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POTENTILLA BRUCEAE (ROSACEAE): A CASE STUDY IN TAXONOMIC SPECIES AS REPEATEDLY MODIFIED HYPOTHESES, WITH AN UPDATED TREATMENT FOR THE CURRENT CIRCUMSCRIPTION

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ABSTRACT

The taxonomic history of *Potentilla bruceae* Rydb. is summarized, representing a case study in the proposition that species are *de facto* hypotheses, which are modified as needed to account for new data. The circumscription and formal description of *P. bruceae* are updated to account for the removal of specimens now relegated to *P. amicarum* Ertter and *P. gracilis* Douglas ex Hook. var. *owyheensis* Ertter & Mansfield, along with other specimens of uncertain placement. The resultant circumscription limits *P. bruceae* sensu stricto to relatively large plants with distinctively incised subpalmate leaves from northeastern California and adjacent Nevada and Oregon, south to the central Sierra Nevada, with the greatest concentration in montane meadows in counties surrounding Lake Tahoe. Biographical information on "Mrs. C. C. Bruce," aka Josephine Cornelia Austin Bruce (1865–1931), is provided beyond what has previously been readily available. In addition, *Potentilla anomalifolia* M. Peck, previously treated as a synonym of *P. drummondii* Lehm. or possibly *P. bruceae,* is reinterpreted as the probable hybrid of *P. gracilis* and *P. millefolia* Rydb.

The average person and even many biologists tend to think of species as fixed entities that are cleanly demarcated from all other species, or, at the other extreme, arbitrary human constructs imposed on the bountiful diversity of the natural world. As the first author has long argued (e.g., Ertter 1997), however, taxonomic species are best understood as scientific hypotheses, basic components in the goal of presenting the oft-times bewildering complexity resulting from evolution-in-action in a simplified conceptual model suitable for a variety of human purposes. The resultant species hypotheses are not arbitrary, but instead based on current understanding of a set of debated criteria, primarily involving a balance of observable characters, hypothesized phylogeny, reproductive isolation, biogeography, and ecology of the proposed species, subject to differing philosophies as to the relative importance of these criteria and the purpose of taxonomy in general.

A key implication of this viewpoint is that species hypotheses, like all scientific hypotheses, are subject to change in the face of new data, which can be as basic as the collection of additional specimens or as sophisticated as the latest molecular analytical technique. Given that many species are initially based on a single collection, and that initial collections of undescribed species are commonly

shoe-horned into already recognized species (Bebber et al. 2010), it should not be surprising that species hypotheses are frequently, and sometimes repeatedly, modified to accommodate new information, especially in groups that are being actively studied. Although frequently bemoaned by users as "botanists can't make up their minds" or "mere opinion," this is actually how science in action operates.

Potentilla bruceae Rydb. (Rosaceae), the subject of the current paper, is a prime example of this general principle in action. Even within the challenging genus *Potentilla*, the circumscription of *P. bruceae* Rydb. has been particularly problematic. Since its initial recognition in 1908, the name has not only varied dramatically in its application but also had a shifting nomenclatural relationship with both *P. drummondii* Lehm. and *P. breweri* S. Wats. Much of this complexity results from a common interpretation that *P. bruceae* owes its origin to hybridization between *P. drummondii* and *P. breweri*, though whether primarily as sporadic recurring hybridization events (i.e., as a nothospecies) or as one or more stabilized hybrids ("hybridogenous species" in Soják's lexicon [e.g., Soják 1986]) remaining unresolved.

Potentilla bruceae was originally described by Rydberg (1908) on the basis of a collection by "Mrs. C.C. Bruce" (No. 2301) from the Warner Mountains of Oregon in 1898; more information on the collector is provided below. In Rydberg's accompanying key, *P. bruceae* was distinguished from *P. breweri* on the basis of subpalmate (vs. pinnate) basal leaves with fewer (5–7 vs. 7–17) leaflets and ternate (vs. pinnate) cauline leaves. Rydberg's proposed new species initially languished in obscurity, with the name not addressed, even in synonymy, by either Jepson (1925, 1936) or Peck (1941) in their respective floras of California and Oregon. Jepson instead used *P. breweri* var. *expansa* S. Wats. to encompass plants in the upper Tuolumne River basin with subpalmate ("leaflets approximate"), sparsely tomentose leaves. Abrams (1944) at least addressed *P. bruceae*, but only in the synonymy of *P. breweri*.

The epithet was brought back into use in conjunction with Clausen, Keck, and Hiesey's (1940) inclusion of a clone of subpalmate-leaved plants from Tuolumne Meadows in their experimental transplants of "cenospecies *Drummondii*," in combination with cytogenetic analysis. The accompanying taxonomic treatment (primarily by Keck) treated these plants as *Potentilla drummondii* subsp. *bruceae* (Rydb.) D.D. Keck, at the same time relegating var. *expansa* to synonymy under *P. breweri.* Keck's circumscription of subsp. *bruceae* encompassed a wide array of specimens from the southern Cascade Mountains in Oregon to the southern Sierra Nevada in California (based on Fig. 69 in Clausen et al. 1940).

Keck's proposed taxonomy was widely accepted in subsequent decades (e.g., Munz 1959; Holmgren 1997 [using the varietal counterpart]), though Peck (1961) evidently was unconvinced by the argument for dividing *Potentilla drummondii* into subspecies. Alternatively, an even broader circumscription of *bruceae* was envisioned by Johnston (1980) in his unpublished dissertation, which analyzed population variability in *Potentilla* sect. *Multijugae* (including *P. breweri* and *P. drummondii*) using multi-character numerical methodology. Johnston concluded that *bruceae* was more appropriately treated as a variety of *P. breweri*, but the combination was never validly published. Although only a limited number of collections from California, Nevada, and Oregon were cited in Johnston's dissertation as representative specimens, his map (Fig. 27) indicated occurrences of *bruceae* as widely distributed as the Canadian Rockies, northern Washington, and eastern Nevada.

The first author's own evolving understanding of *Potentilla bruceae* has been convoluted, in response to new data from field studies and traditional analysis of herbarium specimens (i.e., hypothesis modification in the face of new evidence). Keck's nomenclature and circumscription were essentially retained in the treatment of *P. bruceae* in the revised Jepson Manual (Ertter 1993), albeit preceded by the postulation "that bruceae actually represents a catch-all category for a complicated conglomerate of hybrids between [*P. drummondii* and *P. breweri*], and probably members of the *P. gracilis* [Douglas

ex Hook.] complex as well" (Ertter 1992). Minor adjustments were subsequently made after attempts to locate topotypes of *P. subvillosa* Rydb. failed to locate any fully comparable material in northeastern California (Ertter & Mansfield 2007). Instead, relatively consistent populations of locally abundant plants in Tahoe Meadows (Figs. 1, 2), Washoe Co., Nevada, and several sites in Amador Co., California, were interpreted as prime representatives of *P. bruceae,* with *P. subvillosa* as an outlying variant with palmate leaves and more cottony vestiture. As a result, *P. bruceae* was reinstated as a full species, with *P. subvillosa* in synonymy. *Potentilla anomalifolia* M. Peck was also briefly addressed as a probable synonym, though with more deeply dissected leaves than typical *P. bruceae*; see further discussion on this name below.

Figure 1. Habitat of *Potentilla bruceae* sensu stricto in Tahoe Meadows along Ophir Creek, vouchered by *Ertter et al. 18493* (photo by B. Ertter, 2004).

Figure 2. Habit of *Potentilla bruceae* sensu stricto in Tahoe Meadows along Ophir Creek, vouchered by *Ertter et al. 18493* (photo by B. Ertter, 2004).

Figure 3. Distinctively incised subpalmate leaf from Tahoe Meadows, Nevada (*DiNicola & Ertter 2016-69*; photo by B. Ertter, 2024).

Subsequent treatments of *Potentilla bruceae* (Ertter 2012; Ertter et al. 2015) leaned heavily on the collections from Tahoe Meadows and Amador County, which were relatively large plants with distinctively incised subpalmate leaves (Fig. 3) and petiole vestiture ranging from softly villose to nearly tomentose. This particular kind of subpalmate leaf appears to result from the elaboration of leaflets, especially the central one, on a fundamentally palmate leaf, rather than the addition of proximal pairs on the leaf axis. In addition to these core populations, collections from across northern California and adjacent Oregon, south through the Sierra Nevada, were encompassed in *P. bruceae* in these treatments, including some that diverged from this particular form of subpalmate leaf. The treatment for *P. bruceae* in North America north of Mexico (Ertter et al. 2015) furthermore implicitly rejected the expanded circumscription used by Johnston (1980), though without specifically addressing the disposition of the uncited specimens that underpinned his mapped distribution of *bruceae*.

Although otherwise representative plants of *Potentilla bruceae* can be found growing sympatrically with both *P. breweri* and *P. drummondii,* the FNA treatment (Ertter et al. 2015) nevertheless explicitly back-tracked from the previous view of *P. bruceae* as a "catchall category" for hybrids between *P. drummondii* and *P. breweri*. The species also often co-occurs with superficially similar but palmate-leaved *P. gracilis* var. *fastigiata* (Nutt.) S. Wats., including at Tahoe Meadows and Kirkwood Meadows. At such sites, apparent intergrades are commonly present (e.g., *Ertter et al. 18777* [UC]), but not beyond the norm routinely encountered in populations of other co-occurring *Potentilla* species, especially in sect. *Graciles* (personal observation). It is nevertheless possible that *P. bruceae* has a hybrid origin involving some combination of these species, but if so, it is now sufficiently stabilized to be regarded as a species in its own right.

The circumscription of both *Potentilla bruceae* and *P. drummondii* in Ertter 2012 and Ertter et al. 2015, which was essentially the same as Clausen et al. 1940, was significantly reduced with the publication of *P. amicarum* Ertter (Ertter 2017). This move was the follow-up to a note under *P. drummondii* in Ertter et al. (2015) that "relatively small plants forming uniform populations in the southern Sierra Nevada may represent stabilized hybrids with *P. breweri.*" The majority of these subpalmate-leaved plants in the central and southern Sierra Nevada, previously treated as either *P. bruceae* or *P. drummondii*, are now separated as *P. amicarum*; this includes the "alpine ecotype" of *bruceae* from Mount Dana used by Clausen et al. (1940). Collections from the White and Sweetwater mountains were also incorporated in the new species; more recently, at least one collection from Mount Rose, Washoe Co., Nevada, has also been provisionally moved to *P. amicarum* (Ertter & House 2024).

Updated Circumscription and Description of *Potentilla bruceae*

The flip side of carving out a new species from a more widely circumscribed species is that the circumscription and description of the latter are also affected, especially with the segregation of as significant a component as *Potentilla amicarum.* Another small slice of *P. bruceae* sensu lato has recently been removed with the transfer of *P. subvillosa* from synonymy (Ertter & House 2024), after comparable topotype material was finally located (e.g., *Ertter 21083*); this name is now provisionally being treated as a synonym of *P. gracilis* var. *owyheensis* Ertter & Mansfield (i.e., the epithet with priority at varietal rank). The second portion of the current paper evaluates the remaining components of a previously more broadly defined *P. bruceae,* decides which specimens and populations merit retaining in a relatively cohesive taxon, and provides an updated species description. This is undertaken in conjunction with updating *Potentilla* in the Jepson eFlora (https://ucjeps.berkeley.edu/eflora/; Ertter & House 2024) and the second author's graduate work on the *P. drummondii/breweri* complex.

Since the type of *Potentilla bruceae* from the Warner Mountains of Oregon has the same distinctive leaflet dissection as do the core populations from counties surrounding Lake Tahoe, the name fortuitously remains attached to the specimens that have been treated as primary representative examples and justification of *P. bruceae* as a valid species. This primary core cluster consists of populations in Washoe Co., Nevada, and Amador, El Dorado, Nevada, and Placer cos., California. An

outlier in Butte Co. (*Oswald 4342*) also has the diagnostic leaf shape, but most other specimens from this general part of California that have previously been included in *P. bruceae* have more subpinnate leaves and more cottony vestiture; they might be better treated as components of *P. breweri* sensu lato that are among the subjects of the second author's ongoing studies.

Figure 4. Second author at site of Timberline experimental transplants by Clausen, Keck, and Hiesey. (photo by B. Ertter, 2016)

Figure 5. *Potentilla bruceae* at Timberline site, possibly derived from Tuolumne Meadows clone used in the experimental transplants (photo by B. Ertter, 2016).

A second population cluster is represented by collections in and near Tuolumne Meadows, in eastern Tuolumne and adjacent Mono counties, California. Given that Tuolumne Meadows is the cited

source for the clone representing the "subalpine ecotype" of *Potentilla drummondii* subsp. *bruceae* used in Clausen et al.'s (1940) transplant studies, it is conceivable that the collections cited below from Mono Co., which were collected at or near the Timberline transplant site (Figs. 4, 5), could all be progeny of the original clone. Even within Tuolumne Meadows proper, however, collections span the range of variation between *P. bruceae* sensu stricto and sympatric *P. drummondii* and *P. breweri*, opening the possibility that this population cluster results from an independent hybridization event between the last two species.

The third cluster of reasonably representative populations (including the type of *Potentilla bruceae*) occurs in the Warner Mountains of Modoc Co., California, and adjacent Lake Co., Oregon, supplemented by a couple of collections in the mountains northwest of the Warner Mountains (*Legler et al. 1832* [OSC, WTU], *Leiberg & Coville 2800* [ORE in OSC]). Although the type itself clearly has the same diagnostic leaf dissection as do plants from the Lake Tahoe cluster, some other collections included here in the Warner Mountains cluster have a more ambiguous leaf dissection.

There are also collections from the Warner Mountains that have leaf dissection and vestiture intermediate between *Potentilla bruceae* and *P. breweri* sensu lato; e.g., *DiNicola & Ertter 769* (WIS + to be distributed) and *Ertter & DiNicola 22942* (SRP + to be distributed), both from southeast of Crane Peak on the headwaters of Deep Creek (Figs. 6, 7). Leaves of these plants are more evidently subpalmate, or even subpinnate, with the proximal leaflet pair separated from the others by a span of leaf axis that appears continuous with the petiole. Leaf-blades are accordingly more oblong than those of *P. bruceae* sensu stricto, which are generally round in outline. Other differences include habit and habitat, indicating that further research is needed to determine the optimum disposition of these latter collections.

Figure 6. Plant intermediate between *Potentilla bruceae* and *P. breweri* at site of *Ertter & DiNicola 22942* (photo by B. Ertter, 2017).

Figure 7. Leaf of plant intermediate between *Potentilla bruceae* and *P. breweri* at site of *Ertter & DiNicola 22942* (photo by B. Ertter, 2017).

Although we no longer consider *Potentilla bruceae* to be a "catchall category" for sporadic hybrids between *P. drummondii* and *P. breweri*, it is nevertheless possible that *P. bruceae* has a hybrid origin involving some combination of these two species and/or *P. gracilis* var. *fastigiata* (Nutt.) S. Wats. If so, it is now sufficiently stabilized to be regarded as a species in its own right, at least in the three population clusters addressed above. Even in these sites, however, apparent intergrades are commonly present (e.g., *Ertter et al. 18777* [UC]), but not beyond the norm routinely encountered in populations of other co-occurring *Potentilla* species, especially in sect. *Graciles* (personal observation).

Our resultant conclusion is that no specimens from outside of the three accepted population clusters fall into our current circumscription of *Potentilla bruceae.* Excluded from this more narrowly defined species are all previous reports, including some collections previously annotated as *P. bruceae* by the first author, from the southern Sierra Nevada, northwestern California, most of Oregon, anywhere in Washington, and eastern Nevada. As already noted, the largest group of excluded specimens are those from the central and southern Sierra Nevada that have been transferred to *P. amicarum.* Several other widely scattered collections are more representative of either *P. drummondii* (e.g., *Wheeler 1736* [HSC] from Mendocino Co., California; *Duncan 2847* [SOC] from Jackson Co., Oregon; and *Scullen s.n* [OSC] from Lane Co., Oregon), *P. breweri* sensu lato (e.g., *Denton 2635* [ID, WTU] and *Baker 295* [ID, WTU], both from Josephine Co., Oregon), or possible hybrids between the two species (e.g., *Suksdorf 5252* [WS, WTU] from Yakima Co., Washington). Collections previously assigned the epithet *bruceae* from the Ruby Mountains of Elko Co., Nevada, all appear to be elements of a complex hybrid swarm that has yet to be untangled, rather than a stabilized species.

With the removal of specimens addressed in the previous paragraph from the current circumscription, *Potentilla bruceae* becomes a reasonably well-defined species, both morphologically and ecogeographically. As presented here, *P. bruceae* consists of relatively large sturdy plants with ascending stems, distinctively incised subpalmate leaves with blades nearly round in outline, and openly cymose many-flowered inflorescences (Figs. 2–3, 5). Populations occur in summer-dry montane meadows from the mountains of southwestern Lake Co., Oregon, to Tuolumne Meadows in the central Sierra Nevada of California, with the greatest concentration in counties surrounding Lake Tahoe. An updated full description is provided here, replacing more inclusive descriptions published previously (e.g., Ertter 2012, Ertter et al. 2015).

POTENTILLA BRUCEAE Rydb., N. Amer. Fl. 22: 342. 1908. *Potentilla drummondii* subsp. *bruceae* (Rydb.) D.D. Keck, Publ. Carnegie Inst. Wash. 520: 180. 1940. *Potentilla drummondii* var. *bruceae* (Rydb.) N.H. Holmgren, Intermount. Fl. [Cronquist et al.] 3A: 94. 1997. **TYPE: USA. Oregon.** Lake Co.: Warner Mountains, Jul 1898, *Mrs. C.C. Bruce 2301* (holotype: NY; isotype: DS in CAS).

Plants herbaceous perennials, ± grayish-green, arising from sturdy, compact to elongate caudex branches. **Stems** usually ascending, 2–6 dm, 1.5–3.5 times as long as basal leaves. **Basal leaves** fundamentally palmate but with the central leaflet elaborated so as to appear subpalmate (Fig. 3), other leaflets also often deeply incised, total length (5–)8–25 cm; petiole (3–)6–20 cm, hairs usually abundant, sometimes sparse (can vary on same plant), weak, straight to wavy-tangled, ± appressed to spreading, some often pustulate-based, ± 0.5–2 mm long; blade nearly round in outline, (3–)5–8(–10) × (3–)5–8(–10) cm; leaflets usually 5(–8), ± overlapping, central leaflet deeply incised into 3–5 lobes, sometimes petiolate, other leaflets also often deeply incised, ± broadly obovate in outline, 3–7 cm long, distal ½ to nearly to base of margin toothed ¼–½ to midrib (in addition to deeper incisions), sometimes irregularly so, teeth (3)4–6 per side, broadly and usually bluntly triangular, 3–8(–12) mm, surfaces similar or somewhat greener above, green to more often grayish green, hairs usually straight and appressed to ascending on lower veins, more loosely appressed to ascending elsewhere on surface, sparse to abundant, often with an inconspicuous undercoat of shorter crisped hairs. **Cauline leaves** (1–)2–3. **Inflorescences** (5–)10–25(–30)-flowered, becoming openly cymose; pedicels 0.5–1(–2) cm, straight. **Flowers:** hypanthia 4–6 mm diam., 1.5–2 mm deep; epicalyx bractlets lanceolate-elliptic, 2–4(–5) × 0.8–1.2(–2) mm; sepals 4–7.5 mm, acuminate; petals yellow, 6–9 × 5.5–8 mm; filaments 1.5–2.5 mm; anthers 1–1.5 mm; carpels numerous, styles tapered with papillate base, 2–3 mm. **Achenes** ± 1.5 mm, smooth, pale brown.

Flowering late June to early September. Growing in drier open portions (e.g., borders, elevated sites) of summer-dry meadows (Fig. 1) surrounded by *Pinus contorta* and other conifers, ca. 1820–3000 meters elev.

Chromosomes: Given the retention of collections from Tuolumne Meadows in the current circumscription, the multiplicity of chromosome counts reported for the "subalpine ecotype" of *Potentilla drummondii* subsp. *bruceae* by Clausen et al. (1940) can be assigned to *P. bruceae* sensu stricto, specifically 2*n* = ca. 64, 69, 70, 71, and 98, with a high number of univalents and other anomalies. This group evidently exemplifies the capability of *Potentilla* to propagate in spite of chromosomal irregularities, as already confirmed for several other species in the genus (e.g., Asker 1977).

Additional representative specimens examined. California. Amador Co.: Carson Spur on Hwy 88 ca 2 mi W of Kirkwood, around pond in mixed conifer forest, T10N R17E S21, ca 7800 ft, 10 Sep 2006, *Ertter, Gowen, & Matson 18770* (SD, UC, WIS); Kirkwood Meadows SW of jct of Hwy 88 and road to Kirkwood Ski Area, dried meadow surrounded by mixed conifer forest, T10N R17E S22 NWSW, ca 7700 ft, 10 Sep 2006, *Ertter, Gowen , & Matson 18775* (SBBG, UC[2], UCR), same locality, 7 Jul 2012, *Ertter 21101* (SRP, UC, WIS). Butte Co.: headwaters of E branch of Willow Creek, ca 0.75 mi S of Humbug Summit, ca 4.75 mi E of Jonesville, uncommon among scattered lodgepole pines on E border of summer-dry meadow, red fir forest, T26N R5E S23 NW, 6400 ft, 3 Jul 1990, *Oswald 4342* (CHSC, UC). El Dorado Co.: Lake Valley (near Lake Tahoe), 15 Jul 1904, *Baker s.n.* (UC [mixed collection with *P. gracilis* var. *fastigiata*]); Washoe Meadows State Park, Angora Mdws, 38.879972 -120.026833, 1921 m, 15 Jun 2007, *Dean 3995* (DAV, RENO). Modoc Co.: Pine Creek Trail 2½ mi above trailhead, large meadow complex, 41.36137 -120.24257, 7835 ft, 27 Jul 2017, *DiNicola et al. 766* (WIS + to be determined). Mono Co.: Harvey Monroe Hall Research Natural Area, "Timberline" site of Clausen, Keck, & Hiesey experiments, open meadows, dry now but seasonally wet, 37.69009 -119.28123, 9381 ft, 6 Aug 2016, *DiNicola & Ertter 2016-91* (WIS + to be determined);

Carnegie Inst. Experimental Station N of Tioga Pass, T1N R24E, eroded edge of creeklet through former experimental site, 12 Sep 1993, *Ertter 12271* (UC). Nevada Co.: moist meadow on N side of Prosser Cr, ca 4 aimi W of Hobart Mills, ca 5.2 airmi NW of Truckee, basin of Prosser Creek, Carpenter Valley, 39°23'48.99"N 120°15'56.94"W, 6250 ft, 19 Jul 2017, *Ahart & Dittes 21609* (CHSC, JEPS, SRP); Loney Mdw on Texas Cr 1½ mi S of Bowman Lake, wet mdw along creek at lower end of meadow, 6,000 ft, 14 Jul 1965, *True & Howell 2272* (CAS). Placer Co.: Deer Park, June, July 1912, *Geis 37A* (JEPS) & *Geis 37B* (UC). Tuolumne Co.: Tuolumne Mdws, Yosemite NP, 8700 ft, 20 Jul 1911, *Jepson 4472* (JEPS). **Nevada.** Washoe Co.: Tahoe Mdws on Hwy 431, 10.8 mi above jct with Hwy 28, drier site across hwy from boardwalk trailhead, 39.30271 -119.918.72, 8580 ft, 4 Aug 2016, *DiNicola & Ertter 2016-69* (WIS + to be determined); W side of Mt. Rose Summit on Hwy 27, dry border of meadow and sagebrush, gentle S-facing slope below lodgepole grove, coarse granitic sand, 8 Sep 1989, *Ertter & Carter 8842* (UC); Tahoe Meadows along Ophir Creek, dry flat with *Pinus contorta*, on volcanic rock, 39°17.978'N 119°54.402'W, 8400 ft, 29 Aug 2004, *Ertter et al. 18493* (SBBG, SRP, UC, WIS). **Oregon.** Lake Co.: 2.5 mi NE of Deadhorse Lake, open wet meadow, 42°35.242'N 120°44.489'W, 6809 ft, 2 Jul 2004, *Legler et al. 1832* (OSC, WTU); Cougar Peak, wet meadows, 1900 m, 3 Aug 1896, *Leiberg & Coville 2800* (ORE in OSC).

Who was "Mrs. C.C. Bruce"?

Since very little has previously been written about "Mrs. C. C. Bruce", aka Josephine Cornelia Austin Bruce (1865–1931), we use this opportunity to pull together some of what is known about the woman who first collected *Potentilla bruceae* and for whom it is named. Much of this information is provided by Michael Charters (pers. comm., 21 Nov 2024), including information extracted and synthesized from Find a Grave (https://www.findagrave.com/) records. Additional details have been obtained from biographical sketches of her mother, Rebecca Merritt Smith Austin (1832–1919), who was one of the most active and widely known California botanists of her time (Jepson 1934, Ewan 1955). Rebecca, daughter Josephine, and colleague Mary Pulsifer Ames comprised an accomplished trio of women who were primary contributors to the early botany of northeastern California, along with contemporaries John Gill Lemmon and Sarah Plummer Lemmon (Agnew & Agnew 2020). In addition to collecting plants in northeastern California for sale to the Smithsonian and other herbaria, Rebecca corresponded widely with other biologists (including Darwin and Asa Gray) and wrote scientific papers, most notably on *Darlingtonia californica* Torrey.

Josephine Cornelia Austin was born in 1865 to Rebecca and James Thomas Austin (1837–1918) at Slate Creek near Quincy, Plumas Co., California. She worked as a school teacher before marrying rancher Charles C. Bruce (1861–1936) in 1884 (i.e., at age 19). After their marriage, the Bruces ranched for a time near Chico, California, before moving to Goose Lake Valley in Modoc County for five years. They eventually returned to Chico, where they grew peaches and prunes. Josephine died in 1931 in Alameda, California, several years before the death of her husband Charles.

In spite of her obligations as a farm wife, Josephine devoted much time to gathering plant specimens, presumably both by herself and in company with her mother and Mary Pulsifer Ames. As was common at the time, multiple duplicates were made for wide distribution to prominent herbaria and botanists in the eastern United States and California. Institutions that currently hold significant sets of Josephine's collections include CAS, DOV, GH, KANU, MO, NY, PH, RSA, and US. Many of her collections are among the earliest made from Modoc Co., California, and adjacent Lake Co., Oregon.

In addition to *Potentilla bruceae*, other plants named after Josephine include *Arabis bruceae* M.E. Jones, *Arnica bruceae* Rydb., *Astragalus tener* var. *bruceae* M.E. Jones, *Crepis bruceae* Babc., and *Hamosa bruceae* Rydb. In addition, after citing one of "Mrs. C.C. Bruce's" collections as the type of *Scutellaria austineae*, Eastwood (1903) stated that "It is named in her honor and that of her mother, Mrs. R.M. Austin."

What about *Potentilla anomalifolia*?

Peck (1936) originally described *Potentilla anomalifolia* (as "anomalofolia") for a localized population of distinctive plants growing in a damp meadow near the Klamath Agency in Klamath County, Oregon. He referred to his find as "A remarkable species, in leaf characters quite unlike anything else known to us. One might suspect it of being a hybrid had any possible parent forms been found in the neighborhood. Apparently good seeds occur but not in abundance. Many specimens were found scattered over several acres of ground." He included the species, known only from the type locality, in his subsequent floras of Oregon (Peck 1941, 1961). In his key, Peck distinguished *P. anomalifolia* as having bipinnate leaves and an ample inflorescence, contrasting with *P. bruceae*, *P. drummondii*, and several other pinnate-leaved species.

Clausen et al. (1940) and Hitchcock et al. (1961), however, treated *Potentilla anomalifolia* as simply a "robust form" of *P. drummondii* — this synonymy was also adopted by Abrams (1944) and Johnston (1980). Johnston furthermore associated the name with a form that he believed "appears sporadically throughout the range of *P. drummondii*; it may be a sporadic genetic variant, or less likely a hybrid." His map of *P. drummondii* shows widely scattered occurrences of *anomalifolia*, as the species' "dissected phase," in the Wallowa and Siskiyou mountains of Oregon, the Klamath Mountains and central Sierra Nevada of California, and the Ruby Mountains of Nevada.

Alternatively, the first author has considered *Potentilla anomalifolia* to be a probable synonym of *P. bruceae*, though with more deeply dissected leaves than typical (Ertter & Mansfield 2007). This association carried over to the treatment for Flora of North America (Ertter et al. 2015), in which *P. anomalifolia* is addressed as a possible result of intergradation among *P. bruceae, P. breweri*, and *P. drummondii*. However, after having examined the holotype (*Peck 16819*, WILLU) and two isotypes (OSC, WILLU) of *P. anomalifolia* on loan to WIS, we now have a different interpretation of the anomalous population that Peck vouchered.

First and foremost, the non-montane meadow habitat, large erect habit, many-flowered inflorescence, and stiff vestiture of Peck's collections are well outside the variation within *Potentilla drummondii, P. bruceae, P. breweri*, or any possible combination among the three species. Second, the three type specimens differ significantly among themselves, with the leaves of the holotype less dissected than those of the isotypes. Finally, no comparable collections have subsequently been found, though the area around the Klamath Agency (most of which is now private grazing land) has admittedly not been fully searched.

Given this situation, and the fact that Peck himself noted a paucity of good seed, our conclusion is that *Potentilla anomalifolia* is in fact a hybrid, but not one involving *P. drummondii, P. bruceae*, or *P. breweri*. Instead, our suspicion is that the parentage involves one of the morphotypes of *P. gracilis*, most likely var. *fastigiata* sensu lato, and *P. millefolia* Rydb. Both species are well represented (at least historically) in seasonally saturated bottomlands in this portion of Oregon, and the vestiture of both species is reasonably similar to that of *P. anomalifolia*. However, the two species have very different morphologies, with *P. gracilis* consisting of relatively large, ascending to erect plants with palmate leaves and many-flowered inflorescences, while *P. millefolia* has shorter, prostrate to decumbent stems, pinnate leaves with deeply dissected leaflets, and few-flowered inflorescences with recurved pedicels. Although hybrids between such different species might seem unlikely, we have nevertheless documented apparent hybrids where comparably distinct palmate and pinnate species overlap, resulting in a wide range of anomalous leaf dissection similar to that expressed in the type collection of *P. anomalifolia* (mostly unpublished, but see the discussion of *P. gracilis* var. *indiges* (M. Peck) Ertter & N.M. House and Fig. 4 in Ertter and House 2024).

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