

GENERIC REALIGNMENTS IN TRIBE POTENTILLEAE AND REVISION OF *DRYMOCALLIS* (ROSOIDEAE: ROSACEAE) IN NORTH AMERICA

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ABSTRACT

The convergence of morphology-based research by J. Soják and molecular analysis by T. Eriksson et al. supports the resurrection of *Comarum*, *Dasiphora*, *Drymocallis*, *Sibbaldia*, and *Sibbaldiopsis* from *Potentilla* s.l. These segregate genera, which were used by P.A. Rydberg in the last continent-wide treatment of tribe *Potentilleae* in North America, will be used in the forthcoming treatment of *Potentilleae* in *Flora of North America North of Mexico*. The genus *Drymocallis* in North America is revised to encompass 15 species and seven additional varieties, in place of the three species of *Potentilla* (*P. arguta*, *P. fissa*, *P. glandulosa*) and 11 additional varieties recognized by D.D. Keck. ***Drymocallis pseudorupestris* var. *saxicola*** Ertter (widespread), ***D. pseudorupestris* var. *crumiana*** D.D. Keck ex Ertter (California), and ***D. deseretica*** Ertter (central Utah) are described as new, and several new combinations are made: ***D. lactea* var. *austiniae*** (Jeps.) Ertter, ***D. glandulosa* var. *wrangelliana*** (Fisch. & Avé-Lall.) Ertter, ***D. glandulosa* var. *reflexa*** (Greene) Ertter, ***D. glandulosa* var. *viscida*** (Parish) Ertter, ***D. campanulata*** (C.L. Hitchc.) Ertter, and ***D. cuneifolia* var. *ewanii*** (D.D. Keck) Ertter. The last combination results from the recent rediscovery of *D. cuneifolia* var. *cuneifolia*, which is currently known from a single population in the San Bernardino Mountains of California.

KEY WORDS: Rosaceae, *Potentilleae*, *Drymocallis*, *Dasiphora*, *Comarum*, generic realignment, new species, *Sibbaldiopsis*

RESUMEN

La convergencia entre la investigación basada en la morfología realizada por J. Soják y los análisis moleculares realizados por T. Eriksson et al. soportan la resurrección de *Comarum*, *Dasiphora*, *Drymocallis*, *Sibbaldia*, y *Sibbaldiopsis* desde *Potentilla* s.l. Estos géneros segregados, que se usaron por P.A. Rydberg en el último tratamiento a nivel continental de la tribu *Potentilleae* en Norte América, será usado en el próximo tratamiento de *Potentilleae* en la *Flora of North America North of Mexico*. El género *Drymocallis* en Nore América es revisado para incluir 15 especies y siete variedades adicionales, en lugar de las tres especies de *Potentilla* (*P. arguta*, *P. fissa*, *P. glandulosa*) y 11 variedades adicionales reconocidas por D.D. Keck. ***Drymocallis pseudorupestris* var. *saxicola*** Ertter (de amplia distribución), ***D. pseudorupestris* var. *crumiana*** D.D. Keck ex Ertter (California), y ***D. deseretica*** Ertter (Utah central) se describen como nuevas, y se hacen varias combinaciones nuevas: ***D. lactea* var. *austiniae*** (Jeps.) Ertter, ***D. glandulosa* var. *wrangelliana*** (Fisch. & Avé-Lall.) Ertter, ***D. glandulosa* var. *reflexa*** (Greene) Ertter, ***D. glandulosa* var. *viscida*** (Parish) Ertter, ***D. campanulata*** (C.L. Hitchc.) Ertter, ***D. cuneifolia* var. *ewanii*** (D.D. Keck) Ertter. La última combinación resulta del reciente redescubrimiento de *D. cuneifolia* var. *cuneifolia*, que es conocida actualmente de una única población en las montañas de San Bernardino de California.

Tribe *Potentilleae* Sweet (Rosaceae: Rosaceae) is comprised of *Potentilla* L. and variously recognized segregate and related genera, including *Fragaria* L., *Ivesia* Torrey & A. Gray, and *Sibbaldia* L. All of these genera have at one time or another been included within *Potentilla*, and multiple segregate genera have been proposed. *Potentilla* s.s. is widespread throughout arctic and temperate regions of the northern hemisphere, with southward extensions along the American cordilleran system and mountains of southeast Asia and adjacent Malesian archipelago. The last attempt at a worldwide monograph of *Potentilla* s.l. (excluding *Ivesia*, *Horkelia* Cham. & Schltldl., and related segregate genera endemic to western North America) was by Wolf (1908), who tallied over 300 species along with numerous varieties and hybrids. This number is a poor indicator of the current status, given the significant number of taxa that have been described, reduced to synonymy, or otherwise been subject to taxonomic realignment during the intervening century.

Two relatively recent developments have contributed to an improved understanding of worldwide diversity and generic circumscriptions in *Potentilleae*, one political, one scientific. On the geopolitical front, the collapse of the Soviet bloc and renewed relations between the United States and China made essential comparisons of American and Asian variation significantly easier. Collaboration among researchers with expertise in their respective geographic areas are paving the way for a modern monographic synthesis of

Potentilleae, including the Panarctic Flora project (Elven et al. 2007) and the Flora of China project (*Potentilleae* by Li et al. 2003). In the scientific realm, a molecular phylogenetic underpinning of *Potentilleae* has now been generated by Torsten Eriksson et al. (1995, 1998, 2003) with additional efforts underway by Christoph Dobes (pers. comm. 2006), Bente Eriksen (pers. comm. 2007), and their colleagues.

The present paper summarizes the historical and current nomenclatural framework in *Potentilleae* resulting from these developments. It also provides a revision of one of the resurrected generic segregates, *Drymocallis* Fourr. ex Rydb., including several new taxa and combinations. This synopsis serves to introduce nomenclatural adjustments to *Potentilleae* that will be implemented in vol. 9 of *Flora of North America North of Mexico*, scheduled for publication in late 2008.

NOMENCLATURAL AND PHYLOGENETIC OVERVIEW OF POTENTILLEAE

The last continent-wide treatments of North American *Potentilleae* were by Per Axel Rydberg (1898, 1908), who argued that “Either the whole tribe, *Fragaria* also included, must constitute a single genus, or else both *Potentilla* and *Ivesia* be divided into several genera” (1898, p. 16). Choosing the latter option in his 1898 monograph of North American *Potentilleae*, Rydberg accordingly recognized the genera *Argentina* Hill, *Chamaerhodos* Bunge, *Comarella* Rydb., *Comarum* L., *Comocarpa* Rydb., *Drymocallis*, *Duchesnea* Sm., *Horkelia* (encompassing *Ivesia*), *Sibbaldia*, *Sibbaldiopsis* Rydb., and *Stellariopsis* Rydb., in addition to *Fragaria* and a significantly reduced *Potentilla* s.s. This generic framework was largely retained in his 1908 treatment of Rosaceae for *North American Flora*, except for the replacement of *Comocarpa* with *Dasiphora* Raf., the resurrection of *Ivesia* as distinct from *Horkelia*, and the addition of *Horkeliella* Rydb. and the recently described *Purpusia* Brandegee.

Rydberg was considered a consummate “splitter” by contemporary and later generations of botanists, such that most of his generic segregates disappeared into synonymy in subsequent regional floras in North America. Most European authors also adopted an inclusive circumscription of *Potentilla*, following the world monograph by Theodor Wolf (1908). David D. Keck (1938) retained and revised *Horkelia* and *Ivesia* as distinct genera, but submerged *Comarella*, *Horkeliella*, and *Stellariopsis* within *Ivesia*. Keck (in Clausen et al. 1940) also submerged *Drymocallis* within *Potentilla*, with most of Rydberg’s species reduced to subspecies or synonyms of a single species, *P. glandulosa* Lindl. In the opinion of Keck and his collaborators, “there is no justification for excluding *Drymocallis* from *Potentilla*. Certain species undoubtedly belonging to *Potentilla* closely link *Drymocallis* to the main body of the genus. We do believe, however, that the morphological distinctions of the anther and the position of the style, combined with a homogeneity of form, justify the maintenance of *Drymocallis* as a section or subsection of *Potentilla*.”

Keck’s circumscriptions of genera and species in the *Potentilleae* were largely adopted by subsequent regional floras in North America, though *Ivesia* and *Horkelia* were sometimes included in *Potentilla* (e.g., Howell 1949; Kearney & Peebles 1951). An element of confusion was introduced by Hutchinson (1964), who cited Keck’s revision of *Ivesia* and *Horkelia* in his synthesis of flowering plant genera but failed to incorporate the conclusions in his opus. Hutchinson’s indication of 35 species of *Ivesia*, three species of *Horkeliella*, two species of *Comarella*, and one species of *Stellariopsis* conflicts with Keck’s recognition of only 22 species of *Ivesia* s.l., which includes the species placed in the segregate genera recognized by Hutchinson. Researchers who rely on Hutchinson for generic delineations of these western North American genera are accordingly at odds with current usage as reflected in recent floristic treatments (e.g., Hitchcock & Cronquist 1961; Ertter 1993; Holmgren 1997; Welsh et al. 1993). Subsequent to Keck’s revision of *Ivesia* and *Horkelia*, no flora has used either *Comarella* or *Stellariopsis*, and when *Horkeliella* was resurrected it contained only two species (Ertter 1993). *Purpusia*, which Keck (1938) had retained as a distinct genus, has also been submerged into *Ivesia*, along with several species of *Potentilla* that were morphologically nearly identical to certain species of *Ivesia* except for details of flower structure that apparently form an evolutionary sequence (Ertter 1989).

Further generic resurrections are now supported by the felicitous convergence of independent morphological and molecular studies. In 1989, Czech botanist Jiří Soják published his conclusion that *Potentilleae*

was divided into two fundamental evolutionary lines. The *Fragaria*-line, characterized by sub-basal or lateral styles and anthers with a single horseshoe-shaped theca that opens by a marginal slit, consisted not only of *Fragaria* but also those species sometimes placed in *Comarum*, *Dasiphora* (as *Pentaphylloides* Duhamel), *Drymocallis*, *Sibbaldia*, *Sibbaldiopsis* and two small Asian genera (*Farinopsis* Chrtek & Soják and *Schistophyllidium* [Juz. ex Fed.] Ikonn.). The second evolutionary line, comprised of *Potentilla* s.s., *Ivesia*, and *Horkelia*, was characterized by subterminal styles and anthers with two thecae divided by the connective apex that opens by two lateral slits. The species potentially comprising *Argentina* (e.g., *P. anserina* L.) and the Asian genus *Tylosperma* Botsch. were more problematic.

Soják was then faced with the three options of 1) lumping everything in a single swollen genus, which in his understanding would need to be *Fragaria*; 2) treating the two evolutionary lines as separate genera, with all species of *Potentilleae* included in either *Fragaria* or *Potentilla*; or 3) breaking the components of each line into narrower, more homogeneous genera. Echoing Rydberg's decision, Soják chose the last option, as the simplest, most straight-forward solution that required the least nomenclatural disruption, and accordingly recognized the genera listed above and created the new combinations needed in Eurasian *Drymocallis*. Except for *Drymocallis*, Soják was therefore in concordance with the nomenclature used by his Russian colleague Boris A. Yurtsev in a flora of the arctic Soviet Union (1984). Although Soják's seminal paper was not widely available, being published in the journal of the National Museum in Prague while Czechoslovakia was just emerging from behind the Iron Curtain, his generic conclusions are reflected in more recent papers (e.g., Soják 2004), in which the superfluous and thus illegitimate *Pentaphylloides* is replaced by *Dasiphora* and *Argentina* is sometimes treated as distinct. An unpublished outline of North American *Potentilleae* Soják prepared in 1993 also reflects this generic framework, expanded by the addition of two subtribes to accommodate *Chamaerhodos*, *Alchemilla* L., *Aphanes* L., and *Lachemilla* Rydb.

Several years after Soják first published his generic outline, Torsten Eriksson and Michael Donoghue (1995) presented a molecular phylogenetic analysis of the *Potentilleae* that provided independent confirmation of the fundamental distinction between a potentilloid clade and a fragarioid clade, essentially corresponding to Soják's evolutionary lines. Further studies (Eriksson et al. 1998, 2003) confirmed and expanded the results, showing moreover that *Chamaerhodos* and the alchemilloids were also nested in the fragarioid clade and that the position of *P. anserina* (*Argentina*) was indeed ambiguous. *Comarella*, *Purpusia*, and *Stellariopsis* were specifically targeted for inclusion in further studies, indicating a reliance on Hutchinson (1964) as a generic starting point rather than Keck (1938) and all more recent floras. As it happens, preliminary ITS analysis of representative species of *Ivesia* (including *Comarella*, *Purpusia*, and *Stellariopsis*), *Horkelia*, and *Horkeliella* by the Christopher Baysdorfer lab (California State University, Hayward) results in a monophyletic polytomy (Ertter et al. 1998, unpublished data).

GENERIC DELIMITATIONS FOR FLORA OF NORTH AMERICA

There is no question that the species currently treated as *Potentilla* s.l. that fall into the fragarioid clade cannot be retained in *Potentilla* without that genus being polyphyletic, unless *Fragaria* and possibly *Chamaerhodos*, *Alchemilla*, *Aphanes*, and *Lachemilla* are also included. The two options are towards a more inclusive *Potentilla*, or the removal of all taxa in the fragarioid clade from *Potentilla*. In their discussion of nomenclatural implications, Eriksson et al. (1998, 2003) noted that if all taxa in the clades containing *Potentilla* s.l. were combined in a single genus, *Fragaria* apparently had priority. They were understandably reluctant to do a wholesale transfer of hundreds of species of *Potentilla* s.l. into *Fragaria* and instead, using the situation as an example of the purported advantages of phylogenetic nomenclature, proposed several rankless names for the best resolved clades (e.g., "Fragariinae"). Taking an alternative approach, Mabberley (2002) concluded that *Fragaria* need not take precedence and accordingly provided several new combinations to allow *Fragaria* to be included in *Potentilla* s.l.

Mabberley based his decision on a trend toward more inclusive genera in economically important taxa (e.g., *Prunus* s.l., *Lycopersicon* combined with *Solanum*). In contrast, the dominant trend affecting generic

usage in North America has been in the opposite direction; e.g., Grimes' (1990) work on the *Psoraleeae* (Fabaceae) and Baldwin's (1999) work on the *Madiinae* (Asteraceae), often resulting in the resurrection of generic segregates first proposed by Rydberg and his fellow splitters. This latter approach is easily implemented in *Potentilla*, in that all of the essential generic names are already available and were used in the most recent continent-wide treatment of the family (Rydberg 1908). Initial steps have already been taken towards floristic implementation of the fragarioid generic segregates in both Europe (Kurtto & Eriksson 2003) and North America (e.g., Weber 1987; Weber & Whittman 1992; Pojar 1999; Aiken et al. 2006). Full implementation in North America will occur in volume 9 of *Flora of North America North of Mexico* (scheduled for publication in 2008), in which the following fragarioid genera that have sometimes been included in *Potentilla* will be recognized:

Comarum L.—*Comarum palustre* L. replaces *Potentilla palustris* (L.) Scop. One other Asian species sometimes placed in *Comarum* has been placed in its own genus as *Farinopsis salesoviana* (Stephan) Chrtek & Soják (1984).

Dasiphora Raf.—*Dasiphora fruticosa* (L.) Rydb. replaces *Potentilla fruticosa* L. Several previous treatments that initiated this generic change in North America (e.g., Holmgren 1997; Pojar 1999; Weber 1987) adopted *Pentaphylloides*, but this name has been subsequently interpreted as an illegitimate superfluous name for *Potentilla* (as noted by Kurtto & Eriksson 2003; Reveal et al. 1999).

Drymocallis Fourr. ex Rydb.—*Drymocallis* is the generic segregate from *Potentilla* with the most species, with centers of radiation in western North America, central Asia, and southeastern Europe. My provisional revision (below) recognizes fifteen species with an additional seven varieties in North America. Around thirteen Old World species are currently recognized, with most of the necessary combinations established by Soják (1989) and Kurtto & Eriksson (2003). The elevation of *Drymocallis* to generic status allows it to be used more definitively in making biogeographic comparisons between the southern Rocky Mountains of North America and the Altai of central Asia, as has recently been done by Weber (2003).

Fragaria L.—The treatment of *Fragaria* being prepared by Gündter Staudt will reflect his recent revision of North American strawberries (Staudt 1999).

Sibbaldia L.—*Sibbaldia procumbens* L. var. *procumbens* replaces the nomenclaturally invalid *Potentilla procumbens* (L.) Clairv. (a later homonym of the unrelated *P. procumbens* Sibth.), *P. siboldi* Haller f., and *P. siboldia* Kurtz. Soják (pers. comm. 2006) recognizes only six species of *Sibbaldia*, with most others placed in *Potentilla*.

Sibbaldiopsis Rydb.—*Sibbaldiopsis tridentata* (Soland.) Rydb. replaces *Potentilla tridentata* Soland. Soják (ined.) is also transferring two Asian species (*P. cuneifolia* Bertol. and *P. miyabei* Makino) into this genus, which corresponds to Wolf's (1908) "Grex *Tridentatae*."

The potentilloid segregates *Duchesnea*, *Ivesia*, *Horkelia*, and *Horkeliella* will be retained as in the current treatment for California (Ertter 1993) and the Intermountain Region (Holmgren 1997). Although it has long been assumed that these genera most likely evolved from and are accordingly nested within *Potentilla* s.s., as is now supported by molecular evidence (Eriksson et al. 1995, 1998, 2003), I strongly concur with Brummitt (2002), Diggs and Lipscomb (2002), and Hörandl (2006) that paraphyly alone is insufficient grounds for dictating generic delimitations. *Comarella*, *Purpusia*, and *Stellariopsis* will be retained in *Ivesia*, although Soják (ined.) argues that the distinctive anthers of *Stellariopsis* (= *Ivesia santolinoides* A. Gray), which dehisce by subterminal pores, justify recognition as a separate genus.

REVISION OF NORTH AMERICAN DRYMOCALLIS

The North American members of *Drymocallis*, as *Potentilla glandulosa* and allies, were among those studied by Jens Clausen, David D. Keck, and William M. Hiesey in their seminal experiments on biosystematics (Clausen et al. 1940; Clausen & Hiesey 1958). They confirmed that the complex, which they considered

to be “one of the most satisfactory in the transplant investigations, and ... the most important” (Clausen et al. 1940, p. 26), consists of a wide diversity of ecotypes, often highly localized, differing from one another ecologically, physiologically, and morphologically. They also demonstrated that hybrids between these ecotypes are readily generated, aided by a diploid chromosome number of $n=7$ shared by all species thus far counted, and intergradation zones where ecotypes intersect are the norm. In contrast to the *Potentilla gracilis* complex, which they also investigated, apomixis is not known to play a role in *Drymocallis*. The responsibility of converting this biosystematic complexity into a functional taxonomic framework fell on Keck (in Clausen et al. 1940), whose compromise approach reduced Rydberg’s (1908) 28 species of *Drymocallis* to only three species of *Potentilla* (*P. arguta* Pursh, *P. fissa* Nutt., *P. glandulosa* Lindl.), with most of the ecotypic variation treated as subspecies of *P. glandulosa*.

My initial intent for *Flora of North America* was to adopt Keck’s taxonomy, as modified by Ertter (1993) and Hitchcock et al. (1969), with the requisite new combinations in *Drymocallis* and the description of a new taxon from California. I reluctantly concluded, however, that Keck’s outline did not adequately accommodate current evidence of variation in North American *Drymocallis*, especially outside of central California where the biosystematic experiments had taken place. For one thing, it is not clear that Keck’s subspecies are more closely related within a species than between species, as indicated, for example, by the narrow inflorescences of *P. arguta* subsp. *convallaria* (Rydb.) D.D. Keck and *P. glandulosa* subsp. *hansenii* (Greene) D.D. Keck, or the numerous leaflets of *P. fissa* and *P. glandulosa* subsp. *arizonica* (Rydb.) D.D. Keck. At the same time, there are extremes of variation beyond those addressed by Keck’s abbreviated taxonomic treatment, such as the narrowly opened flowers of *P. glandulosa* subsp. *ewanii* D.D. Keck and *P. glandulosa* var. *campanulata* C.L. Hitchc. Rather than perpetuate an unacceptable taxonomic framework, I accordingly have decided to take the opportunity of a nomenclatural overhaul to introduce an alternate framework. This effort is unabashedly provisional, in that the time frame for *Flora of North America* does not allow for the complete revision that *Drymocallis* clearly deserves. My hope is that it is nevertheless a step forward in approximating the natural variation in *Drymocallis*, until such time as a more complete study can be undertaken that incorporates molecular analysis in combination with extensive studies of variation in the field.

At heart is the question of whether the goals of taxonomy are better served by sharply defined groupings, however polymorphic, or by more finely parsed natural variation, even at the expense of crisp circumscriptions. I have opted for the latter, even though this approach runs counter to that of several recent floristic works (e.g., Holmgren 1997; Welsh et al. 1993), in which many of Keck’s subspecies are relegated to synonymy. My approach, comparable to that currently implemented in some other rosaceous genera (e.g., *Rosa* and sections of *Potentilla* s.s.), is to give taxonomic recognition at the species or subspecies level if a significant core of populations share a relatively cohesive suite of unique characters underpinned by a definable ecogeographic setting. Varieties are used where the core differences are less distinct and/or the intergradations more complex. Such a taxonomic approach can only be done with full understanding that any attempt to recognize formal taxa in North America *Drymocallis* will be compromised by wide zones of intergradation and populations that defy placement. The alternative is to accept such broadly defined taxa that extensive variation within an ecogeographic setting is glossed over, even that which would easily qualify as distinct species if the inconvenient zones of intergradation went extinct. Given this situation, and the current sociopolitical setting, it would be most unfortunate if valid components of biodiversity failed to receive the conservation attention they deserve for lack of sharp boundaries (Ertter 1997). Indeed, my suspicion is that at least some of the purported intergradation actually represents additional unrecognized entities, and that a cleaner taxonomy might result with the recognition of even more, not fewer, taxa. At the very least, I believe that the resultant taxonomic framework will lead to a better appreciation of diversity within *Drymocallis* and encourage more studies on a complex and fascinating genus.

Presented here is a complete synopsis of species of *Drymocallis* that will be recognized in *Flora of North America*. Synonyms used in recent floras are listed, new combinations are provided as needed, three new taxa are described, and some nomenclatural issues are discussed. A complete key, descriptions, and additional

discussion will be available in vol. 9 of *Flora of North America*, and the California species will be covered in the pending new edition of *The Jepson Manual*. Additional synonymy can be found in Clausen et al. (1940), Rydberg (1908), Hitchcock and Cronquist (1961), Holmgren (1997), and the upcoming treatment in *Flora of North America*.

1. *Drymocallis fissa* (Nutt.) Rydb., Mem. Dept. Botany Columbia Coll. 2:197. 1898. = *Potentilla fissa* Nutt.

2. *Drymocallis arizonica* Rydb., N. Amer. Fl. 22:373, 1908. = *Potentilla glandulosa* Lindl. subsp. *arizonica* (Rydb.) D.D. Keck, not *Potentilla arizonica* Greene

3. *Drymocallis arguta* (Pursh) Rydb., Mem. Dept. Bot. Columbia Coll. 2: 192. 1898. = *Potentilla arguta* Pursh.

In his treatment for *North American Flora*, Rydberg (1908) replaced *D. arguta* with *Drymocallis agrimonioides* (Pursh) Rydb., presumably because the conspecific *Geum agrimonioides* Pursh (Fl. Amer. Sept. 351) was on an earlier page than *Potentilla arguta* Pursh (Fl. Amer. Sept. 736). According to the International Code of Botanical Nomenclature, page sequence has no bearing on priority in a single work that was published as a unit, which is the situation for *Flora Americae Septentrionalis* since both volumes were distributed in the last two weeks of 1813 (Reveal et al. 1999). Rydberg's (1898) initial use of *D. arguta*, in which *Geum agrimonioides* is cited in synonymy, confirms that the more familiar epithet can be retained.

4. *Drymocallis convallaria* (Rydb.) Rydb., Mem. Dept. Bot. Columbia Coll. 2:193. 1898. = *Potentilla arguta* Pursh subsp. *convallaria* (Rydb.) D.D. Keck; *P. arguta* Pursh var. *convallaria* (Rydberg) Th. Wolf.

5. *Drymocallis micropetala* Rydb., N. Amer. Fl. 22:375. 1908. = *Potentilla glandulosa* Lindl. subsp. *micropetala* (Rydb.) D.D. Keck; *P. glandulosa* Lindl. var. *micropetala* (Rydb.) S.L. Welsh & B.C. Johnst.

6. *Drymocallis hansenii* (Greene) Rydb., Mem. Dept. Bot. Columbia Coll. 2:200. 1898. = *Potentilla hansenii* Greene; *P. glandulosa* Lindl. subsp. *hansenii* (Greene) D.D. Keck.

7. *Drymocallis lactea* (Greene) Rydb., N. Amer. Fl. 22:369. 1908.

7a. *Drymocallis lactea* var. *lactea* = *Potentilla glandulosa* Lindl. var. *nevadensis* S. Watson; *P. glandulosa* subsp. *nevadensis* (S. Watson) D.D. Keck; not *P. nevadensis* Boiss. (1838).

This taxon has a well-established identity as *Potentilla glandulosa* var. (or subsp.) *nevadensis*, but the epithet *lactea* has priority at species rank and its use avoids possible confusion with *P. nevadensis* Boiss.

7b. *Drymocallis lactea* var. *austiniae* (Jeps.) Ertter, comb. nov. BASIONYM: *Potentilla glandulosa* Lindl. var. *austiniae* Jeps., Fl. Calif. 2:181. 1936.

Jepson (1936) called *P. glandulosa* var. *austiniae* a nom. nov. for *P. glandulosa* var. *fissa* Jepson, the combination he had used in his *Manual* (Jepson 1925). According to K. Gandhi (pers. comm. 2006), var. *austiniae* stands as a legitimate taxon distinct from *P. fissa* Nutt., since this species was explicitly excluded by Jepson (1936), but var. *fissa* Jeps. must be considered a synonym of *P. fissa* and is furthermore an isonym of *P. glandulosa* var. *fissa* (Nutt.) Th. Wolf (1908).

This variety was erroneously treated as *Potentilla glandulosa* subsp. *ashlandica* (Greene) D.D. Keck by Ertter (1993), but I now understand both to be separate entities.

8. *Drymocallis ashlandica* (Greene) Rydb., Mem. Dept. Bot. Columbia Coll. 2:200. 1898. = *Potentilla glandulosa* Lindl. subsp. *ashlandica* (Greene) D.D. Keck; *P. ashlandica* Greene, Pittonia 3:248, 1897; *P. ciliata* Howell, Fl. N. W. Amer. 1:1715. 1898; not *P. ciliata* Raf. (1840) or *P. ciliata* Greene (1887).

Potentilla ashlandica Greene is sometimes said to be a nom. nov. for *Potentilla ciliata* Howell (e.g., Keck in Clausen et al. 1940), the latter illegitimate as a result of being a later homonym, but Greene's name was published first and makes no reference to *P. ciliata*. Both names are based on a collection by Howell from Ashland Butte, the only known collection of which is in Howell's herbarium in ORE (now housed in OSC).

9. *Drymocallis pseudorupestris* (Rydb.) Rydb., Mem. Dept. Bot. Columbia Coll. 2:194. 1898. = *Potentilla*

glandulosa Lindl. subsp. *pseudorupestris* (Rydb.) D.D. Keck; *P. glandulosa* var. *pseudorupestris* (Rydb.) Breitung; *P. rupestris* L. var. *americana* Th. Wolf.

Many populations of *Drymocallis pseudorupestris* from Montana and Wyoming, including the type of *Potentilla pseudorupestris* Rydb. (Long Baldy, Little Belt Mountains, Montana, *Flodman* 598 [NY!]) are significantly larger plants than is the norm elsewhere, with bigger petals and longer filaments. I am treating these populations as *D. pseudorupestris* var. *pseudorupestris*, with further research needed to determine the optimum circumscription and resultant geographic range. Two new varieties are described here: var. *saxicola* to accommodate the majority of populations previously placed in *Potentilla glandulosa* var. *pseudorupestris*, and var. *crumiana* to accommodate a variant from the Sierra Nevada proposed but not published by Keck.

9a. *Drymocallis pseudorupestris* var. *pseudorupestris*

9b. *Drymocallis pseudorupestris* var. *saxicola* Ertter, var. nov. (**Fig. 1, M–R**). TYPE: UNITED STATES. IDAHO: Lemhi Co.: Bighorn Crags ca 30 air mi W of Salmon, head of drainage W of Welcome Lake, at N end of saddle to Barking Fox Lake, ledges in granite, T21N R16E S28 N1/2 of SW, ca 9000 ft, 31 Jul 1990, B. Ertter 9493 with D. Atwood, R. Moseley, S. Bernatas, M. Mancuso (HOLOTYPE: UC; ISOTYPES: BRY, ID, NY).

A var. *pseudorupestris* statura minore (< 2.5 dm), floribus parvioribus, filamentis brevioribus (1–2.5 mm) differt.

Herbaceous perennial from openly branched caudex or spreading rootstocks, sometimes ± rhizomatous, forming clumps to 6 dm across. **Stems** few to many, erect, 0.6–2.5(–3) dm tall, the base 1–2(–3) mm diam. with sparse to abundant peglike glands and septate glandular hairs to 2 mm long, short eglandular hairs sparse to abundant (lacking in some collections from Custer Co., ID). **Basal leaves** 3–9(–16) cm long with (2–)3(–4) pairs of lateral leaflets; sheathing leaf-bases often sparsely strigose; terminal leaflet broadly obovate-cuneate with a ± rounded apex, 0.8–2(–4) cm long, 0.7–2(–3) cm wide, usually with abundant peglike glands and sparse to moderately abundant eglandular hairs to 1.5 mm long, the margins single- to ± double-toothed ca 1/4–1/3 to base with 3–8(–12) teeth per side. **Cauline leaves** 0–1(–2), 2–5(–8) cm long with 2–3 pairs of lateral leaflets. **Inflorescence** relatively open, comprising 1/4–3/4 of plant height, not particularly leafy; subtending bract ± trilobed, 1–2.5(–3) cm long; branches diverging at a (10–)20–40(–50)° angle; pedicels 3–15(–20) mm long, with sparse to abundant (never absent) septate glandular hairs and 0 to abundant eglandular hairs 0.1–0.5 mm long. **Flowers** (2–)3–12(–20); hypanthium saucer-shaped, 2.5–4(–5) mm diam., with highly variable proportions of peglike glands, septate glandular trichomes, and eglandular hairs to 1 mm long; epicalyx bractlets linear-lanceolate to broadly elliptic, 2–5 mm long, ± 1–1.5 mm wide, often toothed or lobed; sepals 4–6(–7) mm long, the vestiture like that of hypanthium, the apex obtuse (to acute), often mucronate, entire; petals cream to ± yellow, not red-tinged, narrowly to broadly obovate, 4–9 mm long (longest in Washington), 3.5–6(–8) mm wide, exceeding sepals, the apex rounded; stamens 20–25, the filaments 1–2.5 mm long, not red-tinged, the anthers ovate-elliptic, 0.7–1.2 mm long; styles ± fusiform, ± 1 mm long, most often golden brown. **Achenes** ± obliquely pyriform, generally short-beaked, ca 1 mm long, light brown.

Ecology and phenology.—Cliffs, ledges, outcrops, ridges, talus slopes, lava beds, and other generally rocky situations, 1000–3400 m elev. Flowering May–Aug.

As circumscribed here, *Drymocallis pseudorupestris* var. *saxicola* accommodates the bulk of specimens previously placed in *Potentilla glandulosa* var. *pseudorupestris*, minus the extremes at the northeastern and southern ends of the range. The current circumscription encompasses significant heterogeneity, which might be resolved into additional taxa upon further analysis. Plants from southeastern Oregon, including the type of *D. pumila* Rydb. from Steens Mountain, combine the habit of *D. pseudorupestris* and the vestiture of *D. lactea*.

REPRESENTATIVE SPECIMENS: **CANADA. ALBERTA:** Bellevue Hill, Waterton Lakes National Park, J. Nagy & W. Blais 682 (DS). **UNITED STATES. CALIFORNIA: Eldorado Co.:** Mt. Tallac, J.T. Howell 22949 (CAS). **Shasta Co.:** ridge overlooking Lake Helen, Lassen Volcanic National Park, H. Bailey & V. Bailey 2949 (UC). **Siskiyou Co.:** W side of Shastina, Mt. Shasta, W.B. Cooke 15372 (UC). **Fresno Co.:** Simpson Meadow, Middle Fork of Kings River, J.T. Howell 33794 (CAS). **Tulare Co.:** Bullfrog Lakes 6 mi SE of Mineral King, B. Rice 430 (CAS). **IDAHO. Adams Co.:** Black Lake, J.H. Christ 8674 (UC). **Boise Co.:** Middle Fork Boise River 2 1/2 mi upstream from Twin Springs,

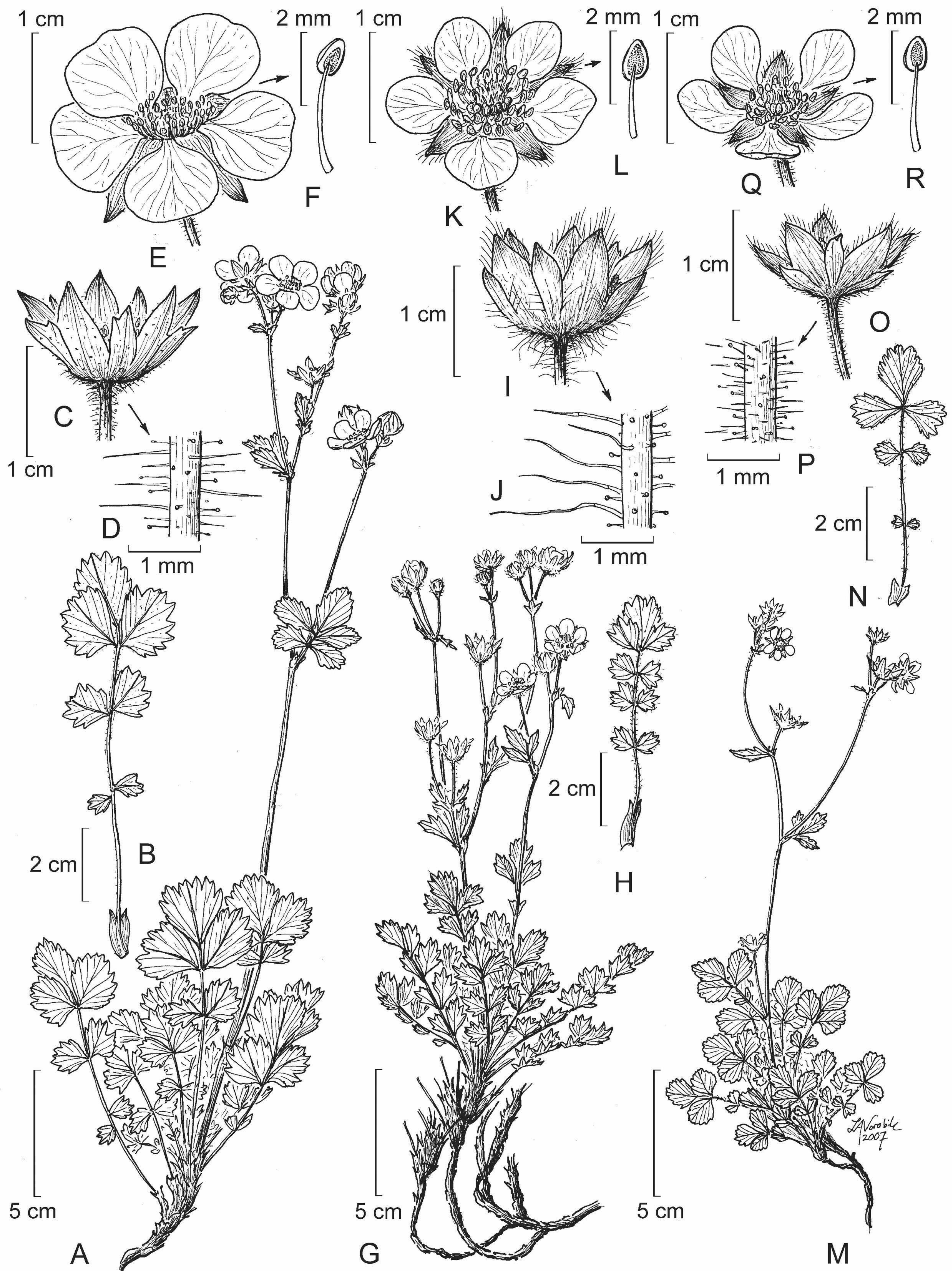


FIG. 1. Varieties of *Drymocallis pseudorupestris*. A–F: *var. pseudorupestris*. A: habit. B: basal leaf. C: hypanthium and calyx. D: vestiture of pedicel. E: flower. F: stamen. G–L: *var. crumiana*. G: habit. H: basal leaf. I: hypanthium and calyx. J: vestiture of pedicel. K: flower. L: stamen. M–R: *var. saxicola*. M: habit. N: basal leaf. O: hypanthium and calyx. P: vestiture of pedicel. Q: flower. R: stamen.

B. Ertter & *C. Prentice* 8703 (UC). **Butte Co.:** 10 mi N of Craters of Moon, 13 May 1941, *G. Williams s.n.* (UC). **Camas Co.:** summit of Featherville-Ketchum road, *C.L. Hitchcock* & *C.V. Muhlick* 10426 (UC, WTU). **Custer Co.:** 3.5 mi SW of Stanley Lake, *C.L. Hitchcock* & *C. V. Muhlick* 9626 (NY, UC, WTU). **Fremont Co.:** Shot Gun, *R.J. Davis* 746 (UC). **Idaho Co.:** Seven Devils Ridge, *J. H. Christ* 12473 (ID, UC). **Lemhi Co.:** Sleeping Deer Mountain, *B. Hayse* 35 (WIS). **Valley Co.:** above Snowslide Lake 10 air mi NE of McCall, *B. Ertter* & *S. D'Alcamo* 7805 (UC; to be distributed). **OREGON: Deschutes Co.:** Broken Top, Cascade Range, *B. Ertter* & *S. Garrett* 15052 (UC). **NEVADA: Elko Co.:** 1.2 km NE of Matterhorn, Jarbidge Mts., *D. Charlet* 445 (UC). **White Pine Co.:** Schell Creek Range, *A. Tiehm* & *S. Crisafulli* 11797 (NY, RM, WIS). **UTAH: Juab Co.:** divide between Toms Creek and Basin Creek drainage, Deep Creek Range, *N.H. Holmgren* & *P.K. Holmgren* 11185 (NY, UC). **Piute Co.:** S of Bullion Creek Canyon, Tushar Mts., *N.H. Holmgren*, *P.K. Holmgren*, & *C.S. Keller* 10897 (NY, UC). **Sevier Co.:** 0.75 mi NW of Mt. Terrill, *S. Goodrich* 24194 (BRY). **WASHINGTON: Asotin Co.:** Big Butte 6 mi W of Anatone, *H. St. John* & *R. Palmer* 9594 (UC). **Chelan Co.:** Mission Ridge, Wenatchee Mts., *J.W. Thompson* 14943 (NY, UC). **WYOMING:** Teton Mts., *A. Nelson* & *E. Nelson* 6578 (RM, UC).

9c. *Drymocallis pseudorupestris* var. *crumiana* D.D. Keck ex Ertter, var. nov. (**Fig. 1, G–L**). TYPE: UNITED STATES. CALIFORNIA: Inyo Co.: Rock Creek Lake Basin, recess or cirque on east side, 11,500 ft, 21 Jul 1934, *F.W. Peirson* 11272 (HOLOTYPE: UC 638452; ISOTYPES: DS 318001, DS 688601).

A var. *saxicola* foliolis plerumque 9, calycis setis conspicuis 1–1.5 mm longis, stylis plerumque vinosis differt.

Herbaceous perennial from openly branched caudex or spreading rootstock, with abundant stalked glands that generate an abundant golden resin. **Stems** few, erect, (0.3–)0.8–2(–2.5) dm tall, the base 1–2 mm diam. with sparse to abundant peglike glands and septate glandular hairs to 2 mm long, eglandular hairs generally lacking. **Basal leaves** (2–)3–9(–15) cm long with 3–4(–5) pairs of lateral leaflets; sheathing leaf-bases ± strigose; terminal leaflet broadly obovate to flabellate with rounded apex, 0.2–1.2(–2) cm long, 0.5–1.5 cm wide, with subsessile golden glands and sparse to moderately abundant spreading to ascending rigid setae 0.5–1 mm long, the margins predominantly single-toothed ca $\frac{1}{3}$ – $\frac{1}{2}$ to base with 2–5 teeth per side. **Cauline leaves** 0–2, 2–3.5(–6) cm long with 2–3 pairs of lateral leaflets. **Inflorescence** open, comprising $\frac{1}{4}$ – $\frac{1}{2}$ (– $\frac{3}{4}$) of plant height, not leafy; subtending bract 0.5–2.5 cm long; branches diverging at a 10–40° angle; pedicels 5–12(–20) mm long, with ± abundant subsessile glands and septate glandular trichomes, eglandular hairs sparse to 0. **Flowers** 2–8; hypanthium saucer-shaped, 4–6 mm diam., with both scattered glandular trichomes and ± rigid spreading setae 1–1.5 mm long; epicalyx bractlets elliptic-ovate to lanceolate, 2–3.5(–4) mm long, 1–2 mm wide; sepals 4–6(–7) mm long, often red-tinged, the vestiture like that of hypanthium, the apex obtuse, generally mucronate, sometimes shallowly erose; petals cream to pale yellowish, often red-tinged, narrowly to broadly obovate, 5–7(–9) mm long, 3–5 mm wide, exceeding sepals, the apex rounded; stamens 25–30, the filaments 1.5–2(–3) mm long, often red-tinged, the anthers ovate-elliptic to nearly round, 0.7–1 mm long; styles thickly to narrowly fusiform, 1.2–1.5 mm long, most often dark red (golden brown in White Mts.). **Achenes** ± obliquely pyriform, ca 1 mm long, pale golden-brown with reddish apex.

Ecology and phenology.—Rocky slopes, talus, and ledges, in metamorphic, granitic, and volcanic substrates, 3200–3900 m elev. Flowering Jul–Aug.

The distinctiveness of this taxon was initially discussed in letters between Frank W. Peirson and Ethel Crum in the 1930's (archives of University Herbarium, University of California, Berkeley). Peirson, an avid collector, had sent specimens of *Potentilla* from Rock Creek Lake Basin in the eastern Sierra Nevada to the University of California at Berkeley for identification by Ethel K. Crum. Crum helped with *Potentilleae* for Jepson's *Flora of California* (1936), where she is described as “a scholarly assistant” who “became ardently attached to *Potentilla*, wherefore certain new varieties bearing her name” (p. 174). According to Mason (1943), Crum “assisted in the organization of the material for many of the larger genera in [vol. 2 of *Flora of California*], but adopted as her own, the genus *Potentilla*, the manuscript of which was accepted with some revisions.” Crum maintained this interest during her tenure as Assistant Curator of the University Herbarium (1933–1943), during which time she was also Secretary to the Editorial Board of *Madroño* (Mason 1943).

In both of two drafts of her letter to Peirson of 15 November 1934, Crum identified his No. 11272 as “*Potentilla* sp. nov. This very interesting specimen of the *Potentilla glandulosa* aggregate with reddish tinged flowers differs in certain particulars from all segregates known to me I believe that in the present state of knowledge [of the] *P. glandulosa* aggregate it will be best to give this form a distinct binomial. If you

wish, therefore, I shall be glad to prepare a description for publication, making your specimen the type of a new species." One draft of this letter (presumably the one sent) then adds the caveat that she first needs to examine the recently published *Potentilla brevifolia* var. *perserverans* A. Nelson. Crum never followed through on describing Peirson's collection, even when supplemented with additional collections, evidently deferring to David Keck and the contemporaneous biosystematics studies on the *Potentilla glandulosa* complex (letter of 5 May 1938). Peirson gave her his support, noting that "You have probably put more work and thought on *Potentilla* than anyone else in the state and it is only just and fitting that you proceed with a synopsis of the genus in spite of publications by others" (letter of 5 Oct 1940). In response, Crum (letter of 8 Oct 1940) indicated that she did not feel prepared to revise the genus, but agreed to return to *Peirson 11272*, "which I examined several years ago and then laid aside." She apologized for holding it up so long, and promised to send a "definite opinion" within the next two weeks.

Instead, Crum sent the specimen to Keck, "who was very much interested considering it was quite aberrant" (letter of 29 Oct 1940). Keck, who had just published his revision of the *P. glandulosa* complex (in Clausen et al. 1940), proposed to name the new taxon after Crum, which Peirson heartily endorsed (letter of 14 Dec 1940). Crum, however, urged Keck not to do so "not only because I don't deserve the honor but because my name is not euphonious" (letter of 20 Dec 1940). She hoped instead that Keck would use some variant of Peirson's name, though there already was a *P. peirsonii* Munz (= *Drymocallis cuneifolia* Rydb.). Following Crum's untimely death in January 1943, her colleague Annetta Carter wrote to Peirson about a letter received from Keck, in which he indicated his intent to use the epithet *crumiana*: "Miss Crum always objected to any publicity, but Dave feels that considering all the work that she did on *Potentilla*, she certainly deserves to have her name commemorated" (letter of 26 Oct 1944).

For whatever reason, Keck likewise never followed through on his intent to describe this distinctive taxon. I take great pleasure in adopting the suggestion of Keck, Peirson, and Carter in giving much-deserved recognition to one of my predecessors in *Potentilla* research, and finally giving a name to Peirson's discovery over 70 years after its original collection. Subsequent collections show the taxon to be both more widespread and perhaps less distinctive than initially believed. The red-tinged petals that first caught Crum's attention are not reliably present, but the leaflet characters provide a distinctive gestalt not found elsewhere in *Drymocallis*, though approaching *D. fissa* in Colorado.

OTHER SPECIMENS EXAMINED: **UNITED STATES. CALIFORNIA. Fresno Co.:** Kings Canyon National Park, Glenn's Pass Trail, 10,580–11,900 ft, 29 Jul 1948, *H. & V. Bailey 2736a* (UC); Kearsarge Pass, 11,500 ft, 15 July 1900, *W.L. Jepson 859* (JEPS); SE corner of Mt. Goddard, very steep stair-step climb, 12,350–12,750 ft, 15 Aug 1957, *C.H. Quibell 6933* (JEPS, RM); W toe of peak facing Goddard Canyon, 12,438 ft, 17 Aug 1957, *C.F. Quibell & A. McCallum 7047* (UC). **Inyo Co.:** Kearsarge Pass trail, 10,500 ft, 7 Aug. 1942, *A.M. Alexander & L. Kellogg 3272* (DS, NY, UC); Seventh Lake, Big Pine Lakes, 11,200 ft, 9 Aug 1947, *J.T. Howell 23963* (CAS); Inconsolable Range above Big Pine Lakes, 12,400 ft, 14 Aug 1947, *J.T. Howell 24093* (CAS, DS, UC); E side of Kearsarge Pass, 11,500 ft, 20 Jul 1948, *J.T. Howell 24790* (CAS); slope above N Fork of Oak Creek between Pk. 12606 and Pk. 10643, 11,500 ft, 6 Aug 1948, *F.L. Jones s.n.* (DS); head of Thibaut Creek, vicinity of Mt. Baxter, 10,600 ft, 16 Oct 1948, *F.L. Jones s.n.* (DS); Kearsarge Trail, 11,000 ft, 16 Aug 1936, *M. Kerr s.n.* (SBBG); Rock Creek Lake basin, cirque on east slope, 11,000 ft, 19 Jul 1931, *F.W. Peirson 9515* (UC); Rock Creek Lake Basin, rocky slopes above East Recess, 11,400 ft, 11 Aug 1937, *F.W. Peirson 12195* (JEPS); Taboose Pass trail, 11,200 ft, 16 Jul 1977, *D.W. Taylor 6604* (JEPS). **Mono Co.:** White Mountains, cirque heading N Fork of Perry Aiken Creek, 0.75 mi due E of White Mt. Peak, 11,900 ft, 25 Jul 1987, *J.D. Morefield & T.S. Ross 4701* (MO, NY, UC). **Tulare Co.:** near summit Arroyo-Kern Divide, region of Kaweah Peaks, 4 Aug 1897, *W.R. Dudley 2417* (DS); Nine Lakes Basin, head of Big Arroyo, cirque just north of Black Kaweah, 11,500 ft, 18 Aug 1938, *C.W. Sharsmith 3792* (DS, MO, NY, UC); W slope Kaweah Peaks Ridge above Nine Lakes Basin, head of Big Arroyo, 12,100 ft, 20 Aug 1938, *C.W. Sharsmith 3805* (CAS, UC).

10. *Drymocallis glabrata* Rydb., Mem. Dept. Bot. Columbia Coll. 2:201. 1898. = *Potentilla glandulosa* Lindl. subsp. *glabrata* (Rydb.) D.D. Keck; *P. glandulosa* Lindl. var. *intermedia* (Rydb.) C.L. Hitchc.

Potentilla glandulosa β *incisa* Lindl. (Bot. Reg. t. 1973. 1837) is in all likelihood another synonym for *D. glabrata*, although Keck (in Clausen et al. 1940: 48) concluded that var. *incisa* "is beclouded with doubt, and does not stand for any of the preceding natural units [of *P. glandulosa*]." In his earlier revision of *Horkelia* and *Ivesia*, Keck (1938, p. 83) stated that *P. glandulosa* β *incisa* was "surrounded by confusion and should doubtless be rejected." Keck's conclusions at first seem justified: most collections labeled as corresponding to Tab. 1973 in Edward's Botanical Register, including that annotated by Keck as holotype of *P. glandulosa* β *incisa* in the

Lindley Herbarium at Cambridge (CGE), consist of *Horkelia californica* subsp. *frondosa* (Greene) Ertter. This taxon, which grows in central California, is superficially similar to the image in Tab. 1973 but differs in significant regards, including petal color (white, not yellow). During my visit to Cambridge in 2002, however, I found a different collection of “B.R. 1973,” also from the Lindley Herbarium, filed as an unidentified *Potentilla*. This sheet, which is an excellent match for the illustration and description of *P. glandulosa* β *incisa*, has the diagnostic features of *D. glabrata*: i.e., leafy spreading inflorescence, large yellow petals, and septate glandular hairs as the dominant vestiture. The purported California origin of *P. glandulosa* β *incisa* remains a problem, but Douglas also collected within the range of *D. glabrata* in eastern Oregon. Given the potential for mix-ups in collections and data following Douglas’s death in 1834, as evident in the confusion with *H. californica* subsp. *frondosa*, it is realistic to suspect that the specimens on which Tab. 1873 were based may have originated in eastern Oregon, within the range of *D. glabrata*.

11. *Drymocallis deseretica* Ertter, sp. nov. (**Fig. 2**). TYPE: UNITED STATES. UTAH: Summit Co.: Uinta Mts., in the notch of Notch Mt., 28 km (17.5 mi) airline distance E (75°) of Kamas, T1S R9E S30 (NE1/4), 3250 m (10,650 ft) elev.; locally common on rocky W slope of notch, 22 Aug 1984, N.H. Holmgren & P.K. Holmgren 10750 (HOLOTYPE: UC 1583251; ISOTYPES: BRY 342384, NY, RM).

A *D. glabrata* inflorescentiis contractioribus, sepalis elongatis, pedicellis velutinis differt.

Herbaceous perennial from \pm branched caudex. **Stems** few, erect, (1.5–)2.5–6(–6.5) dm, the base 2–3(–4) mm diam., with sparse to abundant septate glandular hairs to 2(–3) mm long, inconspicuous short eglandular hairs sparse or lacking. **Basal leaves** (5–)7–20 cm long with (2–)3 pairs of lateral leaflets, sometimes with a much-reduced fourth pair; sheathing leaf-bases glabrous or \pm glandular, rarely sparsely strigose; vestiture of rachis similar to that of stem; terminal leaflet \pm petiolulate, the blade obovate to rhombic with an acute to obtuse apex, (1.5–)7–20 cm long, (1–)1.5–3 cm wide, both surfaces with a sparse mixture of sessile glands, short glandular trichomes, and simple hairs \pm 0.5 mm long, the margins single- to \pm double-toothed with 5–9 teeth per side. **Cauline leaves** 1–2, sometimes equaling or exceeding basal leaves, 3–15 cm long with 2–3 pairs of lateral leaflets. **Inflorescence** relatively compact, comprising (1/6–)1/5–1/2 of plant height, relatively leafy; subtending bract trilobed, rarely pinnate, 2–7 cm long; branches diverging at a 10–20° angle; pedicels 2–15(–20) mm long, with abundant short spreading hairs \pm 0.2 mm long and sparse to moderately abundant septate glandular hairs. **Flowers** 3–15(–20); hypanthium shallowly saucer-shaped, 4–7 mm diam., with abundant short simple hairs \pm 0.2 mm long and \pm sparse glandular trichomes; epicalyx bractlets linear to lanceolate or narrowly elliptic, (2.5–)3–8 mm long, 0.5–2(–3) mm wide, rarely notched; sepals (5–)6–12(–15) mm long, the vestiture like that of hypanthium or more sparse, the apex acute (to obtuse); petals cream to pale yellow, narrowly to broadly obovate, (4–)6–10 mm long, (2.5–)3.5–6(–7) mm wide, equaling or more often shorter than mature sepals, the apex rounded; stamens 20–25, the filaments 1–3 mm long, the anthers \pm elliptic; styles very thickly fusiform, slightly $>$ 1 mm long, golden-brown, attached just below middle of achene. **Achenes** \pm obliquely pyriform with a slight beak, 1.2–1.5 mm long, light brown.

Ecology and phenology.—Openings among sagebrush, aspen, fir, and/or spruce, often where moist or rocky, and below cliffs, 2000–3250 m elev. Flowering (May) Jun–Sep.

Drymocallis deseretica is common in the northern Wasatch and western Uintah mountains of Utah, where it has generally been treated as *Potentilla glandulosa* var. *intermedia* (= *D. glabrata*) or *P. glandulosa* var. *pseudorupestris* (= *D. pseudorupestris* var. *saxicola*). It differs from both species in its more compact inflorescence, velutinous pedicels, and conspicuously enlarged acute sepals, which create a very distinctive gestalt. Plants with a comparable gestalt, but shorter obtuse sepals, occur in the Raft River Mountains of Utah. The species intergrades with *D. glabrata* to the north and *D. arizonica* to the south, with the exact range not yet determined. Petal color is rarely recorded on labels and needs to be confirmed.

REPRESENTATIVE SPECIMENS: **UNITED STATES. UTAH: Cache Co.:** Intervale, 1 mi from mouth of Pine Canyon, Wellsville Range, 19 Jun 1932, B. Maguire 2991 (UC). **Duchesne Co.:** W fork of Duchesne River, 44 mi E of Heber, T1N R7E S33, 27 Jul 1978, D. Atwood 7018 (BRY); Uinta Mts., head of Duchesne River near Mirror Lake, 4 Aug 1980, S. Goodrich 14717 (BRY). **Juab Co.:** Mt. Nebo, jct. Willow Creek and Cottonwood Campground trails, 23 Jul 1976, F. Peabody 645 (BRY). **Salt Lake Co.:** Bells Canyon, near reservoir, 20 Jul 1959, W.P. Cottam et al. 15802 (WIS); Alta Pass above Twin Lake, 7 Aug 1939, B. Maguire 17363 (UC); above Salamander Lake, Lamb’s Canyon, 10

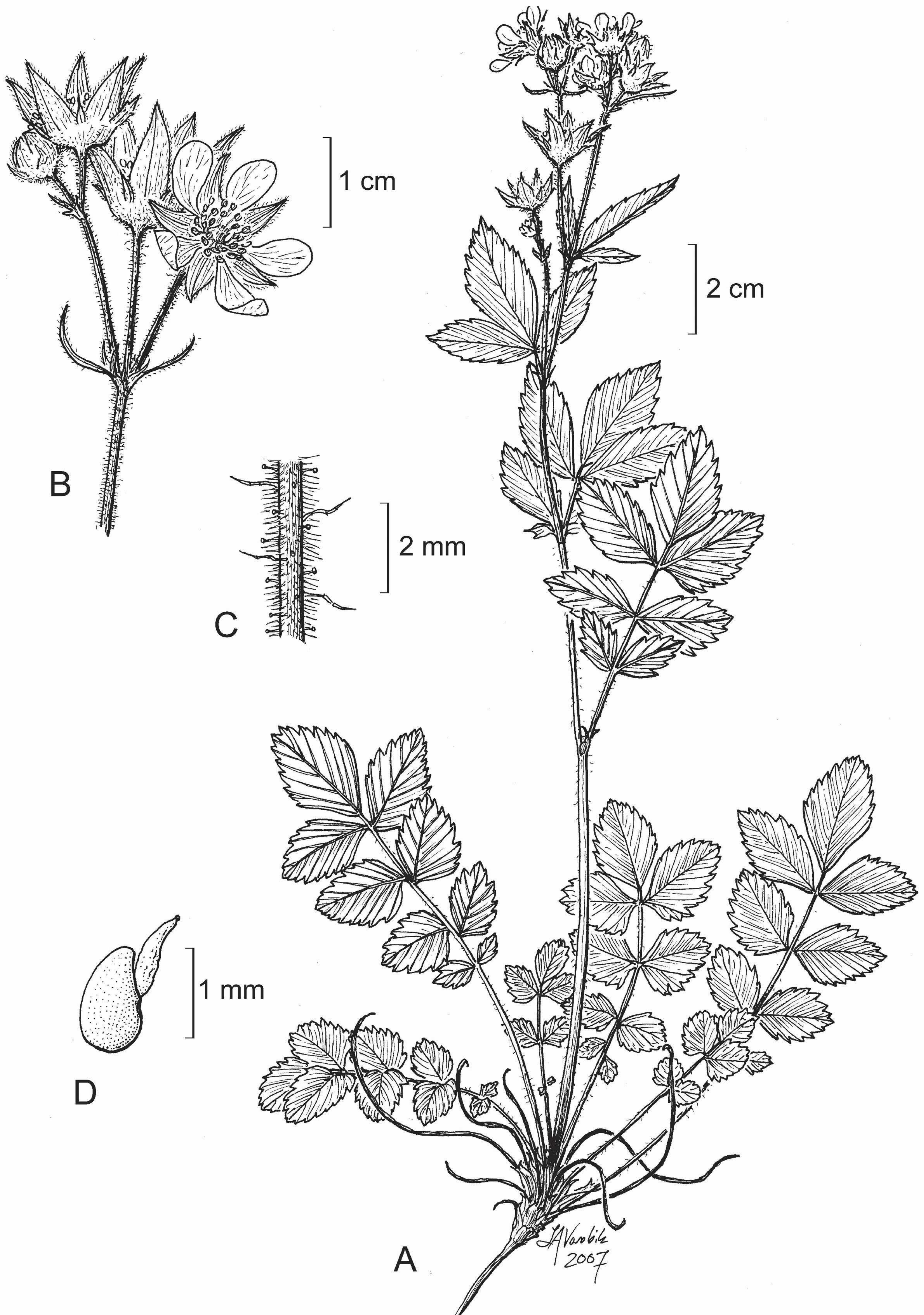


FIG. 2. *Drymocallis deseretica*. A: habit. B: inflorescence. C: vestiture of pedicel. D: achene and style.

May 1958, R.K. Vickery 2073 (UC). **Sanpete Co.:** top of Log Hollow Canyon, San Pitch Mts., 3 Jul 1979, R. Collins 301 (BRY); 13 km air distance ENE of Fairview, Hwy 30, upper Gooseberry Creek drainage, 19 Jun 1985, N.H. Holmgren et al. 10880 (UC); Upper Horseshoe Flat, 28 Jul 1962, H. Johnson s.n. (BRY). **Summit Co.:** Stillwater Basin, head Bear River, Uinta Mts., 18 Aug 1933, B. Maguire et al. 4172 (UC); due W of parking lot at head of Bald Mt. Trail, summit of Mirror Lake Pass, 1 Aug 1970, P.A. Replogle 200 (BRY). **Tooele Co.:** Mill Fork of South Willow Canyon, Stansbury Mts., T4S R7W S14, 4 Jul 1980, A. Teye 990 (BRY). **Utah Co.:** Pika Cirque, Mt. Timpanogos, 12 Jul 1974, K. Allred 1027 (BRY); along Timpanogos trail between 1st and 2nd falls, 30 Jun 1964, A. C. Blauer & J. Brotherson 44 (BRY); Little Cottonwood Canyon, Albion Basin campground, 20 Aug 1984, N.H. Holmgren & P.K. Holmgren 10721 (UC); Provo, 8000 ft., 3 Jul 1894, M.E. Jones 5575 (UC); 1 mi NE of Springville Crossing on Diamond Fork Creek, T7S R6E S31, 21 Jun 1969, J.W. Thomas 155 (BRY). **Wasatch Co.:** Strawberry Valley, T3S R12W, 16 Jul 1964, V.B. Matthews 89 (BRY).

12. *Drymocallis glandulosa* (Lindl.) Rydb., Mem. Dept. Bot. Columbia Coll. 2:198. 1898. = *Potentilla glandulosa* Lindl.

The original illustration of *Potentilla glandulosa* in Edwards's Botanical Register (19: pl. 1583. 1833), drawn from living material "in the Chiswick Garden in August last," has bright yellow petals. It is therefore probable that David Douglas collected the seeds from which the specimen was grown somewhere in Oregon, since coastal populations in California (treated here as var. *wrangelliana*) are predominantly white-petaled. Variation in *D. glandulosa* s.s. outside of California is unclear, with no evident pattern to differences in petal size and color; as default, these have largely been assigned to var. *glandulosa*. Sporadic collections have been made in Idaho, Montana, Nevada, and Utah; disjunct populations in Arizona south of the Mogollon rim may represent an undescribed variety.

12a. *Drymocallis glandulosa* var. *glandulosa*

12b. *Drymocallis glandulosa* var. *wrangelliana* (Fisch. & Avé-Lall.) Ertter, comb. nov. BASIONYM: *Potentilla wrangelliana* Fisch. & Avé-Lall., Ind. Seminum Hort. Petrop. 7:54. 1841.

12c. *Drymocallis glandulosa* var. *reflexa* (Greene) Ertter, comb. nov. BASIONYM: *Potentilla glandulosa* Lindl. var. *reflexa* Greene, Flora Francisc. 65. 1891. = *P. glandulosa* subsp. *reflexa* (Greene) D.D. Keck.

A disjunct collection from a major mining area in central Idaho (Boise Co., Clear Creek–Grimes Creek, 28 Jun 1959, L. Maydale s.n., CIC) most likely results from dispersal via the transport of mining equipment from California, parallel to a comparable speculation for *Eriogonum inerme* (S. Watson) Jeps. (Ertter & Moseley 1993). The variety, with its small reflexed yellow petals, is otherwise known only from the mountains of California and southern Oregon.

12d. *Drymocallis glandulosa* var. *viscida* (Parish) Ertter, stat. et comb. nov. BASIONYM: *Drymocallis viscida* Parish, Bot. Gaz. 38:460. 1904.

This overlooked variety combines the flower and vestiture of *Drymocallis glandulosa* var. *reflexa* with the narrow inflorescence and predominately single-toothed leaflets of *D. lactea* var. *lactea*.

13. *Drymocallis campanulata* (C.L. Hitchc.) Ertter, stat. et comb. nov. BASIONYM: *Potentilla glandulosa* var. *campanulata* C.L. Hitchc., Vasc. Pl. Pacific NorthW. 1:861. 1969.

The epithet "campanulata" was used provisionally as a species of *Potentilla* in the treatment of Rosaceae (Hitchcock & Cronquist 1961) in volume 3 of *Vascular Plants of the Pacific Northwest*, "in anticipation of its publication by Dr. Keck," but the validating publication in "Additions and Corrections" in volume 1 (Hitchcock et al. 1969) treated the new taxon as a variety of *P. glandulosa*. This entity was referred to as the John Day race in Clausen and Hiesey (1958).

14. *Drymocallis rhomboidea* (Rydb.) Rydb., Mem. Dept. Bot. Columbia Coll. 2: 203. 1898. = *Potentilla rhomboidea* Rydb.; *P. glandulosa* Lindl. subsp. *globosa* D.D. Keck.

Keck (in Clausen et al. 1940) identified the type of *P. rhomboidea* as *P. glandulosa* subsp. *glandulosa* and therefore described *P. glandulosa* subsp. *globosa* to accommodate this distinctive taxon.

15. *Drymocallis cuneifolia* Rydb., Mem. Dept. Bot. Columbia Coll. 2:204. 1898. = *Potentilla cuneifolia* (Rydb.) Th. Wolf, not *P. cuneifolia* Bertol.; *P. peirsonii* Munz.

Rydberg (1898) described *Drymocallis cuneifolia* on the basis of a collection by Samuel B. Parish in the San Bernardino Mountains of San Bernardino County, California, “probably near Green Lead Mines,” in June 1886 (F, GH, NY). The collection, distributed as *Potentilla glandulosa* var. *nevadensis*, was numbered and cited as *Parish 1818* (which is also the number given to a collection of *Phlox dolichantha* A. Gray, another rare plant endemic to the San Bernardino Mountains). Rydberg noted that the species “differs from the others in the small flowers with erect petals and the cuneate-flabelliform leaflets”; it also had filiform styles that are very unusual in *Drymocallis*. When comparable (though much smaller) specimens were found in 1919 by F. W. Peirson in the San Gabriel Mountains in Los Angeles County, Munz and Johnston (1925) adopted *Potentilla cuneifolia* (Rydb.) Th. Wolf for both forms. Since this name was a later homonym of *P. cuneifolia* Bertol., however, Munz (1932) renamed the species *P. peirsonii*, noting that Peirson had “rediscovered a plant that had not been collected for many years.”

The continued lack of comparable new collections from the San Bernardino Mountains led Keck (in Clausen et al. 1940) to conclude that the type of *Drymocallis cuneifolia* was merely an immature specimen of *Potentilla glandulosa* subsp. *nevadensis* (= *D. lactea* var. *lactea*). As a result, he described *P. glandulosa* subsp. *ewanii* to accommodate populations in the San Gabriel Mountains. He did, however, note that “the type of *D. cuneifolia* is fragmentary, and since neither *Ewanii* nor *cuneifolia* is well represented in herbaria as yet, the possibility exists that the differences which now appear impressive may eventually lose importance.”

Serendipitously, a small population of plants comparable to the type of *Drymocallis cuneifolia* has recently been discovered in the San Bernardino Mountains, not far from Parish’s original collection: San Bernardino Co., San Bernardino Mts., Grout Creek, NE of Butler Peak, 200 m W of creek crossing along FS road 2N13, 0.3 mi W of FS road 2N70, 34°16'08"N, 116°58'40"W, 2195 m/7200 ft, 30 June 2004, Mark A. Elvin 3555 (IRVC, UCR). These plants were identified as *P. glandulosa* subsp. *ewanii* and have the diagnostic small narrow corollas and elongate styles of this taxon. These features, however, also characterize the type of *D. cuneifolia*, which was collected in the same general area. Both *Elvin 3555* and the type of *D. cuneifolia* are larger plants than is the norm in the San Gabriel Mountains, with more elongate leaflets. As a result, I am treating the San Bernardino Mountain and San Gabriel Mountain populations as varieties of a single species, *D. cuneifolia*.

15a. *Drymocallis cuneifolia* var. *cuneifolia*

As indicated above, this variety is currently known from a single extant population and must therefore be considered extremely rare and potentially threatened. Although not known from limestone substrates, its occurrence on alluvial benches in an area known for a cohort of federally listed carbonate endemics (e.g., *Erigeron parishii* A. Gray, *Astragalus albens* Greene) opens the possibility that *D. cuneifolia* var. *cuneifolia* might have similar limitations.

15b. *Drymocallis cuneifolia* var. *ewanii* (D.D. Keck) Ertter, stat. et comb. nov. BASIONYM: *Potentilla glandulosa* Lindl. subsp. *ewanii* D.D. Keck, Carnegie Inst. Wash. Publ. 520:47. 1940.

ACKNOWLEDGMENTS

Foremost I wish to thank the curatorial staff at the multiple herbaria who prepared loans used in this study, tracked down additional information upon request, remained patient with the length of time the specimens have been in my hands, and generally went the extra mile in their curatorial obligations: ALA, ARIZ, ASC, ASU, BRY, CAS/DS, F, GH, ID, MICH, MO, NDG, NY, OSC, RM, RSA/POM, SBBG, UCR, US, UTC, WIS, WTU. I also wish to acknowledge the curatorial staff at UC/JEPS, who have processed my seemingly unending loans; and the courtesy offered me at other herbaria that I visited and used during the course of this study: BM, CGE, CIC, K, LE, PR, SRP, W. I am indebted to Jiří Soják (PR) for freely sharing his extensive knowledge and insights on *Potentilleae*, and to Adolf Ceska, Lenka Drabkova, and the late Otto Winkler for

serving as translators and intermediaries. I wish to thank Kanchi Gandhi (GH) for deciphering a steady stream of nomenclatural tangles; J.G. Murrell (CGE) for checking vestiture on the type of *Potentilla glandulosa* β *incisa*; Dick Brummitt (K) and John McNeill (E) for hosting me during my visits to British herbaria; and Mark Brunell (CPH) and Mark Elvin (IRVC) for bringing my attention to the new collection of *Drymocallis cuneifolia*. The excellent illustrations by Linda Vorobik are greatly appreciated, as always, and support from the Lawrence R. Heckard Endowment Fund of the Jepson Herbarium is gratefully acknowledged.

Note added in proof.—In a recently published paper, Soják (2006) provides new combinations in *Drymocallis* of all subspecies of the *Potentilla glandulosa* complex as recognized by Keck (in Clausen et al. 1940), with no change in rank or taxonomic arrangement.

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