

REDEFINITION OF *HESPERODORIA* (ASTERACEAE: ASTEREAEE) AND
THE SEGREGATION OF *COLUMBIADORIA*, A NEW MONOTYPIC GENUS
FROM THE WESTERN UNITED STATES

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ABSTRACT

The genus *Hesperodoria* is ditypic with the inclusion of *Hesperodoria salicinus* *comb. nov.* This species, which is endemic to northern Arizona, has not formerly been treated outside of *Haplopappus*. *Hesperodoria scopulorum* occurs in northern Arizona and southern Utah. The only other species to have been included in *Hesperodoria* is here described as a monotypic genus, *Columbiadoria*, with the new combination *Columbiadoria hallii*. This species occurs in Oregon and Washington, and has been placed in *Haplopappus*, *Pyrrocoma*, *Aster*, and *Hoorebekia*. Both *Hesperodoria* and *Columbiadoria* are members of the *Petradoria* group of the Solidagininae, although they are not closely related to each other within it. A key distinguishes both species of *Hesperodoria* along with those of *Petradoria*, *Vanceleva*, and *Stenotus*, the genera most similar to *Hesperodoria*. The phylogenetic position of *Columbiadoria* apparently is near *Tonestus*.

KEY WORDS: *Haplopappus*, *Columbiadoria*, *Hesperodoria*, Asteraceae, Astereae, Solidagininae

In a summary of the disposition of the North American segregates of *Haplopappus* (Nesom & Morgan 1990), the taxonomic status of the genus *Hesperodoria* E. Greene was noted to be poorly understood. The type species, *Hesperodoria scopulorum* (M.E. Jones) E. Greene is a relatively well known plant from northern Arizona and southern Utah. Another species, *Haplopappus salicinus* S.F. Blake, although clearly similar to *Hesperodoria*, was not assigned to a genus outside of *Haplopappus* because it was known to us only from the relatively immature specimens of the type collection. Recent material available for study, however, has clarified the identity of this species, and it is here transferred to *Hesperodoria*.

Hesperodoria salicinus (S.F. Blake) Nesom, *comb. nov.* BASIONYM: *Aplopappus salicinus* S.F. Blake, Proc. Biol. Soc. Washington 48:171. 1935. TYPE: UNITED STATES. Arizona. [Coconino Co.], Bright Angel Trail, Grand Canyon, 22 Oct 1905, A. Eastwood 10 (HOLOTYPE: US!).

As noted by Blake (1935) in the original description of *Haplopappus salicinus*, Hall (1928) cited the type (*Eastwood 10*) as a specimen of *H. scopulorum*. I have studied the type as well as a more recent, mature and ample collection of *H. salicinus*: United States. Arizona: Mojave Co., above S shore of Lake Mead, 26 Oct 1973, Martin & Van Devender s.n. (NY). Duplicates of this collection were distributed as "*Haplopappus cf. acradenius*." A more detailed study and taxonomic treatment of *Hesperodoria* is now being undertaken (Gary Baird in prep.).

Hesperodoria possesses a suite of characters that identify it as a member of the subtribe Solidagininae Hoffm., as outlined by Nesom (1991b). Within the subtribe, it is a part of the "*Petradoria* group," which comprises *Petradoria* E. Greene, *Vanclavea* E. Greene, *Hesperodoria*, *Stenotus* Nutt., *Tonestus* A. Nelson, *Columbiadoria* Nesom (see below), *Eastwoodia* Brandegee, *Acamp-topappus* A. Gray, and *Amphipappus* Torr. & Gray. Taxonomic studies or overviews of a number of these genera are available (Porter 1943; Anderson 1963; Anderson & Weberg 1974; Lane 1988; Nesom & Morgan 1990; Nesom 1991a).

The taxa of the *Petradoria* group are confined to the western United States, except for *Stenotus*, which has one species endemic to Baja California, another that reaches into western Canada, and one endemic to Canada. Seven genera of the group are monotypic or ditypic; *Stenotus* and *Tonestus* have six and nine species, respectively. Within the Solidagininae, the *Petradoria* group can be recognized by its style appendages, which have massively thickened vascular traces, except in *Petradoria*, *Vanclavea*, *Columbiadoria*, and a few species of *Stenotus* and *Tonestus*, where the traces are not so massively thickened. The vascular traces of the style shaft are mostly 3-5 cells wide and maintain this width as they enter the style branches. Upon entering the appendages, however, each trace abruptly widens to 15-20 cells, forming a distinctly clavate terminal portion. This feature apparently does not occur in any other American Astereae.

Hesperodoria is most closely similar to *Petradoria* (in line with Greene's original assessment and in contradiction to Hall's reassessment) and to *Vanclavea*. The plants of these three genera are herbs or small shrubs that produce coriaceous, linear to linear lanceolate leaves with three(-five), parallel, raised veins; the leaves are mostly punctate-glandular, and the margins and lamina are glabrous or sometimes hirtellous-scabrous. Anderson & Weberg (1974) found that the leaves of these taxa are similar in their isolateral

mesophyll and massive sclerenchymatous bundle sheaths that completely surround the vascular tissue. The capitulescences are mostly cymose, the ray flowers absent or with short ligules. *Petradoria* and *Vancleavea* both have a chromosome base of $x = 9$ (Anderson 1963, Anderson & Weberg 1974) but there is no documented report for either species of *Hesperodoria*. All other chromosome numbers reported for plants of the *Petradoria* group are also on a base of $x = 9$, and the same is predicted for those species yet unstudied.

As noted above, *Petradoria* and *Vancleavea* both lack the massively thickened vascular traces of the disc style appendages that are characteristic of almost all of the rest of the *Petradoria* group, including *Hesperodoria*. Also, the disc corolla lobes of both genera are deltate rather than long-lanceolate, although the lobes of *H. scopulorum* are variable in length and some are relatively short. *Petradoria* differs further from *Hesperodoria* in habit, capitulescence, head shape, and achene vestiture. *Vancleavea* differs further from *Hesperodoria* in its attenuate phyllary apices and pappus of broad, strongly flattened awns. Of the two, however, *Vancleavea* is more similar to *Hesperodoria* in its habit, capitulescence, and head shape.

Anderson (1963) observed that the sclerenchymatous bundle sheaths of *Stenotus* are similar to those of *Petradoria* and *Hesperodoria*. This is true in both *Stenotus acaulis* (Nutt.) Nutt., the species studied by Anderson, and *S. armerioides* Nutt., but the foliar venation of the other species is not so conspicuously sclerified and raised. Further, although the major foliar veins in all species of *Stenotus* are parallel, the interconnecting veins tend to be much more prominent than in *Hesperodoria*, *Petradoria*, and *Vancleavea*. If *Stenotus* is a fourth member of this group, as seems likely, the other three genera are more similar among themselves in their leaf morphology, polycephalous capitulescence, and extreme reduction of the ray flowers.

In the present treatment, the genus *Hesperodoria* comprises two species, although yet another species was originally referred to it by Greene (see below, "A new monotypic genus"). The similarities and differences between *H. scopulorum* and *H. salicinus*, as well as among all the species of *Vancleavea* and *Petradoria*, are summarized in the key below. The two species of *Hesperodoria* are very different from each other, particularly in their glandularity and head, flower, and fruit size, so much so that in this taxonomic region of monotypic and ditypic genera, I originally thought that they might be better classified as two separate genera. They are more similar between themselves, however, than to any other species. The large difference between them is paralleled by that between the two species of *Petradoria*. Despite marked disparities among all five species of these three genera, they are morphologically and geographically similar among themselves and so clearly distinct as a group that they might be combined into a single genus. On the other hand, until additional lines of evidence might show otherwise, they may be justifiably distinguished as the taxa in the key below.

KEY TO THE TAXA MOST CLOSELY RELATED TO *HESPERODORIA*

1. Heads solitary; ray flowers with conspicuous ligules (except *Stenotus pulvinatus*). *Stenotus*
1. Heads more than one, mostly in flat topped capitulescences; ray flowers absent or if present, with very inconspicuous ligules. (2)
 2. Above ground stems annual or perennial; heads turbinate to cylindrical; disc corolla lobes deltate, shallowly cut; vascular trace of disc style branches narrow, unthickened; ray flowers present or absent; pappus bristles apically narrowed, dilated in one species. (4)
 2. Above ground stems perennial, the basal portions woody; heads turbinate, disc corolla lobes narrowly triangular, deeply cut; vascular trace of disc style branches massively thickened; ray flowers absent; pappus bristles apically dilated. (3) *Hesperodoria*
3. Leaves ascending, eglandular and not resinous, the margins scabrous, the lamina glabrous or scabrous; heads 6-10 mm high, sessile to subsessile or on pedicels up to 1 cm long; (1-)3-5 in a cymose capitulescence; disc corollas 5-7 mm long, with lobes cut $\frac{1}{3}$ - $\frac{1}{2}$ the length of the limb; phyllaries slightly convex, with a glandular midline from base to tip, without a strongly developed apical glandular area; achenes 4 mm long, 6-8 nerved; northern Arizona and southern Utah.
 *Hesperodoria scopulorum*
3. Leaves spreading to deflexed, punctate-glandular and resinous, glabrous; heads 4-5 mm high, on pedicels 2-5 mm long, numerous in a number of barely cymoid clusters, these associated in a loose panicle; disc corollas 2.8-3.2 mm long, with lobes cut to the base of the limb; phyllaries strongly convex, without a glandular midline but with a glandular apex; achenes 1 mm long, 5 nerved; northern Arizona.
 *Hesperodoria salicinus*
4. Above ground stems perennial, the basal portions woody; leaves arcuate; heads turbinate, 9.5-12.5 mm high, solitary or 2-5 and loosely cymoid; phyllary apices attenuate; ray flowers absent; achenes sparsely strigose; pappus of broad, strongly flattened, linear-lanceolate awns; northern Arizona and southern Utah.
 *Vanclvea stylosa*
4. Above ground stems annual, the basal portions mostly herbaceous; leaves ascending; heads cylindrical, usually in a dense flat topped capitulescence; phyllary apices rounded to obtuse; rays present or absent; achenes glabrous; pappus of capillary bristles.
 (5) *Petradoria*

5. Leaves eglandular; heads 11-13 mm high; phyllaries slightly convex, apically truncate-apiculate; rays absent; disc flowers hermaphroditic, fully fertile, the corollas 9-12 mm long; pappus bristles strongly flattened, apically dilated; east central California and southern Nevada.
 *Petradoria discoidea*
5. Leaves punctate-glandular; heads 5-9 mm high; phyllaries strongly convex, apically obtuse to acute; ray flowers present; disc flowers staminate, with abortive ovaries, the corollas 4- 6 mm long; pappus bristles terete, not apically dilated; southeastern California, Nevada, northern Arizona and New Mexico, Colorado, Utah, and southwestern Wyoming and Idaho.
 *Petradoria pumila*

A new monotypic genus of Solidagininae

The original description of *Hesperodoria* E. Greene (1906) was only of two sentences regarding the type (*H. scopulorum*) and its putative relationship to *Petradoria* E. Greene. Greene included one other species in *Hesperodoria*, appended with the following comments, which completed the entire discussion of his new genus: "Along with this I place tentatively a type which remained in *Aplopappus* as I left it, that is [*Haplopappus hallii* A. Gray]. That this has rays while the type is rayless does not with me count for much; but the involucre are not quite the same, neither is the pappus, nor even the style-tips." The only other comments ever published regarding the relationship between the two species of *Hesperodoria* apparently have been those of Hall (1928), who included both species as sect. *Hesperodoria* (E. Greene) Hall of the genus *Haplopappus*. "This section comprises two relict species so unlike each other and each so distinct from those of any other group that little can be said as to their relationships" (p. 218). "The wide separation of this species [*Haplopappus hallii* A. Gray] from any other, both geographically and morphologically, probably means that its exact phylogenetic position never will be determined" (p. 221).

While *Haplopappus hallii* is clearly a member of the Solidagininae and a member of the *Petradoria* group, Hall's assessment of its isolated position was correct. It is not closely similar to any other species of the subtribe and is recognized here as a distinct, monotypic genus. The proposed generic name juxtaposes the geographic home of the species with "Doria," an early name for the goldenrod (*Solidago*).

Columbiadoria Nesom, *gen. nov.* TYPE: *Haplopappus hallii* A. Gray

Subfrutices perennes e basi maxime ramosi. Caules ad basim lignei 3-6 dm alti stricti plerumque non ramosi sub capitulescentia. Folia oblanceolata integra dictyophlebia redacta versus apicem caulis. Capitula cylindrici-turbinata 8-11 mm alta plerumque 5-10 in capitulescentia laxa spicata vel leniter cymoidea. Flores radii 5-8 corollis 6-10 mm longis. Flores discii lobis deltatis; appendices ramorum stylinorum lineis stigmaticis 5-6-plo longiores. Achae-
nia 4-5 mm longa 8-nervia moderate strigosa; setae pappi graciles teretes attenuatae ad apices.

Columbiadoria hallii (A. Gray) Nesom, *comb. nov.* *Haplopappus hallii* A. Gray, Proc. Amer. Acad. Arts 8:389. 1872. TYPE: UNITED STATES. Oregon, [Wasco Co.], bluffs of Columbia River at The Dalles, 1871, *E. Hall* 257 (HOLOTYPE: GH!). *Aster howellii* Kuntze [*nom. nov.*], Rev. 316. 1891. *Hesperodoria hallii* (A. Gray) E. Greene, Leaf. Bot. Observ. 1:175. 1906. *Hoorebekia hallii* (A. Gray) Piper, Contr. U.S. Natl. Herb. 11:560. 1906. *Pyrocoma hallii* (A. Gray) Howell, Fl. N.W. Amer. 1:299. 1900.

Perennial subshrubs with woody, highly branched bases, arising from a stout taproot. Stems 3-6 dm tall, strict, mostly unbranched below the capitulescence. Leaves eglandular or obscurely punctate-glandular, not resinous, sparsely scabrous-hispidulous, oblanceolate, entire, net veined, sessile and petiolate, ascending, the largest 2-5 cm long, 4-7(-11) mm wide, gradually reduced in size upwards. Heads cylindric-turbinate, 8-11 mm high, 5-15 or more in a loosely spicate to broadly and loosely cymoid capitulescence; phyllaries in 5-6 strongly graduated series, convex, lanceolate, slightly glutinous, with a green viscid apex, not keeled or slightly so on the upper half, the lower $\frac{2}{3}$ white indurated. Ray flowers 5-8, pistillate, fertile, the corollas yellow, 6-10 mm long, the ligules 6-7 mm long and ca. 2 mm wide, weakly if at all coiling. Disc flowers hermaphroditic, all fertile, the corollas 6-7 mm long, the lobes erect, deltate, cut ca. $\frac{1}{10}$ the length of the limb; style branches 1.5-2.0 mm long, the appendages 5-6 times longer than the stigmatic lines, with short, closely set sweeping hairs, these merely papillate near the apex, vascular traces of appendages barely thickened distally. Achenes 4-5 mm long, narrowly oblong, slightly compressed, 8 nerved, moderately strigose with stiff hairs; pappus bristles slender, terete, the apices attenuate.

The species primarily occurs in the eastern Columbia River Gorge in northern Oregon and southern Washington, but it also is found in scattered localities in the Cascade Mountains of Oregon to about 100 km south of the river. Cronquist (1955) noted that the southern populations, outside of the gorge, are variants perhaps deserving recognition at varietal rank.

Columbiadoria clearly is a member of the *Petradoria* group of the Solidagininae, based on the morphology of its disc style appendages and its disc corollas with the filaments inserted at midtube (Nesom 1991b). Its oblanceolate, net veined, little sclerified leaves contrast strongly with the linear-lanceolate, parallel veined leaves of *Hesperodoria*, as well as those of the closely related *Petradoria*, *Vancleavea*, and *Stenotus*. Among the genera of the *Petradoria* group, only *Tonestus* has obviously net veined leaves, and only *Tonestus* and *Stenotus*, besides *Columbiadoria*, have ray flowers with long, conspicuous ligules. Additionally, both *Columbiadoria* and *Tonestus* tend to produce a racemoid capitulescence, verging toward a narrowly cymoid one. This tendency is particularly noticeable in *T. aberrans* (A. Nels.) Nesom & Morgan and *T. graniticus* (Tiehm & Shultz) Nesom & Morgan, although in other *Tonestus*, the heads are usually solitary.

The features common to *Tonestus* and *Columbiadoria* appear to be unspecialized ones, since they are also found in at least some species of *Solidago*. Although the distinctive style branch morphology of the first two places them as members of the *Petradoria* group, they may be phylogenetically basal elements, independently derived within it. *Tonestus* is the only genus of either the *Petradoria* group or the *Gutierrezia* group that produces leaves with toothed margins (two species produce entire leaves); in this aspect of its foliar morphology, however, it is similar to *Solidago*, where the leaves characteristically are net veined and toothed. *Tonestus* also differs from *Columbiadoria* in its herbaceous above ground parts, leaves in persistent basal rosettes, stipitate glandular vestiture in most of the species, and strongly keeled phyllaries with prominently strongly glandular apices.

The genera *Eastwoodia*, *Acamptopappus*, and *Amphipappus* appear to constitute a lineage apart from *Columbiadoria* and the genera of the *Petradoria* group discussed above. *Eastwoodia* and *Acamptopappus* are similar in their solitary heads and the long, apically acute sweeping hairs of their disc style appendages. All three genera produce strongly flattened pappus bristles and uninerved leaves (Lane 1988).

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