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TWO NEW NORTH AMERICAN GENERA SEGREGATED FROM *HAZARDIA* (ASTERACEAE: ASTEREAE)

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ABSTRACT

Adeia Nesom, gen.nov., includes *Hazardia whitneyi* var. *whitneyi* (California) and *H. whitneyi* var. *discoidea* (California and Oregon), which are recognized as separate species, Adeia whitneyi (A. Gray) Nesom, comb. nov., and Adeia discoidea (J.T. Howell) Nesom, comb. nov. The plants are herbaceous perennials (vs. shrubs in *Hazardia*) and have a chromosome number of 2n = 8 (vs. 2n = 10 in *Hazardia*); they also differ from *Hazardia* in vestiture, floral morphology, and flavonoid chemistry, and DNA indicates that they are as closely related to *Pyrrocoma, Benitoa, Corethogyne*, and *Lessingia* as to *Hazardia*. Adiaphila Nesom, gen. nov., comprises the single species *Hazardia brickellioides* (California and Nevada) as Adiaphila brickellioides (Blake) Nesom, comb. nov. The species has not been included in DNA analyses but it differs from *Hazardia* sensu stricto in significant ways: white bark, stipitate-glandular vestiture, apically spinulose leaf teeth and phyllaries, short style branch appendages, short, turbinate achenes, lack of flavones, and a chromosome number of 2n = 12. Distribution maps and photos of plants (in situ/herbarium specimens) are provided for both new genera, and pertinent molecular phylogenies are diagramatically summarized.

Hazardia Greene in recent treatments includes 13 species (Clark 1979, 2006), two with infraspecific taxa (*H. squarrosa* and *H. whitneyi*). Five species are endemic to California and Nevada, two occur in the USA and Mexico, with the rest restricted to Baja California.

Eleven of the *Hazardia* species have a chromosome number of 2n = 10 — these have been divided among sect. *Hazardia* (8 species) and sect. *Bracteofolia* Clark (3 species; disc flowers with sterile ovaries and heads with immediately subtending, toothed, foliaceous bracts). *Hazardia whitneyi* with 2n = 8 constitutes monotypic sect. *Machaerantheroides* Clark. *Hazardia brickellioides* with 2n = 12 was included by Clark with the 2n = 10 species of sect. *Hazardia*.

Hazardia in phylogenetic analyses of Astereae based on DNA (e.g., Markos & Baldwin 2001; Moore et al. 2012) has been represented only by *H. cana*, *H. detonsa* and *H. squarrosa* (all of sect. *Hazardia*), and *H. whitneyi*. The three species of sect. *Hazardia* represent a single clade, while *H. whitneyi* is more closely related to species of other genera (Figs. 1, 2). Morphological evidence also indicates that *H. whitneyi* should not be included within *Hazardia*. A molecular-phylogenetic hypothesis is not available for *H. brickellioides*, but the divergent chromosome number and a range of morphological features indicate that it is also outside the bounds of *Hazardia*. Each of the two species is placed here in a newly described genus, *Adeia* (*H. whitneyi*) and *Adiaphila* (*H. brickellioides*). Both new genera are members of subtribe Machaerantherinae (sensu Nesom 2020) and are among those informally recognized as the *Haplopappus*, *Xanthocephalum*, and *Lessingia* groups (see Fig. 2) in the subtribal summary. This larger set of genera is referred to here as the "Haplopappus clade."

Nesom: Genera segregated frm Hazardia

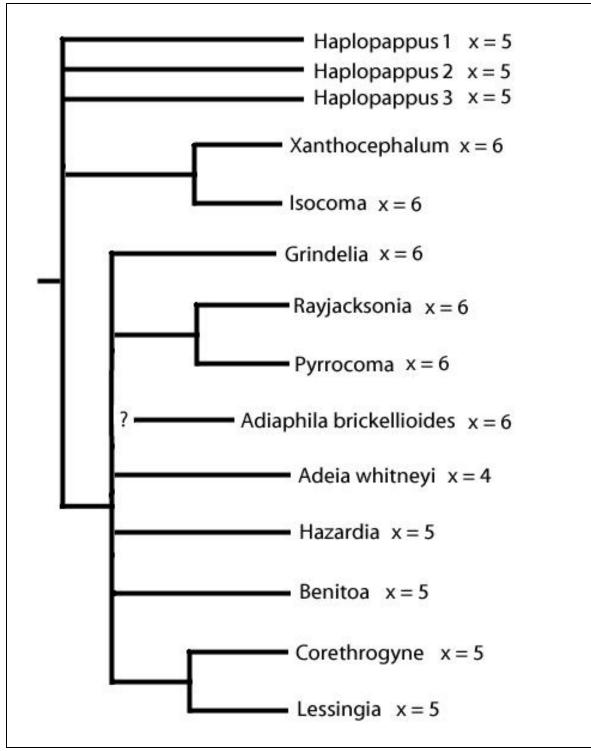


Figure 1. Phylogenetic relationships of *Hazardia* and closely related genera, including *Adeia* and *Adiaphila*, showing base chromosome number. Topology from Brouillet et al. (2009, Fig. 37.1E, from "GenBank-available nrDNA ITS sequence data"). *Adiaphila* (Hazardia) *brickellioides* has not been included in molecular-phylogenetic analyses and its position here is speculative (see text). <u>Haplopappus 1</u> = *H. macrocephalus*; <u>Haplopappus 2</u> = *H. foliosus* and *H. marginalis*; <u>Haplopappus 3</u> = *H. glutinosus* and *H. paucidentatus*. Species of *Haplopappus* with x = 6 (e.g., sensu Grau 1976) have proved to be *Grindelia* (Moore et al. 2012), where the number is consistent with all other species.

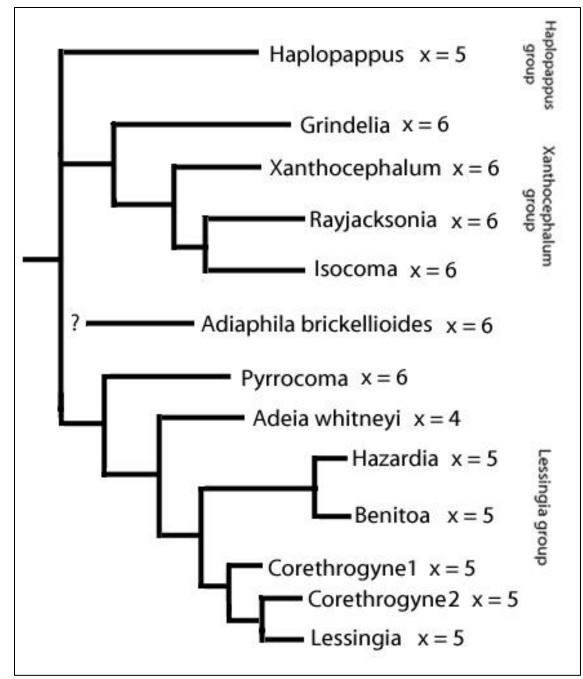


Figure 2. Phylogenetic relationships of *Hazardia* and closely related genera, including *Adeia* and *Adiaphila*, showing base chromosome number. Topology from Moore et al. (2012, Fig. 3B, maximum likelihood bootstrap consensus from nrDNA data). *Adiaphila* (Hazardia) *brickellioides* has not been included in molecular-phylogenetic analyses and its position here is speculative (see text). The *Haplopappus* sample includes 11 species, including the 5 from Figure 1. Corethrogyne 1 and 2 both are samples from *Corethrogyne filaginifolia*. All of numerous chromosome counts from *Lessingia* species have been 2n = 10, (e.g., Markos 2006), except for one, reported as an infra-population variant in *L. nemaclada* from Trinity Co. (Raven et al. 1960). The Haplopappus, Xanthocephalum, and Lessingia groups, as marked here, are slightly different in composition from those in Nesom (2020): <u>Haplopappus group</u>: *Grindelia, Haplopappus, Hazardia.* Xanthocephalum group: *Isocoma, Pyrrocoma, Rayjacksonia, Stephanodoria* (not included in molecular analyses), *Xanthocephalum.* Lessingia group: *Benitoa, Corethrogyne, Lessingia*.

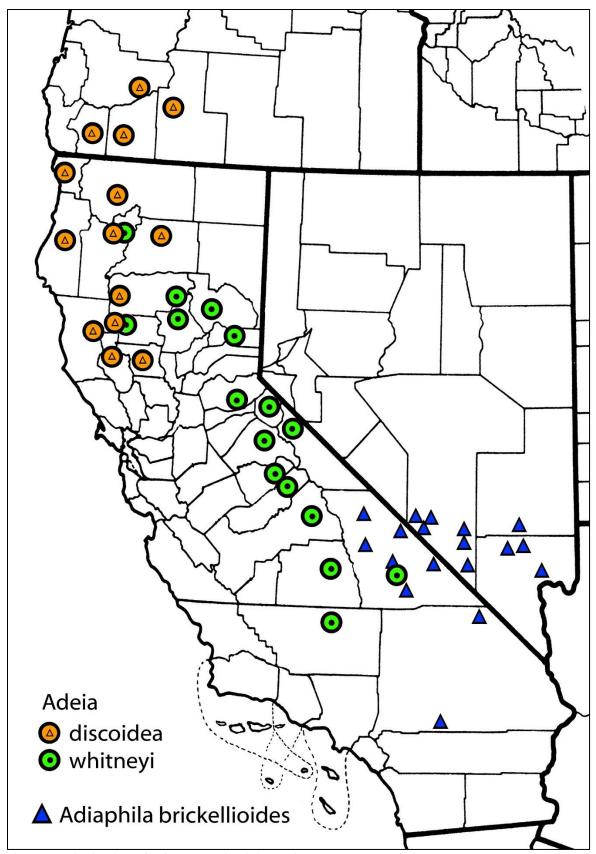


Figure 3. Distribution of Adeia and Adiaphila species.

1. Hazardia whitneyi as a new genus

DNA molecular data and analyses are unequivocal in placing *Hazardia whitneyi* within the *Haplopappus* clade but outside of *Hazardia* sensu stricto (Figs. 1, 2). The analysis of Moore et al. (2012) places it as sister to the x = 5 genera of the *Lessingia* group, where *Hazardia* sensu stricto is more closely related to *Benitoa*.

Clark's name (1978) for the monotypic sect. *Machaerantheroides* alluded to the superficial resemblance of *Hazardia whitneyi* to *Xanthisma* (Machaeranthera) grindelioides — but even with acknowledgement of a superficial resemblance, he considered *H. whitneyi* to be "an ancient aneuploid derivative from an element, in the phyletic sense, of both *Machaeranthera* and *Hazardia*" (p. 113). This could now be seen as true only in a broad sense — within subtribe Machaerantherinae (sensu Nesom 2020), the *Haplopappus* clade is sister to the *Machaeranthera* group (comprising *Dieteria, Leucosyris, Machaeranthera, Oonopsis, Xanthisma*, and *Xylorhiza*).

Among species of *Hazardia* sensu stricto, *H. squarrosa* (Fig. 15) is perhaps the species most closely resembling *H. whitneyi*. As with *H. whitneyi*, leaves of *H. squarrosa* are stipitate-glandular, while other hazardias have glandular-punctate and resinous leaf surfaces, or glands appear to be totally absent in the densely canescent *H. cana* and *H. detonsa*.

Placment of *Hazardia whitneyi* within *Hazardia* is conspicuously problematic because of its perennial-herbaceous habit, as the other species are woody-stemmed shrubs. Other morphological features also set it apart, as summarized below.

- Perennial herbs; ray florets with sterile ovaries; style branch (disc florets) collecting appendages linear to narrowly linear-lanceolate; achenes elliptic-oblong to narrowly oblong-obovate, strongly flattened, 8– 12-nerved; base chromosome number x = 4

Clark (1979, p. 108) noted that *Hazardia whitneyi* also stands apart in flavonoid chemistry from the other species of *Hazardia*: "Except for *H. whitneyi*, which accumulates only flavonol derivatives, *Hazardia* species consistently produce a complex array of glycoflavones and O-glycosides of flavones and flavonols, and usually a number of highly methoxylated flavonol aglycones (Clark & Mabry 1978)" (but see comments below on *H. brickellioides*).

ADEIA Nesom, gen. nov. TYPE: Adeia whitneyi (A. Gray) Nesom

Hazardia sect. Machaerantheroides W.D. Clark, Madroño 26: 111. 1979.

Similar to species of *Hazardia* in its toothed leaves, the upper not strongly reduced in size, phyllaries graduate in length and with a thickened-herbaceous distal region, yellow rays, disc corollas gradually expanded in the throat region, and pappus a single series of terete bristles. Different in its perennial-herbaceous habit, stipitate-glandular leaves, ray florets with sterile ovaries, with style branches (disc florets) with linear-lanceolate collecting appendages, chromosome number of 2n = 8, and different flavonoid chemistry. DNA analyses indicate that *H. whitneyi* is not part of *Hazardia* sensu stricto.

Perennials from a slender woody caudex, apparently taprooted; stems 20–50 cm high, pilose with vitreous, viscid, multicellular hairs, some gland-tipped. **Leaves** alternate, epetiolate, subclasping (distally), blades broadly oblong to oblanceolate, 25–50 long, 7–16 mm wide, thick-herbaceous to subcoriaceous ("scarcely coriaceous" fide A. Gray in the protologue of *H. whitneyi*), abaxial venation raised when dry, apex acute to obtuse or rounded, margins serrate with ca. (5–)8–15 pairs of sharp-pointed teeth, teeth apices indurate-spinulose but not bristle-tipped, surfaces glabrous or usually sparsely puberulent to hirsutulous with gland-tipped hairs. **Heads** in panicles, racemes, or spikes, or (with suppression of proximal branches) sometimes solitary. **Involucres** subcylindric or (pressed) campanulate, 11–13 mm long, 8–12 mm wide

(pressed). **Phyllaries** in 4–5 series of unequal length, narrowly oblong-lanceolate, apices acute, proximal 1/2-2/3 indurate and narrowly keeled, inner scarious, whitish or sometimes with pink inflections, and glabrous, outer with a herbaceous, stipitate-glandular distal region, sometimes recurving. **Receptacles** flat, shallowly pitted, epaleate. **Ray florets** 0 (*Adeia discoidea*) or 5–18 (*Adeia whitneyi*) and sterile, ligules yellow, much longer than the involucre. **Disc florets** 15–30; corollas 8–10 mm long, tubular, slightly widening into the throat; style branches with linear-lanceolate collecting appendages equal to or slightly longer than the stigmatic portion. **Cypselae** 6–8 mm long (*whitneyi*) or 7–10 mm long (*discoidea*), elliptic-oblong to narrowly oblong-obovate, strongly flattened, 8–14-nerved (Figs. 7, 8, confirming the description by Munz & Keck 1959), or "5-angled and striate between the ribs" (fide Clark 1979), glabrous. **Pappus** a single series of reddish brown, barbellate bristles 7–10 mm long. **Chromosome number**, 2n = 8 (*H. whitneyi*; Solbrig et al. 1969, voucher from Kern Co.); unknown for *Adeia discoidea*.

The genus name, directly from the Greek word, means safety, security, freedom from fear — an antonymic allusion to one of the meanings of "hazard," although Greene's genus *Hazardia* commemorates the California botanist Barclay Hazard.

Since the description of *Haplopappus whitneyi* var. *discoideus* (Howell 1950), its taxonomic rank not been critically evaluated or discussed (e.g., Munz & Keck 1959; Clark 1979, 2006; Brown & Clark 1993; Keil et al. 2021). Yet var. *whitneyi* and var. *discoidea* are different both in morphology and geography, classical criteria for the recognition of species. Howell noted that "Because of the important biological and geological differences between [the "Sierra Nevada" and the "Klamath Area of the Coast Ranges"], it has seemed entirely proper to accord varietal value to an otherwise formal character [lack of rays] and to recognize for each of these major regions an endemic variety." The two are similar in habitat but essentially allopatric (Fig. 3), although in Glenn and Trinity counties, they apparently are contiguous in range or even slightly overlapping — suggesting the possibility of a post-zygotic isolating mechanism.

There is little doubt that var. *whitneyi* and var. *discoidea* are evolutionary sisters, and, as nearly explicit in Howell's protologue comments, the reason for regarding them as conspecific varieties, rather than species, is the small morphological difference (lack of ray flowers in var. *discoidea*). Reliance on degree of difference, however, is subjective and there is a wide range in the degree of difference between closely related, accepted species. The two taxa of *Adeia* are recognized here at specific rank.

Adeia whitneyi (A. Gray) Nesom, comb. nov. Haplopappus whitneyi A. Gray, Proc. Amer. Acad. Arts 7: 353. 1868. Aster whitneyi (A. Gray) Kuntze, Rev. Gen. Pl. 1: 318. 1891. Hazardia whitneyi (A. Gray) Greene, Pittonia 3: 43. 1896. Type: USA. California. Mono Co.: Mono Trail and Sonora Pass, open woods in large tufts, 9000 ft, 1866, H.N. Bolander 6008 (holotype: GH; isotypes: BM, F, K, MO, NY, UC, US, YU). Images seen of all.

Flowering Jul–Sep. Rocky slopes, ridges, summits, talus, outcrops, sometimes over serpentine, hard soil, roadbanks and trailsides, open woods, chaparral; (950–)1200–3650(–4000) m; Calif.

Adeia discoidea (J.T. Howell) Nesom, comb. nov. Haplopappus whitneyi var. discoideus J.T. Howell, Leafl. W. Bot. 6: 84. 1950. Haplopappus whitneyi subsp. discoideus (J.T. Howell) Keck, Aliso 4: 103. 1958. Hazardia whitneyi (A. Gray) Greene var. discoidea (J.T. Howell) W.D. Clark, Madroño 26: 112. 1979. TYPE: USA. California. Siskyou Co.: Marble Mountains, Shackleford Creek trail S of Sky High Valley, ca. 6000 ft, 9 Aug 1939, J.T. Howell 15236 (holotype: CAS; isotypes: DS, GH, US). Images seen of all.

Flowering Jul–Sep. Rocky sites and outcrops, scree and slopes, crevices, ridges and summits, sometimes on serpentine, open sites, meadows, and within woods; (550–) 900–2300 m.

Hall (1928) saw *Hazardia brickellioides* as closely related to *Machaeranthera* (now *Xanthisma*) sect. *Blepharodon* (x = 2, 3, 4, 5) — noting that "the character of involucre and flowers leave no doubt," despite its distinct habit and leaves. Clark (1979) noted that *Hazardia brickellioides* and *Xylorhiza frutescens* are similar in base chromosome number (x = 6), habit (woody, white-barked shrubs), and leaf morphology (stipitate-glandular with spinulose-dentate margins) but discounted a close evolutionary relationship. Clark speculated, however, that "*H. brickellioides* probably represents a distant link to *Isocoma*," alluding to their similar base chromosome number.

Jackson (1968) attempted unsuccessfully to make crosses between *Hazardia brickellioides* and *Xanthisma arenarium* and *X. spinulosum* (x = 4) and *Isocoma vernonioides* (x = 6), but he did create hybrids between *H. brickellioides* and *Hazardia squarrosa* (x = 5) and grew three F1s to maturity. The hybrids were intermediate in morphology; meiosis was highly abnormal, although there were indications that "rather long chromosome segments of the parents were homologous." Jackson (1979) also created artificial hybrids between *Hazardia squarrosa* (x = 5) and *Xanthisma arenarium* (x = 4) and, again, observed large homologous segments. Based on these observations, he regarded *Xanthisma* and *Hazardia* as congeneric (within larger *Haplopappus*). Jackson also noted (1979, p. 160, but apparently never provided documentation) that "as I have obtained hybrids between sections *Hazardia* and [sect.] *Polyphylla*, and between *Hazardia* and section *Haplopappus* there appears to be no sound morphological or genetic basis for considering *Hazardia* as a separate genus."

Brown and Clark (1981, p. 1220) also observed that *Haplopappus* sect. *Polyphylla*, "being the group most closely related to *Hazardia* and probably being derived from broad-leaved, *Hazardia*-like ancestors, is the most primitive of the South American sections. *Hazardia* and *Polyphylla* may merit congeneric treatment, separate from true *Haplopappus*." By now, however, representative species from *Haplopappus* sect. *Gymnocoma* (*H. setigerus*), sect. *Haplopappus* (many), and sect. *Polyphylla* (*H. foliosus*, *H. multifoliosus*) have been included in broad-based molecular-phylogenetic analyses (e.g., Markos & Baldwin 2001; Moore et al. 2012) and results indicate that they constitute a monophyletic group apart from *Hazardia*. Study of *Haplopappus* sect. *Xylolepis* is a priority toward understanding the origin and evolution of *Haplopappus* sensu stricto.

Recently phylogenies of Machaerantherinae (e.g., the summary by Brouillet et al. 2009) show that segmental homologies observed by Jackson reflect common ancestry but do not provide evidence of proximity of relationship. Further, while *Hazardia brickellioides* clearly evolved from within the Machaerantherinae, hybridization and phyletic reticulation have been factors in the history of the group (Morgan et al. 2009) and may lead to conflicting interpretations without intensive study.

The phylogenetic position of *Hazardia brickellioides* remains to be identified but significant features indicate that it is out of place within *Hazardia*. If considered part of *Hazardia*, the base chromosome number of x = 6 suggests that it would be the most primitive species and sister to the others. And unlike the species of sect. *Hazardia*, where it was placed by Clark, *H. brickellioides* does not accumulate flavones (Clark & Mabry 1978). Morphological contrasts are in the couplet below.

- 1. Bark distinctly white; leaves stipitate-glandular, 3-veined from the base; heads mostly restricted to short, distal branches; phyllaries and leaf teeth apically spinulose; style branch appendages much shorter than the stigmatic portion; achenes turbinate, 2-3 mm long; base chromosome number x = 6 Adiaphila

ADIAPHILA Nesom, gen. nov. Type: Adiaphila brickellioides (Blake) Nesom

Similar to species of *Hazardia* in its shrubby habit, toothed leaves, the upper not strongly reduced in size, phyllaries graduate in length and with a thickened-herbaceous distal region, yellow rays, disc corollas gradually expanded in the throat region, and pappus a single series of terete bristles. Different in its white bark, stipitate-glandular leaf vestiture, 3-veined leaves, heads mostly restricted to short, distal branches and subtended by bracteal leaves much reduced in size from the cauline, apically spinulose phyllaries, style branches with appendages much shorter than the stigmatic portion, short, turbinate achenes, chromosome number of 2n = 12, and different flavonoid chemistry.

Shrubs; stems 20–80 cm high, often much-branched proximally, white-barked, scabrous to hispid, some hairs gland-tipped. Leaves alternate, subsessile to subpetiolate, not clasping to barely subclasping, evenly distributed on stems, blades elliptic to obovate or obovate-cuneate, 10-35 long, 5-25 mm wide, coriaceous, weakly 3-veined from near the base, abaxial venation raised when dry, margins usually coarsely serrate with 3–6 pairs of coarse, sharp-pointed, spinulose teeth, very rarely entire, apices acute, surfaces pilose-hirsute to scabrous with gland-tipped hairs. Heads solitary or few in loose clusters on short, distal branches, subtended by bracteal leaves. Involucres cylindric, 6–7 mm long, 4–5 mm wide (pressed); phyllaries in 6–7(–8) imbricate series of unequal length, narrowly oblong-lanceolate, apices sharply acute and spinulose, slightly to strongly recurving, green-herbaceous and densely stipitate-glandular on the distal half, white-indurate below, innermost with scarious margins. Ray florets 5-8, fertile; ligules 2-4 mm long, yellow, shorter than involucres and inconspicuous. Disc florets 8–12, fertile, corollas 6–8 mm long, tubular, gradually widening into the throat; style branches 1.4–1.7 mm long, with triangular-ovate collecting appendages ca. 1/3 as long as stigmatic portion. Cypselae 2-3 mm long, turbinate, 5-nerved, strigosesericeous. Pappus a single series of white to tan barbellate bristles 5–7 mm long. Chromosome number, 2n = 12 (Jackson 1966, voucher from Nye Co., Nevada; Anderson et al. 1974, voucher from Inyo Co., California).

The genus name is from Greek *adeia* (freedom from fear) and *philia* (affection, fondness) — an allusion to *Hazardia* in parallel with that of the new genus *Adeia*.

Adiaphila brickellioides (Blake) Nesom, comb. nov. Haplopappus brickellioides Blake, Proc. Biol. Soc. Wash. 35: 173. 1922. Hazardia brickellioides (Blake) W.D. Clark, Madroño. 26: 125. 1979. TYPE: USA. Nevada. [Nye Co.]: Sheep Mountain, Ash Meadows, felsen [rocks], 3000-4000 ft, May 1898, C.A. Purpus 6022 (holotype: US not seen; isotype: NY image). The label has "May-October 1898" but 6022 is within the range of collection numbers by Purpus in May from Nevada.

Flowering (May–)Jun–Oct(–Nov). Rocky hillsides, outcrops, talus, cliffs, ridges, canyon bottoms, almost always on limestone, gravelly washes, roadsides; 650–2150 m.

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Figure 4. Adeia whitneyi. Tuolumne Co. California. Photo by Debra Cook, July 2012.





Figure 5. Adeia whitneyi. Fresno/Tulare Co. California. Photo by Debra Cook, 12 August 2015.



Figure 6. Adeia whitneyi. Mountains about the headwaters of the Sacramento River, California. Pringle s.n. (PH).



Figure 7. *Adeia whitneyi*. Mountains about the headwaters of the Sacramento River, California. *Pringle s.n.* (PH).



Figure 8. Adeia whitneyi. Mountains about the headwaters of the Sacramento River, California. Pringle s.n. (PH).



Figure 9. *Adeia discoidea*. Tehama Co. (North Yolla Bolly Mountains), California. Photo by Steve Matson, 16 July 2017.



Figure 10. *Adeia discoidea* — detail from Figure 6. Tehama Co., California.



Figure 11. Adeia discoidea. Tehama Co., California. Photo by Steve Matson, 16 July 2017.



Figure 12. Adeia discoidea. Tehama Co., California. Photo by Steve Matson, 16 July 2017.



Figure 13. Adeia discoidea. Sisyou Co., California. Photo by Julie Kierstead Nelson, 22 August 2011.

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Figure 14. Adeia discoidea. Josephine Co., Oregon. Photo by Maureen Jones Jules, 23 August 2006.





Figure 15. Hazardia squarrosa. Representative morphology, disc corollas long-extended beyond involucre.

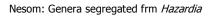


Figure 16. Adeia whitneyi. Mariposa Co., California. Congdon s.n. (MINN).





Figure 17. Adeia whitneyi. Mariposa Co., California. Congdon s.n. (MINN).



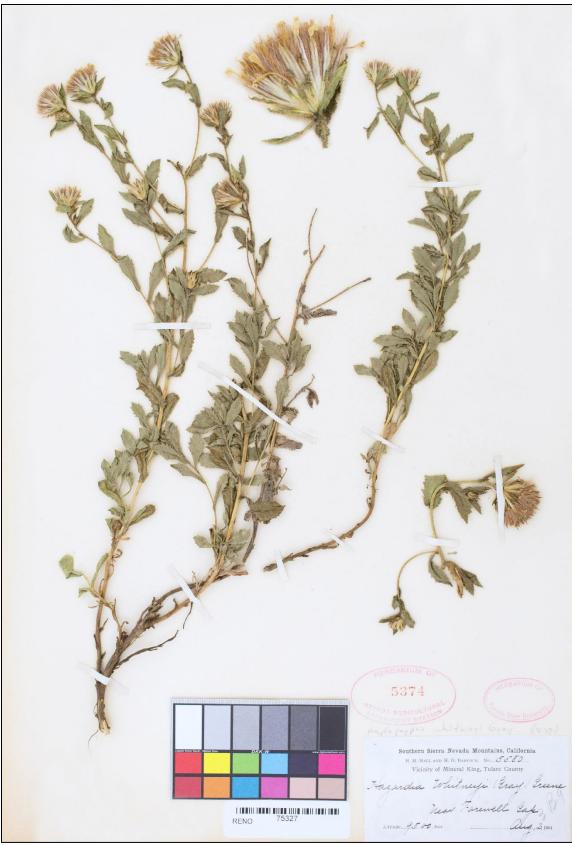


Figure 18. Adeia whitneyi. Tulare Co., California. Hall & Babcck 5580 (RENO).



Figure 19. Adeia whitneyi. Tulare Co., California. Ferris & Lorraine 11192 (COLO).





Figure 20. Adeia discoidea. Siskyou Co., California. Rolle 479 (SOC).

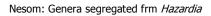




Figure 21. Adiaphila brickelloides. Inyo Co. California. Photo by Matt Berger, 28 September 2019.



Figure 22. Adiaphila brickelloides. Inyo Co. California. Photo by Matt Berger, 30 August 2020.



Figure 23. Adiaphila brickelloides. Inyo Co., California. Photo by Matt Berger, 28 September 2019.

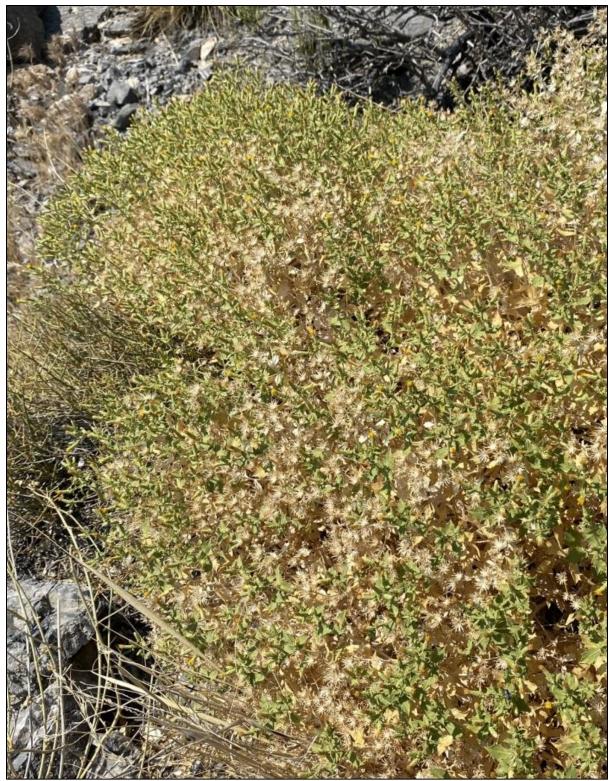


Figure 24. Adiaphila brickelloides. Inyo Co. California. Photo by Matt Berger, 30 August 2020.



Figure 25. Adiaphila brickelloides. Inyo Co. California. Photo by Matt Berger, 28 September 2019.



Figure 26. Adiaphila brickellioides. Inyo Co., California. Ferris & Ernst 13163 (US).



Figure 27. Adiaphila brickellioides. Inyo Co., California. Gilman 2031 (US).



Figure 28. *Adiaphila brickellioides*. Inyo Co., California. *Gilman 1698* (US). Note the pair of lateral veins emerging from the leaf base.

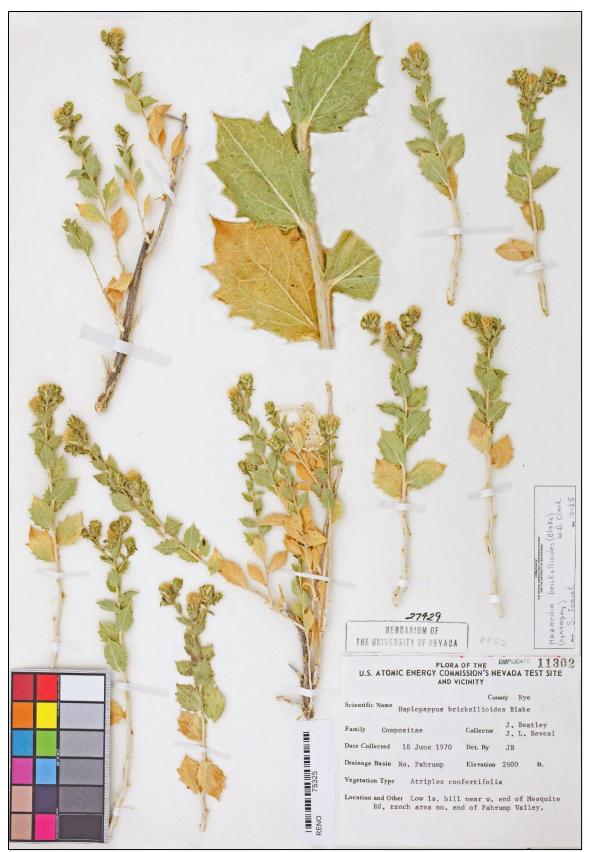


Figure 29. Adiaphila brickellioides. Nye Co., Nevada. Beatley 11302 (RENO).



Figure 30. Adiaphila brickellioides. Nye Co., Nevada. Beatley 9764 (NY).



Figure 31. Adiaphila brickellioides. Nye Co., Nevada. Beatley 9731 (NY).