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PONDEROSA PINE REVISITED

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ABSTRACT

We here recognize a new variety, **Pinus ponderosa** var. **pacifica**, in the Pacific portion of the species' distribution and present a new combination for Washoe pine as a variety, **Pinus ponderosa** var. **washoensis**. In this treatment, we reject the neotype of *Pinus ponderosa* selected by Lauria and designate instead the branch collected by David Douglas with mistletoe (*Arceuthobium campylopodum*) as lectotype for *Pinus ponderosa*. Table 1 compares the distinguishing characters of the North Plateau (typical) variety, the Pacific variety, and the Washoe variety of *Pinus ponderosa* with a closely related species, *Pinus jeffreyi*. Figure 1 illustrates the cones of the three varieties of *Pinus ponderosa* discussed here and the cone of *Pinus jeffreyi.*

Key words: California, David Douglas, lectotype, neotype, nomenclature, Pinaceae, *Pinus*, ponderosa pine, taxonomy, Washoe pine, John Work.

Pinus ponderosa Douglas ex Lawson & C.Lawson (ponderosa pine) is a conspicuous native component of foothill woodlands and montane coniferous forests in all of the contiguous western states of the United States, as well as southwestern British Columbia, Canada, and northern Mexico (Griffin and Critchfield 1973; Eckenwalder 2009). Rocky Mountain populations occurring from northern Mexico to southern Colorado have usually been called var. *arizonica*, while those from central Colorado to southwestern North Dakota have been called var. *scopulorum*, and a number of other varietal names have been proposed from the Pacific states, but are not in wide use (for a detailed discussion of varietal names, see Lauria 1996*a*).

David Douglas, collector for the Royal Horticultural Society of London, England, is credited with discovering, collecting, and naming this species before any of its Rocky Mountain populations were recognized, so Douglas' specimen became the basis for the descriptions of *Pinus ponderosa.* Douglas first collected *Pinus ponderosa* in 1826 in the area of the Spokane River, Washington. He collected a specimen for the mistletoe growing on the branches. Douglas recognized the new mistletoe; however he did not recognize the new species of *Pinus* at the time of collection. In his field notes, Douglas (1914) lists the branches as those of *Pinus resinosa* Aiton, a pine with 2 needles per bundle in the eastern United States. When Douglas collected plants that he recognized as being new, such as *Pinus lambertiana* Douglas—sugar pine (Douglas 1827), he made numerous collections of branches, cones, and seeds from the type locality. Douglas did not do this with the first *Pinus ponderosa* collections. Only later did Douglas recognize the pine as being new and corrected his field descriptions from *Pinus resinosa* to *Pinus ponderosa* (written in 1829; Douglas 1914, 1959).

Douglas intended to collect eight species of conifer that he thought to be widespread. He hired a Hudson Bay Company fur trapper named John Work to collect seed of four of these species, among them *Pinus resinosa* (Douglas 1914). John Work and David Douglas met at Kettle Falls, Washington, in the spring of 1826. There are no surviving notes of where Work collected his seed samples. It is known from an entry in the Fort Colville logs that John Work stayed at the fort and was headed to the Pend Oreille River, north of and at higher elevations than where Douglas collected the branches with mistletoe in the area of the Spokane River. In the spring of 1827, Douglas again met Work. We presume, but have no direct evidence such as a bill of sale or a field notation, that the seed collected by Work was transferred from Work to Douglas at this time.

The seed collected by Work was then carried by Douglas back to England (arriving in October 1827). This seed was turned over to the Royal Horticultural Society of London to be germinated and distributed. The horticulturalist Charles Lawson of Peter Lawson & Co. took the seed and germinated what he could. By this time, Douglas had recognized *Pinus ponderosa* as a new species, and he annotated his sheets of the branches with the new mistletoe as *Pinus ponderosa.* William J. Hooker began giving talks on "the new mistletoe on a new pine" (Hooker 1836). The seedlings grown by Charles Lawson were referred to as "Douglas's ponderosa pine." At this point (1829), Douglas was under pressure to write up his notes from his trip before he returned to North America to continue collecting. Douglas completed his work, with the help of W. J. Hooker, submitted his field notes and his journal account to the Royal Horticultural Society in 1829, and returned to North America (Douglas 1914). In 1932, while in Hawaii, Douglas sent his California collections to England. He then resigned as a collector for the Royal Horticultural Society. In 1834, David Douglas died in Hawaii (Wilks 1914).

By the time of his death, Douglas had recognized *Pinus ponderosa* as a new species, had annotated the sheet of the branch with mistletoe as *P. ponderosa*, and had written his journal account of his trip, including an expanded description of *P. ponderosa* as a new species. He had corrected the references to *P. resinosa* in his field notes to *P. ponderosa* in his expanded journal. The description of ponderosa pine had been written but not published. His manuscript remained in the files of the Royal Horticultural Society for another 85 years before seeing the light of day. In Douglas' honor, J. C. Loudon took on the

task of completing the formal botanical description of this new species, then undescribed but widely planted.

In 1836, C. Lawson put an announcement in the Peter Lawson & Co. newsletter, the Agriculturalist's Manual, for the availability of the seedlings of ''Douglas's ponderosa pine'' and noted that the seedlings had three needles in a fascicle. We now have seed collected by John Work, carried to England by Douglas, grown to seedlings, and distributed by C. Lawson.

When Loudon published his description in 1838, he cited Douglas as the sole author. The botanical community accepted Loudon's description of ponderosa pine for many years. Forestry botanist John Gill Lemmon (1888) and Willis Lynn Jepson (1907) cited ponderosa pine as *Pinus ponderosa* Douglas. As greater emphasis was given to priority of publication in accepting descriptions and authorship, and as the manuscript by Douglas remained unpublished, the citation for authorship of *Pinus ponderosa* became Douglas in Loudon.

In 1892, the nomenclatural rules changed to refer to the first publication of a name with a morphological description. It was no longer necessary that a complete botanical description be given priority. This meant the first publication of ''3 needles'' in the now 9-year-old seedlings of ''Douglas's ponderosa pine'' by Charles Lawson in 1836 in the Agriculturalist's Manual was the first publication of the name *Pinus ponderosa* with a morphological description. The observation of three-needle fascicles was enough to correct the early misidentification of *Pinus resinosa* (which has two-needle fascicles). However, there are many three-needled pines in western North America, as well as a few five-needled pines with three needles in the juvenile stage. Therefore the description of the three-needled fascicles applies to many western pines. The authorship at this point changed to Douglas ex C.Lawson. There was an impassioned plea by young Jepson (1893) to retain the Douglas authorship in honor of the first collector and the specimens designated by Douglas.

Later, the nomenclatural rules were tightened, and the reference to Douglas (whose treatment had still not been published) was dropped. Since the 1836 publication was jointly published by Peter and Charles Lawson, the accepted authority became Lawson & C.Lawson. By removing any reference to the Douglas collection of the branches with the mistletoe, there was now a name, and no specimen, to typify this name. The description was of the seedlings and young trees grown from the seed collected by Work that had been distributed by the Royal Horticultural Society.

Lauria (1996*a*) completed the sequence upon the discovery of ''Douglas's ponderosa pine'' cones from numerous pineta in England. Lauria carefully connects the history of the seeds collected by John Work, seedlings and plants grown from these seeds by C. Lawson, to the cones in the Vienna Natural History Museum cone collection. The neotype designated by Lauria relies solely on the seeds collected by John Work, not on any collections by Douglas. The problem with this new type became clear when the cones were examined by the authors in 2005 at the Vienna Natural History Museum and were found to fit more closely the description of Washoe pine, not the North Plateau ponderosa pine collected by Douglas. Cones of the Washoe pine are denser, more compact, have more series of seed-bearing cone scales, can be quite conical in shape, the prickles face downward, and the seed-to-wing ratio is higher (Table 1 and Fig. 1).

We do not know where John Work collected his seeds. The variation in characters of the resulting trees and cones (Lauria 1996*a*) suggests that Work either collected from more than one site or collected in a population with mixed taxa. Trees with Washoe pine characters are found in the Warner Mountains of northeastern California, Nevada, Oregon, Washington, and into British Columbia, Canada, well beyond the original distribution range described by Mason and Stockwell (1945). We now know that at least some of the cones produced by trees grown from Work's seeds (*P. ponderosa* var. *washoensis*) were not from the same taxon as the branches collected by Douglas (*P. ponderosa* var. *ponderosa*). There were no cones on the young tree Lawson was describing in 1836, so cones were not included in his protologue. Moreover, the cones (collected in 1849) of trees planted from seed collected by John Work were not available to Peter and Charles Lawson at the time of their description in 1836. However, the cones on the branch collected by Douglas were available and were being described and illustrated by Loudon at that time. The description by Lauria of trees grown from Work's seed includes both Washoe pine characters—shorter needles, denser cones, a higher phyllotaxy of 8/13, and deeper fissures in the bark—as well as North Plateau pine characters—longer needles, open and less dense cones, cone scale prickles pointing outward, and plate formation with shallower fissures in the bark (Table 1; Fig. 1). This suggests that at least two taxa were represented in Work's seed.

The better choice for the typification of Douglas' ponderosa pine would therefore be the branch collected by Douglas with mistletoe. Although the branch is today without the cones, it retains the needles with three to a fascicle as described by Lawson. We have available to us the supplemental information of descriptions and cone illustrations provided by Loudon in 1838, as well as Douglas' own description, published in 1914. Using this material, that was unavailable to the authors [P. and C. Lawson] at the time of their description, we therefore reject the neotype for Douglas' ponderosa pine designated by Lauria in 1996 as being in conflict with Lawson's protologue, on account of the source material being of mixed taxonomic origin (McNeill et al. 2006). Instead, we designate the branch with mistletoe collected by Douglas as the lectotype for *Pinus ponderosa* var. *ponderosa* Douglas ex Lawson & C.Lawson (North Plateau variety), Douglas' ponderosa pine. This branch is today in the Herbarium of the Royal Botanical Gardens at Kew, filed under the type specimen for the mistletoe *Arceuthobium campylopodum* W.J.Hooker, Loranthaceae. The name *Pinus ponderosa* is annotated on the sheet by W. J. Hooker. Hooker notes on the sheet: ''Parasitical on Pinus ponderosa, Amer. Boreali ou. Douglas 1829'' (Lauria 1996*a*). This is Hooker's ''new mistletoe on a new pine'' (Hooker 1836).

The neotypification of *Pinus ponderosa* with a Washoe cone by Lauria underscores the need for descriptive criteria to distinguish among infraspecific forms of ponderosa pine, yet the variation across its 2000 km range is gradual. The clinal gradation of characters from the North Plateau variety at lower elevations to the characters of the Washoe variety with increasing elevation or colder habitats (Haller 1984) shows a close relationship between these varieties, with distinct characters at the ends of the cline (Table 1). The denser, more compact cones of Washoe pine and its greater cold tolerance and growth at higher elevations have suggested to some authors that this is simply an environmentally stressed plant of

Table 1. Distinguishing characteristics of three Western varieties of *Pinus ponderosa* and *Pinus jeffreyi*.

	P. ponderosa var. *ponderosa*	*P. ponderosa* var. *pacifica*	*P. ponderosa* var. *washoensis*	*Pinus jeffreyi*
Needle length	14–26 cm	15–28 cm	12–17 cm	13–27 cm
Needle diameter	1.7–2.3 mm	1.4–1.9 mm	1.9–2.4 mm	1.7–2.2 mm
Needle color	Grayish green	Shiny deep green	Light green	Grayish blue-green
Needle surface	±glaucous	Not glaucous	Scarcely glaucous	Glaucous
Seed cone length	Gen 7–12 cm	Gen 8–15 cm	Gen 5–11 cm	10–26 cm
Immature seed cone color	Greenish-brown to dark purple	Light yellowish-green	Dark reddish-purple	Light green to reddish-purple
Seed cone shape	Ovoid to ±conical	Gen ovoid	Ovoid to distinctly conical	Ovoid to ±oblong
Seed cone scale arrangement	Moderately separated	Well separated	Very crowded	±crowded
Seed cone scale phyllotaxy (number of spiral rows)	5 in one direction, 8 in the other	5 in one direction, 8 in the other	5 & 8, 8 & 13, or 5, 8, and 13	8 in one direction, 13 in the other
Seed cone scale color	Upper surface brown, sometimes with black streaks, lower surface gen black, occasionally dark brown streaked with black	Upper surface brown, lower surface gen uniformly black	Upper surface brown, lower surface black or brown streaked with black	Upper and lower surfaces similarly brown
Terminal prickles on cone scales (from mid-cone)	Gen curved outward	Gen curved outward	Point straight down (parallel to cone axis)	Inwardly curved
Seed wing extends beyond seed length	2.3–4.5×	3.0–4.5×	1.4–2.5×	<2.5×
Cold tolerance	High	Low	Very high	High
Correlation of quantitative characters with elevation	High	Low	High	Low
Bark characters:				
Bark odor	Resinous (not sweet or spicy)	Resinous	Resinous	Sweet or spicy (not resinous)
Mature bark characters:				
Fissure depth	Intermediate	Shallow	Intermediate	Very deep
Plates	Broad	Very broad	Narrow	Very narrow
Color of bark scales:				
Outer surface	Tawny red	Light yellowish-tan	Brownish-red to purplish-red	Dark purplish-red
Inner surface	Yellow	Bright yellow	Yellow	Pinkish-red
Ease of removing bark scales	Moderate	Sheds easily	Moderate	Difficult

P. ponderosa (Brayshaw 1997). The close genetic relationship between *P. ponderosa* vars. *washoensis* and *ponderosa* (Critchfield 1984; Lauria 1997), and the typification of ponderosa pine with a Washoe cone by Lauria, has led recent authors to sink Washoe pine into synonymy as an alpine ecotype of ponderosa pine (Eckenwalder 2009). Yet the growth of the seedlings collected by Work in the carefully tended pineta in England provides an inadvertent common garden experiment. The retention of the distinctive cone characteristics of Washoe pine when grown in cultivation in England is strong evidence for the genetic basis of the Washoe characters.

We take this opportunity to formally recognize two varieties in *P. ponderosa*, the first in the Pacific portion of the species' distribution (Pacific variety), and the second as a new combination for Washoe pine (Washoe variety). In Table 1, we list characters that, when used in combination, reliably distinguish between the (typical) North Plateau, Washoe, and Pacific varieties of ponderosa pine.

PINUS PONDEROSA Douglas ex Lawson & C.Lawson var. **pacifica** J.R.Haller & N.J.Vivrette, var. nov.—TYPE: USA, California. Lassen Co.: 26.2 mi N of Susanville along the eastern shore of Eagle Lake on CA Highway 139, 5200 ft, associated species *Pinus jeffreyi*, *Juniperus occidentalis* var. *occidentalis*, *Artemisia tridentata*, 2 Aug 1959, *J. R. Haller 10205* (holotype UCSB 69943).

Folia 15–28 cm longa, tenues et pervirides, non glauca. Strobili immaturi pallide flavo-virentes, nec rubelli nec purpurascentes. Strobili maturi generatim ovoidei, generatim 8–15 cm longi; bracteae bene separatae, paginae adaxiales brunnei, abaxiales ateri, aculei terminales extrinsecus curvi. Alae seminibus 3–4.5-plo longiores.

Leaves 15–28 cm long, thin, shiny and deep green, not glaucous. Immature strobili light yellowish-green, neither reddish nor purplish. Mature strobili generally ovoid, generally 8–15 cm long; scales well separated, surfaces adaxially

Fig. 1. Illustration of the cones of three varieties of ponderosa pine and Jeffrey pine. Far left: *Pinus ponderosa* var. *ponderosa*: North Plateau variety, Douglas' ponderosa pine (Spokane, Washington, *J. R. Haller 10122-9*). Middle left: *Pinus ponderosa* var. *pacifica*: Pacific variety (type of the variety: Eagle River, California, *J. R. Haller 10205*). Middle right: *Pinus ponderosa* var. *washoensis*: Washoe pine (type locality: Mt Rose, Nevada, *J. R Haller 10040-33*). Far right: *Pinus jeffreyi*: Jeffrey pine (Ebbetts Pass, California, *J. R. Haller 10045-2*).

brown, abaxially uniformly black, the terminal prickles generally curved outward. Wings of the seeds 3–4.5-times longer than the seed.

Pinus ponderosa var. *pacifica* is described as new. This variety is most common on coastal draining slopes of the major mountain ranges, in elevations from 1200 to 2100 m, from the Cuyamaca Mountains, just north of the U.S.–Mexico Border, north through the Peninsular Ranges, then west along the Transverse Ranges and north along the western slopes of the Sierra Nevada, where forest dominated by *Pinus ponderosa* var. *pacifica* forms a continuous but open band at elevations of 1100–2100 m in the middle of the range (Yosemite National Park) and 500–1500 m in the north (Cascade Range). Forests similar to these Sierra–Cascade stands also are common in the North Coast Ranges. East of the Sierra Nevada, at the crest and south of Tioga Pass, var. *pacifica* appears only as a component of the riparian vegetation lining the banks of perennial streams with sources among the snowfields and peaks of the Sierra Nevada, only a few kilometers distant but 2400 m higher. Table 1 summarizes the characters that distinguish the new Pacific variety of ponderosa pine from the typical variety (North Plateau variety), the Washoe pine variety, and Jeffrey pine (*Pinus jeffreyi* Grev. & Balfour). Figure 1 illustrates the type cone of the new Pacific variety (middle left), compared to the ponderosa typical variety (far left), the Washoe pine variety (middle right), and Jeffrey pine (far right). The name "pacifica" is derived from the distribution, because the Pacific variety is the westernmost variety of ponderosa pine and has been used by foresters informally as the Pacific race for years (Critchfield 1984).

Pinus benthamiana Hawth. and *Pinus ponderosa* var. *benthamiana* (Hawth.) Vasey (typified by Lauria [1996*b*]) are names that have been applied to a few local populations of *P. ponderosa* var. *pacifica* found on deep sandy soils in the Santa Cruz Mountains of California. These populations have some trees with very large cones and other trees that contain aldehyde compounds similar to *Pinus jeffreyi*. At this time, there is not yet sufficient evidence to recognize these populations as a separate species or as a variety of ponderosa pine. The names *Pinus benthamiana* and *Pinus ponderosa* var. *benthamiana* would here be considered synonyms of *Pinus ponderosa* var. *pacifica*.

Pinus ponderosa Douglas ex Lawson and C.Lawson var. **washoensis** (H.Mason & Stockw.) J.R.Haller and N.J.Vivrette, comb. et stat. nov.—TYPE: USA, Nevada. Washoe Co.: Sierra Nevada, E side of Mount Rose, 2 Aug 1940, *Herbert L. Mason 12370* (UC 692993).

Basionym: *Pinus washoensis* H.Mason & Stockw. *Madroño* **8(2)**: 61–63 (1945).

Ting (1966) used the name *Pinus ponderosa* var. *washoensis* in his paper describing the differences in the pollen of Washoe pine and other pine species. He did not cite the basionym as required for recognition of the variety, so this new combination is not recognized (Ting 1966: 114).

Elevation (1400) 2000–3000 m. Most distinct above 2100 m, upper montane to subalpine zones with Jeffery pine, white bark pine, red fir, and white fir, Warner Mountains, higher elevations in the northern Sierra Nevada (Babbit Peak), Mt. Rose, Nevada (type locality); intergrading with var. *pacifica* and/or var. *ponderosa*; low-lying flats subject to cold air drainage, spring waterlogging from snowmelt, and summer drought at 1400–1900 m (Haller 1961), higher elevations in the northern Sierra Nevada, Cascade Range, and Modoc Plateau, with Jeffrey pine, lodgepole pine and western juniper; to North Warner Mountains, Crater Lake, Burns, Wolf Mountain, Blue Mountain, Grande Rande River, Oregon; Kettle River Range, Washington; Boston Bar, Manning Park, Merritt, Princeton, and Promontory Mountain, British Columbia, Canada.

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