CYTOLOGICAL, MORPHOLOGICAL, ECOLOGICAL AND
PHENOLOGICAL SUPPORT FOR SPECIFIC STATUS OF
CRATAEGUS SUKSDORFII (ROSACEAE)

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ABSTRACT

Field and herbarium studies have revealed the presence of 20-stamen black-fruited hawthorns (Crataegus) from 29 sites in the northern Rocky Mountains. This entity has often been treated as a variety of the 10-stamen species, C. douglasii, and was formerly believed to be essentially restricted to west of the Cascade/Sierra Range. We present evidence that the 20-stamen form is diploid whereas C. douglasii is tetraploid, and that the two differ substantially in morphology, ecology and phenology. These lines of evidence strongly support Kruschke’s treatment of the 20-stamen entity as a distinct species, C. suksdorfii.

The black-fruited hawthorns, Sect. Douglasii Loud., constitute the most widespread and abundant members of Crataegus L. in western North America. The group consists of three entities that have been treated as distinct species (Kruschke 1965), or as varieties of one species, Crataegus douglasii Lindl. (e.g., Hitchcock et al. 1961; Scoggan 1978). Crataegus suksdorfii (Sarg.) Kruschke (C. douglasii var. suksdorfii Sarg.) is distinctive in having 20 stamens, and was previously thought to be distributed: “entirely west of the Cascades except inland somewhat in the Fraser R. Valley and Columbia R. Gorge” (Hitchcock et al. 1961); and confined to the “Coastal Douglas-Fir” zone in British Columbia (Taylor and MacBryde 1977). The second form, C. douglasii (var. douglasii), has 10 stamens and is widespread in the northern Rocky Mountain region, occurring occasionally west of the Cascades in the Puget Sound and the Columbia River Gorge, and also disjunct in northern Michigan and southwestern Ontario (Hitchcock et al. 1961). The third form, C. rivularis (var. rivularis), has 10 stamens, is distributed in the central Rocky Mountains, and differs from C. douglasii in its leaf shape and branching pattern. Crataegus rivularis is poorly understood and will not be considered further in this paper.

Differences in stamen number, especially 10 vs. 20 stamens, are found in many species groups in Crataegus. Some early workers (e.g., Eggleston 1908; Palmer 1946) considered this variation relatively trivial and did not use stamen number as an important basis for distinguishing species. Kruschke (1965), however, placed con-
sizable weight on this trait; he stated “a 10-stamen entity can not
be a variety of a 20-stamen entity or conversely so”. On this basis,
and perhaps other unmentioned characters, he elevated many taxa,
including *C. suksdorfii*, to specific status. Phipps and Muniyamma
(1980) have noted that taxa differing in stamen number generally
have other associated distinguishing features.

The recent discovery of 20-stamen hawthorns sympatric with 10-
stamen forms in the northern Rocky Mountains has prompted a
reevaluation of the taxonomy of these two entities. Our investiga-
tions provide evidence from cytology, morphology, ecology, and
phenology that *C. suksdorfii* should indeed be considered a distinct
species.

**Distribution**

Since 1981, when a specimen of 20-stamen *Crataegus* from Idaho
first came to our attention (Wellner 2258), we have gathered exten-
sive field and herbarium data (ID, IDF, MONTU, MRC, ORE, WS,
WU) on the black-fruiting hawthorns of the northern Rocky Moun-
tain region. Figure 1 illustrates the formerly-known western distribu-
tion of *C. suksdorfii*, and the locations of 29 newly-confirmed
northern Rocky Mountain populations (representative specimens
are given in Table 1). The disjunct range extends from about latitude
49° to 53°N, a distance of about 1000 km. Inland Rocky Mountain
and coastal populations are disjunct 200–400 km from one another
throughout most of their range, but the gap is somewhat bridged by
populations in the Fraser R. drainage in interior British Columbia,
and three isolated collections from east of the Cascade crest in central
Washington and Oregon (Fig. 1). The two Washington sites are from
the east slope of Cascades, east of the formerly-described range, but
following a pattern seen in many other “west side” species such as
*Cornus nuttallii* and *Acer circinatum* (Hitchcock et al. 1961). The
third outlier, in central Oregon, appears to be a continuation of the
Columbia River Gorge eastward extension of range. The type locality
of *C. suksdorfii*, indicated by an open circle in Figure 1, is at the
east end of the Columbia River Gorge in Klickitat Co., Washington.
Figure 1 also shows the principal range of *C. douglasii*, which is
partially sympatric with the disjunct inland *C. suksdorfii* element
reported here. Herbarium data also confirm that there is localized
sympathy in the Puget Sound/Vancouver Island region and the Co-
lumbia River Gorge. We have not examined the extent of sympathy
or the ecological relationships between the species at these western
points of contact.

**Evidence for Specific Status of *Crataegus suksdorfii***

Species concepts in *Crataegus* have been notoriously variable. For
example, estimates by various workers for the number of *Crataegus
species in Ontario range from 8 to 91 (Phipps and Muniyamma 1980). Until recent years species concepts were based largely on the principal data at hand: morphology seen on herbarium sheets. In modern biosystematic studies decisions on what constitutes a species are generally based on assessments of the reproductive biology and the overall genetic divergence of the populations under consider-
Table 1. Representative Specimens of *Crataegus suksdorfii* from the Interior/Rocky Mountain Region.


ation. If a group of populations is reproductively isolated and possesses significant genetic distinctions, as manifested by morphology, ecology, phenology, molecular measures, etc., the criteria of both the biological species concept and the taxonomic species concept are satisfied (Grant 1981). We present four lines of evidence that together strongly support the treatment of *C. suksdorfii* as a biological and taxonomic species.

1) Cytology. Polyploidy is a common phenomenon in plants, and it generally results in speciation because ploidal differences effectively end most gene exchange (Grant 1981). The 10- and 20-stamen hawthorns considered here exist at different ploidal levels, and thus likely have a high degree of reproductive isolation. *Crataegus suksdorfii* is diploid (2*n*=34) in its distribution west of the Cascade Range (Calder et al. 1968: Queen Charlotte Islands, B.C., 2*n*=34). *Crataegus douglasii* has been reported to be tetraploid (2*n*=68). The tetraploid count, however, was from a plant of unknown origin cultivated in Leningrad, USSR (Gladkova 1968). The chromosome number of *Crataegus douglasii* is listed as 2*n*=51 in the Flora of Alberta (Moss 1983), but no additional information is given.

We sought to confirm differences in ploidy level of 10- and 20-stamen populations from the sympatric Rocky Mountain region. Flower buds were fixed using standard techniques (Soltis 1980), and mitotic figures were obtained from preparations of tissue from young, meristematic petals (Dickinson and Phipps 1986). No pretreatment of the buds was performed. Counts were obtained from a site where both the 10- and 20-stamen entities occur: USA, Idaho, Adams Co., Goose Ck. near Last Chance Campground, Cronk 205—*Crataegus suksdorfii*, 2*n*=34 (ID, IDF); Cronk 192—*Crataegus douglasii*, 2*n*=68 (ID, IDF). An additional count of *C. douglasii* was obtained from
Table 2. Conspectus of Morphological Characters of *Crataegus douglasii* (var. *douglasii*) and *C. suksdorfii*.

<table>
<thead>
<tr>
<th>Character</th>
<th><em>C. douglasii</em></th>
<th><em>C. suksdorfii</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Flower width, dried (mm)</td>
<td>14–16</td>
<td>12–13</td>
</tr>
<tr>
<td>Stamen number</td>
<td>10</td>
<td>20</td>
</tr>
<tr>
<td>Mature fruit, fresh diameter (mm)</td>
<td>9–10</td>
<td>7–8</td>
</tr>
<tr>
<td>Pyrene length (mm)</td>
<td>5.0</td>
<td>4.5</td>
</tr>
<tr>
<td>Pyrene shape</td>
<td>dorsally rounded, plump, shallowly sculpted laterally</td>
<td>dorsally keeled, narrow, deeply sculpted laterally</td>
</tr>
<tr>
<td>Leaf shape on short shoots</td>
<td>obovate, lobed above middle, truncate apex</td>
<td>elliptic to obovate, unlobed, rounded apex</td>
</tr>
<tr>
<td>Thorn length on older branches (mm)</td>
<td>13–18</td>
<td>8–12</td>
</tr>
</tbody>
</table>

a population about 280 km to the north: USA, Washington, Whitman Co., vic. Pullman-Moscow Airport, *Brunsfeld 3012*, 2n=68 (IDF). Photomicrographs and camera-lucida drawings are on file with the authors. We conclude from this evidence that *C. suksdorfii* and *C. douglasii* are diploid and tetraploid, respectively. However, the possible triploid count for *C. douglasii* reported from Alberta may indicate that hybridization, or apomixis and fertilization of unreduced gametes occurs in this species as it does in some other polyploid hawthorns (Dickinson and Phipps 1986; Campbell and Dickinson 1990).

2) Morphology. Based on our field and herbarium observations, especially on Rocky Mountain populations, *Crataegus suksdorfii* differs substantially from *C. douglasii* in its floral and vegetative morphology (Table 2, Fig. 2). Because the species differ in flower, fruit, leaf and thorn, they can be distinguished with some certainty throughout the year. Thus they appear to be more clearly differentiated than a number of other recognized species pairs in *Crataegus* (Phipps and Muniyamma 1980).

3) Ecology. The discovery of numerous sympatric populations of these two entities allows a comparison of their ecological amplitudes. It has been observed that polyploid species often occupy a wider range of habitats than their diploid relatives (Stebbins 1971; Lewis 1980; Levin 1983). Thus polyploids are often able to tolerate temperature, moisture or soil conditions unsuitable to the diploid. This is clearly the case in this species pair.

In the northern Rockies, *C. suksdorfii* is almost exclusively found in cool, moist stream- and lakeside habitats within forest communities ranging from mid-montane (*Abies grandis, Thuja plicata*, and
Tsuga heterophylla) to the lower subalpine (Abies lasiocarpa) zones. The geographic distribution of C. suksdorfii (Fig. 1) conforms to the extent of maritime (coastal) climates in the Rocky Mountains, as manifested by the distribution of Abies grandis.

Crataegus douglasii has a substantially broader ecological amplitude in both temperature and moisture regimes. Habitats in the sympatric region range from low-elevation grassland and sagebrush zones, through the montane and lower subalpine forest zones. It inhabits streamside and bottomland sites, but also is common in seasonally drier, mesic, forested and nonforested upland habitats. For example, Cooper et al. (1987) present data for its occurrence beneath near climax upland stands of Pinus ponderosa, Pseudotsuga menziesii var. glauca, Abies grandis, and Thuja plicata. Daubenmire (1970) describes communities dominated by Crataegus douglasii in both riparian and upland habitats of the steppe region of Washington.

Crataegus douglasii is so ubiquitous in the Rocky Mountains, it not surprising that it was found in close proximity to many C.
suksdorfii populations. At these sites the species tend to be segregated: C. suksdorfii at lake or streamside, C. douglasii in adjacent meadows and uplands.

4) Phenology and reproductive biology. Where we have observed the species occurring together, C. douglasii begins flowering one to two weeks before C. suksdorfii, though there is some overlap in flowering times. Other workers have also documented differing phenologies for different Crataegus species at a site (e.g., Phipps and Muniyamma 1980; Dickinson and Phipps 1986). Fruiting phenology is reversed, with ripe, black fruits present on C. suksdorfii, while at the same time and site the fruits of C. douglasii are still largely immature. Apparently the larger fruits of tetraploid C. douglasii take several weeks longer to develop. Such developmental differences have been observed in other diploid/tetraploid species pairs (Levin 1983).

Despite the large number of populations in the newly-reported range, several lines of evidence suggest a limited reproductive potential for C. suksdorfii in this region. Most of the 29 populations reported here contain relatively few individuals and are of restricted geographic extent. This may reflect limited suitable habitat at many sites, but may also be the result of low seed output. We observed a high rate of seed abortion in C. suksdorfii, something also noted by Sargent (1907). In many populations we found that frequently at least 3 of the 5 pyrenes per fruit were unfilled. Crataegus suksdorfii has been reported to be self-incompatible (Love and Feigan 1978), which combined with small, isolated populations could affect fecundity. We did not observe a notable incidence of seed abortion in C. douglasii. Although many of the C. suksdorfii populations reported here are in close proximity to larger C. douglasii populations, C. suksdorfii appears be largely maintaining its identity, probably due to intersterility conferred by ploidal differences and phenological and habitat separation. However, at several locations plants were collected that appear be intermediate or atypical in thorn length and/ or leaf characteristics. Additional study of the reproductive biology of these species is needed, particularly to the assess the role of apomixis in C. douglasii.

DISCUSSION

The discovery of widespread populations of C. suksdorfii in the Rocky Mountains is not only of phytogeographical interest, but also provides insights into the relationship between C. suksdorfii and its sister taxon C. douglasii. Although it is remarkable that such a widespread and conspicuous species could go undetected until now, the presence of another Pacific coastal species in the northern Rocky Mountain flora is no surprise. Montane vegetation of the western
portion of the northern Rocky Mountains is basically a disjunct extension of a coastal ecosystem that was fragmented by the climatic changes created by the uplift of the Cascade Range in the Pliocene. *Crataegus suksdorfii* joins a long list of plant and animal species whose principal distribution is west of the Cascades, but which also occur in the region of maritime climate in the northern Rocky Mountains (Lorain 1988).

The sympatry between *C. suksdorfii* and *C. douglasii* in the northern Rocky Mountains provides us with an opportunity to make more profound judgments of their biological relationships. We now believe that these entities are reproductively isolated by virtue of their ploidal differences likely supplemented by phenological and ecological separation. They can be easily distinguished by a suite of floral and vegetative traits, which in concert with phenological and ecological differences indicate significant genetic divergence. These entities would appear to qualify as segregate species by the criteria of both the biological and taxonomic species concepts.

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**Literature Cited**


ANNOUNCEMENT
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