

---

# New Combinations and New Genera in the North American Tarweeds (Compositae–Madiinae)

Bruce G. Baldwin

Jepson Herbarium and Department of Integrative Biology, University of California, Berkeley, California 94720-2465, U.S.A.

---

**ABSTRACT.** New combinations and new genera for species in *Hemizonia* DC., *Madia* Molina, and *Raillardiopsis* Rydberg allow for a revised, practical taxonomy of Madiinae that better reflects phylogenetic relationships. Reinstatement of *Anisocarpus* Nuttall, *Centromadia* Greene, *Deinandra* Greene, and *Hemizonella* A. Gray, abandonment of *Raillardiopsis* Rydberg, and recognition of four new genera (*Carlquistia*, *Harmonia*, *Jensia*, *Kyhosia*) for tarweed lineages without available generic names result from changes in circumscription based on monophyletic groups.

Results of phylogenetic, biosystematic, and cytogenetic studies in Madiinae (Kyhos et al., 1990; Baldwin et al., 1991; Baldwin, 1992, 1993, 1996, unpublished; Carr et al., 1996) indicate that *Hemizonia* DC. sensu Keck (1959), *Madia* Molina sensu Keck (1959), and *Raillardiopsis* Rydberg are not monophyletic. *Hemizonia* sensu Keck (1959) comprises a minimum of three monophyletic groups that correspond to section *Centromadia* (Greene) D. D. Keck, section *Hemizonia*, and section *Madiomeris* Nuttall sensu Tanowitz (1982) plus the informal “Fruticosae” or “Zonamra” (cf. Clausen, 1951; Keck, 1959). *Madia* sensu Keck (1959), *Raillardiopsis*, and the monophyletic Hawaiian silversword alliance (*Argyroxiphium* DC., *Dubautia* Gaudichaud-Beaupré, *Wilkesia* A. Gray; see Carr, 1985) constitute a clade lacking a formal name (the “*Madia*” lineage in Baldwin, 1996) that is extremely heterogeneous and difficult to diagnose morphologically. The Hawaiian group comprises trees, shrubs, subshrubs, large rosette plants, mat plants, cushion plants, and vines that are strikingly divergent in morphological and ecological characteristics from the primarily Californian herbs in *Madia* sensu Keck (1959) and *Raillardiopsis* (see Carr, 1985; Baldwin & Robichaux, 1995; Baldwin, 1997). In addition to the distinctive Hawaiian lineage, a minimum of seven monophyletic groups can be reliably diagnosed from morphological and molecular data within the clade comprising *Madia* sensu Keck (1959), *Raillardiopsis*, and the silversword alliance.

Recognition at the generic level of each of the three lineages in *Hemizonia* sensu Keck (1959) and each of the seven lineages in the paraphyletic group comprising *Madia* sensu Keck (1959) plus *Raillardiopsis* in the traditional (only) sense results in a practical taxonomy that conforms to the criterion of monophyly (= holophyly) of taxa. The revision of *Madia* sensu Keck (1959) plus *Raillardiopsis* (hereafter, MADRAIL) also allows for continued generic distinction of the unusual Hawaiian species in the silversword alliance without maintaining non-monophyletic California tarweed genera. I realize that additional nomenclatural changes in the silversword alliance are necessary to achieve a taxonomy of the Hawaiian species that includes only monophyletic genera. The new combinations herein focus only on genera relevant to treatments in preparation for the *Flora of North America North of Mexico*.

## REVISION OF MADRAIL

In my revised taxonomy of MADRAIL, *Madia* is restricted to an  $x = 8$  lineage of radiate, epappose annuals with compressed or 3-angled ray cypselsae, i.e., the informal section “*Madia*” sensu Keck (1959), minus *M. minima* (A. Gray) D. D. Keck. *Madia minima*, with obcompressed ray cypselsae, falls outside *Madia*, as circumscribed here, and is returned to the monospecific genus *Hemizonella* A. Gray. All of the widespread, ruderal taxa of *Madia* sensu Keck (1959) fall within *Madia* in the new sense. *Madia* remains the most widely distributed genus of Madiinae, with species found across much of western North America, in Chile and Argentina, and (mostly naturalized) in other parts of the world.

*Anisocarpus* Nuttall is resurrected for a taxon comprising both perennial (sister) species in MADRAIL with  $2n = 7$  II: *M. madioides* (Nuttall) Greene (= *A. madioides* Nuttall, the type species of *Anisocarpus*) and *R. scabrida* (Eastwood) Rydberg (= *A. scabridus* (Eastwood) B. G. Baldwin), the type species of *Raillardiopsis*. Members of *Anisocarpus* in the new sense are the only perennial herbs in Madiinae that combine well-distributed cauline

leaves, radiate heads, ellipsoid or spheric involucre, and yellow anthers.

*Anisocarpus* is a western North American genus found from southern California to southern British Columbia. The two species constituting the genus are allopatric and ecologically divergent. *Anisocarpus madioides* is found in understories of evergreen forests at low to mid elevations, primarily in the coast ranges and on the outer coast of California, Oregon, Washington, and British Columbia. In contrast, *A. scabridus* is restricted to metamorphic scree slopes at high elevations in the inner North Coast Ranges and southern Cascade Range in California.

***Anisocarpus scabridus*** (Eastwood) B. G. Baldwin, comb. nov. Basionym: *Raillardella scabrida* Eastwood, Bull. Torrey Bot. Club 32: 216. 1905. *Raillardiopsis scabrida* (Eastwood) Rydberg, N. Amer. Fl. 34: 320. 1927. TYPE: U.S.A. California: Snow Mountain, 25 Aug. 1892, K. Brandegees s.n. (holotype, CAS).

Four new genera are erected for the remaining MADRAIL lineages. *Carlquistia*, for *Raillardiopsis muirii* (A. Gray) Rydberg ( $2n = 8$  II), recognizes Sherwin Carlquist for his contributions on systematic anatomy in Madiinae, work that led him to determine that *Raillardella* A. Gray in the traditional sense (including *Raillardiopsis*) and the Hawaiian silversword alliance are tarweeds. *Harmonia*, *Jensia*, and *Kyhosia* recognize Harvey Monroe Hall, Jens Clausen, and Donald W. Kyhos for their contributions to Madiinae biosystematics across three successive generations of botanists. *Harmonia* corresponds to the lineage of four species of yellow-anthered, pappose annuals with  $2n = 9$  II. *Jensia* encompasses two (sister) species of dark-anthered, pappose annuals with  $2n = 8$  II. *Kyhosia* is a monospecific genus to which the montane perennial *Madia bolanderi* (A. Gray) A. Gray ( $2n = 6$  II) is transferred.

***Carlquistia*** B. G. Baldwin, gen. nov. TYPE: *Raillardella muirii* A. Gray, Bot. Calif. 1: 618. 1876.  $\equiv$  *Carlquistia muirii* (A. Gray) B. G. Baldwin.

A Madiinae ceteris differt characteribus conjuncte: habitu perenni, herbaceo; rhizomatibus lignosis; foliis caulinis, foliis proximalibus oppositis; capitulis discoidis; squamis papporum subulatis, ciliato-plumosis;  $2n = 8$  II.

Perennials, clumped to mat-forming, white-hirsute to villous and glandular; rhizomes woody, loosely branched; aerial stems greenish yellow to dark purplish, sometimes woody at base, ascending

to erect, leafy throughout, simple or branched, 7–54 cm high; leaves sessile, opposite from base to beyond middle of stem, alternate distally; blades green to gray-green, linear to lanceolate, mostly 9–42 mm long, entire, flat to strongly crisped-coiled, the apices acute; heads discoid, borne singly or in leafy, loosely corymbiform or rounded capitulescences; peduncles 0–8 cm long; “involucre” elliptic-campanulate, campanulate, or turbinate, 8–13 mm high; “phyllaries” (5) 7 to 16, uniseriate, green to purple, subequal; receptacles flat, setulose; “paleae” none; florets 7 to 29, bisexual, the corollas yellow, tubular, 6.5–10 mm long, constricted basally; anthers yellow; style branches hispidulous; cypselae black, terete, linear, straight or slightly curved at acute base, 4–7.5 mm long, covered with white, antrorse hairs; pappus of 9 to 17, purplish white to tawny, subulate scales 5–11 mm long, ciliate-plumose to tip;  $2n = 8$  II.

Members of *Carlquistia* are the only rhizomatous perennial herbs in Madiinae with both well-distributed cauline leaves and discoid heads. As in other members of Madiinae with discoid heads, true phyllaries are absent—the bracts surrounding the florets and functioning as an involucre are homologous with receptacular bracts (Carlquist, 1959).

*Distribution, ecology, and relationships.* *Carlquistia* is restricted to granitic exposures and granitic alluvium of mid- to high-elevation montane habitats of the southern Sierra Nevada and Ventana Double Cone in the Santa Lucia Range of California. *Carlquistia* appears to be most closely related to *Madia*, which shares the common base chromosome number of  $x = 8$  (Baldwin, 1996, & unpublished). Members of the two genera are so disparate in habit, capitular morphology, and ecology that treating them as congeners is impractical, i.e., would result in a group difficult to diagnose with macroscopic characteristics.

***Carlquistia muirii*** (A. Gray) B. G. Baldwin, comb. nov. Basionym: *Raillardella muirii* A. Gray, Bot. Calif. 1: 618. 1876. *Raillardiopsis muirii* (A. Gray) Rydberg, N. Amer. Fl. 34: 320. 1927. TYPE: U.S.A. California: Sierra Nevada, “the station unknown,” J. Muir s.n. (holotype, GH).

***Harmonia*** B. G. Baldwin, gen. nov. TYPE: *Madia hallii* D. D. Keck, Madroño 3: 5. 1935.  $\equiv$  *Harmonia hallii* (D. D. Keck) B. G. Baldwin.

A Madiinae ceteris differt characteribus conjuncte: habitu annuo; capitulis radiatis; phyllariis omnibus ovario radii perfecte cingentibus, phyllariis omnibus hirsutis irregulariter, apicibus pilorum rectis; bracteis receptaculo-

rum in annulo inter flosculos radiorum et flosculos discretis vel unitis infirme; antheris luteis; cypselis radiorum teretibus vel compressis; squamis papporum  $\pm$  subulatis, ciliato-plumosis;  $2n = 9$  II.

Annuals; stems erect, often reddish purple, slender, to 2.7(–4) dm high, hirsute; leaves sessile, mostly cauline, evenly distributed or congested at bases of subumbelliform capitulescences, opposite in proximal half or at base, alternate distally; blades narrowly linear, entire or shallowly toothed, often revolute, mostly hirsute, eglandular or minutely stipitate-glandular, the glands black (or yellowish); capitulescences loosely corymbiform or rounded to subumbelliform, or heads borne singly; peduncles erect or reflexed, 1–60 mm long, minutely stipitate-glandular, the glands black (or yellowish); involucre obconic to obovoid, 3–6 mm high; phyllaries 3 to 8, uniseriate (1 per ray floret), herbaceous, each completely enveloping a ray ovary, not bulging downward at base, the apices acute to acuminate, <half the length of enfolded basal portion of phyllaries, flat or revolute; abaxial faces mostly sparsely to densely hirsute, often with broadly arching or somewhat appressed hairs, often sericeous to villous near margins, ciliate with soft hairs interlocking the enfolded margins, eglandular or minutely stipitate-glandular, the glands black (or yellowish); receptacles flat to slightly convex, glabrous or sparsely setulose; paleae not persistent, restricted to ring at periphery of receptacle (encircling the disc florets), the margins free or weakly fused; ray florets 3 to 8, pistillate, the corollas bright yellow, the laminae flabelliform to obovate, 3-lobed; disc florets 7 to 30, bisexual or functionally staminate, the corollas bright yellow, 5-lobed, glabrous or the tube sparsely villous; anthers yellow; style branches elongate, hispidulose; ray cypselae black, terete to compressed, faintly or prominently adaxially angled, clavate, kyphotic (i.e., strongly bowed out abaxially and slightly concave adaxially) or weakly arcuate, glabrous, beakless to distinctly beaked, attachment scar basal; ray pappus none or of rudimentary broad or subulate scales,  $\leq 1$  mm long, fimbriate to plumose; disc cypselae black, terete, clavate, straight or weakly arcuate, glabrous or with antrorse hairs; disc pappus of 7 to 10, stramineous or purplish, lance-attenuate to subulate,  $\pm$  flat (not crisped), fimbriate or ciliate-plumose scales 0.2–4 mm long;  $2n = 9$  II.

Members of *Harmonia* are the only annuals in Madiinae that combine yellow anthers, phyllaries each completely surrounding a ray ovary, terete to compressed ray cypselae, and pappose disc ovaries.

Unlike *Jensia*, *Harmonia* has phyllaries irregularly hirsute and lacking uncinata hairs, receptacular bracts free or weakly fused, anthers yellow, pappus elements plane, and  $2n = 9$  II.

*Distribution, ecology, and relationships.* *Harmonia* is restricted to soils derived from volcanic ash or serpentine in the North Coast Ranges and Klamath Ranges, California. The volcanic-ash endemic *H. nutans* is apparently sister to the remaining three, serpentine-endemic species (Baldwin, 1993, & unpublished).

***Harmonia doris-nilesiae*** (T. W. Nelson & J. P. Nelson) B. G. Baldwin, comb. nov. Basionym: *Madia doris-nilesiae* T. W. Nelson & J. P. Nelson, Brittonia 37: 394. 1985. TYPE: U.S.A. California: Trinity County, along Shasta-Trinity Forest road 1N40, 0.25 mi. E of junction with road 1N35 (T1N, R7E, S2), 3600 ft., 14 June 1983, T. W. Nelson & B. Williams 7422 (holotype, HSC; isotypes, CAS, JEPS; also GH, MO, NY, US, WTU, not seen).

***Harmonia hallii*** (D. D. Keck) B. G. Baldwin, comb. nov. Basionym: *Madia hallii* D. D. Keck, Madroño 3: 5. 1935. TYPE: U.S.A. California: Napa County, "Near Knoxville," 27 May 1931, H. M. Hall 13094 (holotype, DS; isotypes, UC; also B, CI, GH, K, MO, NY, US, not seen).

***Harmonia nutans*** (Greene) B. G. Baldwin, comb. nov. Basionym: *Callichroa nutans* Greene, Pittonia 2: 227. 1892. *Blepharipappus nutans* Greene, Pittonia 2: 247. 1892. *Layia nutans* (Greene) Jepson, Fl. W. Mid. Calif., ed. 2. 449. 1911. *Madia nutans* (Greene) D. D. Keck, Madroño 3: 5. 1935. TYPE: U.S.A. California: Sonoma County, "Hood's Peak" (on label), 15 May 1892, F. T. Bioletti s.n. (holotype, NDG).

***Harmonia stebbinsii*** (T. W. Nelson & J. P. Nelson) B. G. Baldwin, comb. nov. Basionym: *Madia stebbinsii* T. W. Nelson & J. P. Nelson, Brittonia 32: 323. 1980. TYPE: U.S.A. California: Trinity County, along Shasta-Trinity National Forest road to Hell-to-Find Lake (T29N, R11W, S27, NE1/4), 23 June 1978, T. W. Nelson & J. P. Nelson 4337 (holotype, HSC; isotypes, CAS, DAV, JEPS, UC; also GH, MO, NY, RSA, US, WTU, not seen).

***Jensia*** B. G. Baldwin, gen. nov. TYPE: *Madia yosemitana* Parry ex A. Gray, Proc. Amer. Acad. Arts 17: 219. 1882.  $\equiv$  *Jensia yosemitana* (Parry ex A. Gray) B. G. Baldwin.

A Madiinae ceteris differt characteribus conjuncte: habitu annuo; capitulis radiatis; phyllariis omnibus ovario radii perfecte cingentibus, phyllariis omnibus hirsutis  $\pm$  uniformiter, apicibus pilorum uncinatis; bracteis receptaculorum in annulo inter flosculos radiorum et flosculos discorum, unitis valde; antheris purpureis; cypselis radiorum compressis; squamis papporum subulatis, crispis irregulariter, ciliatis;  $2n = 8$  II.

Annuals; stems erect, stramineous to reddish purple, usually slender, to 6 dm tall, hirsute; leaves sessile, mostly cauline, evenly distributed or congested at bases of subumbelliform capitulescences, opposite in proximal half or at base, alternate distally; blades linear to narrowly spatulate, entire or inconspicuously toothed, plane or slightly revolute, strigose or hirsute, eglandular or the distalmost minutely stipitate-glandular, the glands yellowish or reddish (or black); capitulescences loosely corymbiform or rounded to subumbelliform, or heads borne singly; peduncles erect, to at least 1 dm long, hirsute or not, eglandular or minutely stipitate-glandular, the glands yellowish or reddish or rarely black; involucre obconic to spheric, 3–5 mm high; phyllaries 2 to 10 in 1 series (1 per ray floret), herbaceous, each completely enveloping a ray ovary, usually bulging slightly downward at base, the apices acuminate, revolute, abaxial faces hirsute (the stout hairs usually uncinata at tips, often from pustules), usually eglandular, minutely farinose near margins, ciliate with soft hairs interlocking the enfolded margins; receptacles flat to slightly convex, glabrous or sparsely setulose; paleae not persistent, restricted to ring at periphery of receptacle (encircling the disc florets),  $\pm$  strongly fused most of length; ray florets 2 to 10, pistillate, the corollas bright yellow, often with purplish lines on abaxial surface of laminae, the laminae obovate, 3-lobed; disc florets 1 to 65, functionally staminate, corollas bright yellow, 5-lobed, glabrous or nearly so; anthers dark purple; style branches elongate, hispidulose; cypselae black, compressed, adaxially angled, clavate, kyphotic, glabrous, distinctly beaked, attachment scar slightly oblique; ray pappus a minute crown of subulate scales, to 1 mm long; disc ovaries glabrous; disc pappus of 5 to 7, white or purplish tipped, subulate, crisped, ciliate scales 2.5–4 mm long;  $2n = 8$  II.

Members of *Jensia* are the only annuals in Madiinae that combine phyllaries each completely surrounding a ray ovary, dark purple anthers, terete to compressed ray cypselae, and pappose disc ovaries. Unlike *Harmonia*, *Jensia* has phyllaries more or less uniformly hirsute with hairs usually uncinata, receptacular bracts strongly united, anthers

dark purple, pappus elements crisped, and  $2n = 8$  II.

*Distribution and ecology.* *Jensia* is found from foothill woodlands to mid-montane meadows in the western Sierra Nevada, California. The showy, self-incompatible *J. rammii* and the diminutive, self-compatible *J. yosemitana* are allopatric sister-species. *Jensia rammii* occurs in the Sierra foothills; *J. yosemitana* occurs in montane Sierran habitats.

***Jensia rammii*** (Greene) B. G. Baldwin, comb. nov.  
Basionym: *Madia rammii* Greene, Bull. Calif. Acad. Sci. 1: 90. 1885. *Anisocarpus rammii* (Greene) Greene, Fl. Francisc. 415. 1897.  
TYPE: U.S.A. California: Nevada City, July 1884, C. A. Ramm s.n. (holotype, CAS).

***Jensia yosemitana*** (Parry ex A. Gray) B. G. Baldwin, comb. nov. Basionym: *Madia yosemitana* Parry ex A. Gray, Proc. Amer. Acad. Arts 17: 219. 1882. *Anisocarpus yosemitana* (Parry ex A. Gray) Greene, Fl. Francisc. 416. 1897.  
TYPE: U.S.A. California: "foot of the Upper Yosemite Fall," June 1881, C. C. Parry s.n. (holotype, GH; isotype, DS).

***Kyhosia*** B. G. Baldwin, gen. nov. TYPE: *Anisocarpus bolanderi* A. Gray, Proc. Amer. Acad. Arts 7: 360. 1868.  $\equiv$  *Kyhosia bolanderi* (A. Gray) B. G. Baldwin.

A Madiinae ceteris differt characteribus conjuncte: habitu perenni, rhizomatoso, herbaceo; capitulis radiatis; phyllariis omnibus ovario radii  $\pm$  cingentibus; bracteis receptaculorum in annulo inter flosculos radiorum et flosculos discorum; antheris atropurpureis; squamis papporum  $\pm$  subulatis, ciliatis;  $2n = 6$  II.

Herbs, perennial, with acrid odor; stems erect, stramineous to reddish purple, usually robust, to 12 dm tall, sparsely to densely hirsute proximally, stipitate-glandular distally, the glands yellowish brown to black; leaves sessile, basal and cauline, congested near base, opposite from base to beyond middle of stem, alternate distally; blades linear or lance-linear, to 35 cm long, to 1.5 cm wide, the distal shorter and more widely spaced than on proximal stem, entire, sparsely to densely hirsute, the distalmost stipitate-glandular; capitulescences loosely corymbiform or rounded, usually of 8 or fewer heads; peduncles erect, to 15(–25) cm long, stipitate-glandular, the glands yellowish brown to black; involucre campanulate to hemispheric, 7–14 mm high; phyllaries 8 to 12, uniseriate (1 per ray floret), herbaceous, each  $\pm$  completely enveloping a ray ovary, ciliate, often  $\pm$  hirsute, coarsely

stipitate-glandular; phyllary apices acuminate, up to half the length of enfolded basal portion, revolute; receptacles convex, glabrous or sparsely setulose; paleae not persistent, mostly free or weakly united, restricted to ring encircling the disc florets at periphery of receptacle; ray florets 8 to 12, pistillate, the corollas bright yellow, the laminae conspicuous, oblanceolate to obovate, deeply 3-lobed, the tubes hirsute and minutely glandular; disc florets 30 to 65, bisexual, the corollas bright yellow, 5-lobed, sparsely hirsute and minutely glandular; anthers dark purple; style branches elongate, hispidulose; ray cypselae brown to black,  $\pm$  terete, weakly 5-ridged (with adaxial angle evident), clavate, arcuate, about 5–7 mm long, glabrous or sparsely hispidulose, constricted apically, attachment scar basal; ray pappus absent or a minute crown of subulate scales; disc cypselae brown to black, terete, weakly 5-ridged, clavate, straight or arcuate proximally, ca. 5–9 mm long, brownish hispid (the hairs ascending); disc pappus of 5 to 10, stramineous or purplish, broadly lanceolate to subulate, ciliate to ciliate-plumose scales ca. 2–5 mm long;  $2n = 6$  II.

Members of *Kyhosia* are the only rhizomatous perennial herbs in Madiinae that combine radiate heads, paleae restricted to a ring at the periphery of the receptacle, bisexual disc florets, and dark purple anthers.

*Distribution and ecology.* *Kyhosia* is endemic to the California Floristic Province, where it occurs in mid-montane wet meadows and on streambanks of the western Sierra Nevada and in the southern Cascade Range and Klamath Ranges of California and southern Oregon.

***Kyhosia bolanderi*** (A. Gray) B. G. Baldwin, comb. nov. Basionym: *Anisocarpus bolanderi* A. Gray, Proc. Amer. Acad. Arts 7: 360. 1868. *Madia bolanderi* (A. Gray) A. Gray, Proc. Amer. Acad. Arts 8: 391. 1872. TYPE: U.S.A. California: "Mariposa Big-tree Grove," *H. N. Bolander s.n.* (holotype, GH; isotype, DS).

#### REVISION OF *HEMIZONIA* SENSU KECK (1959)

Under my revised taxonomy for species in *Hemizonia* sensu Keck (1959), *Hemizonia* includes only the hayfield tarweeds, i.e., *H.* sect. *Hemizonia* sensu Keck (1959)—the *H. congesta* DC. (the type species of *Hemizonia*) complex. *Hemizonia* in the new sense comprises the annual members of Madiinae with receptacles chaffy throughout, disc florets

functionally staminate, and cypselae without well-developed beaks. The hayfield tarweeds are endemic to seasonally dry, low- to mid-elevational habitats of the northern and central California Floristic Province, and are most diverse in the North Coast Ranges of California. Based on results of phylogenetic analyses, *Hemizonia* in the new sense is apparently most closely related to *Blepharizonia* Greene, also with  $2n = 14$  II (Baldwin, unpublished).

*Centromadia* Greene is resurrected to accommodate the spikeweeds [*Hemizonia* sect. *Centromadia* sensu Keck (1935, 1959)], the only members of Madiinae with spine-tipped or apiculate leaves. Members of *Centromadia* are annual or rhizomatous-perennial herbs found in grassland or woodland habitats at low elevation, mostly in poorly drained, somewhat alkaline sites. The spikeweeds are endemic to the California Floristic Province; *C. pungens* subsp. *septentrionalis* has become naturalized in the interior Pacific Northwest of Oregon and Washington. New infraspecific combinations in *Centromadia* are provided below for practical convenience, prior to critical systematic re-evaluation of the infraspecific taxa.

***Centromadia parryi*** (Greene) Greene subsp. ***australis*** (D. D. Keck) B. G. Baldwin, comb. nov. Basionym: *Hemizonia parryi* Greene subsp. *australis* D. D. Keck, Madroño 3: 15. 1935. *Hemizonia australis* (D. D. Keck) D. D. Keck, Aliso 4: 110. 1958. TYPE: U.S.A. California: Orange County, Seal Beach, 29 Sep. 1933, *D. D. Keck* 2537 (holotype, DS; isotype, CAS).

***Centromadia parryi*** (Greene) Greene subsp. ***congdonii*** (B. L. Robinson & Greenman) B. G. Baldwin, comb. nov. Basionym: *Hemizonia congdonii* B. L. Robinson & Greenman, Bot. Gaz. 22: 169. 1896. *Centromadia congdonii* (B. L. Robinson & Greenman) C. P. Smith, Muhlenbergia 4: 73. 1908. *Centromadia pungens* (Hooker & Arnott) Greene var. *congdonii* (B. L. Robinson & Greenman) Jepson, Man. Fl. Pl. Calif. 1087. 1925. *Hemizonia parryi* Greene subsp. *congdonii* (B. L. Robinson & Greenman) D. D. Keck, Madroño 3: 15. 1935. *Hemizonia parryi* Greene var. *congdonii* (B. L. Robinson & Greenman) Hoover, Fl. Vasc. Pl. San Luis Obispo Co., Calif. 288. 1970. TYPE: U.S.A. California: Monterey County, Salinas, 26 May 1886, *J. W. Congdon* 151 (holotype, GH).

**Centromadia parryi** (Greene) Greene subsp. **rudis** (Greene) B. G. Baldwin, comb. nov. Basionym: *Centromadia rudis* Greene, Man. Bot. San Francisco 197. 1894. *Hemizonia parryi* Greene subsp. *rudis* (Greene) D. D. Keck, Madroño 3: 15. 1935. TYPE: U.S.A. California: Solano County, Vacaville, 20 Aug. 1892, *W. L. Jepson s.n.* (lectotype, selected here, NDG 61004; isolectotype, JEPS 38135). Three potential syntypes at NDG conform to Greene's protologue ("Sacramento Valley, near Vacaville, *Jepson*"). The date and locality of NDG 61004, annotated in D. D. Keck's handwriting as the type, are the same as on JEPS 38135, annotated in *Jepson*'s handwriting as "part of original collection."

**Centromadia pungens** (Hooker & Arnott) Greene subsp. **laevis** (D. D. Keck) B. G. Baldwin, comb. nov. Basionym: *Hemizonia pungens* (Hooker & Arnott) Torrey & A. Gray subsp. *laevis* D. D. Keck, Madroño 3: 14. 1935. *Hemizonia laevis* (D. D. Keck) D. D. Keck, Aliso 4: 110. 1958. TYPE: U.S.A. California: San Bernardino Valley, 300 m, 8 July 1916, *S. B. Parish 10972* (holotype, DS; isotype, CAS).

**Centromadia pungens** (Hooker & Arnott) Greene subsp. **maritima** (Greene) B. G. Baldwin, comb. nov. Basionym: *Centromadia maritima* Greene, Man. Bot. San Francisco 196. 1894. *Hemizonia pungens* (Hooker & Arnott) Torrey & A. Gray subsp. *maritima* (Greene) D. D. Keck, Aliso 4: 110. 1958. TYPE: U.S.A. California: "Alameda," Oct. 1881, *E. L. Greene s.n.* (lectotype, selected here, NDG 61021). Two potential syntypes at NDG, both from "Alameda," conform to Greene's protologue ("Borders of salt marshes about San Francisco Bay," no date or collector indicated). The collection selected here as lectotype was annotated as the apparent type by D. D. Keck.

**Centromadia pungens** (Hooker & Arnott) Greene subsp. **septentrionalis** (D. D. Keck) B. G. Baldwin, comb. nov. Basionym: *Hemizonia pungens* (Hooker & Arnott) Torrey & A. Gray subsp. *septentrionalis* D. D. Keck, Aliso 4: 110. 1958. *Hemizonia pungens* (Hooker & Arnott) Torrey & A. Gray var. *septentrionalis* (D. D. Keck) Cronquist, Fl. Pacific Northwest 529. 1973. TYPE: U.S.A. California: Siskiyou County, Shasta Valley, *H. M. Hall 12907* (holotype, DS; isotype, DS).

*Deinandra* Greene is reinstated to accommodate

the species in *Hemizonia* sect. *Madiomeris* sensu Tanowitz (1982) plus the informal "Fruticosae" or "Zonamra" (see Clausen, 1951; Keck, 1959). Members of *Deinandra* in the new sense are the only annuals, and non-rhizomatous perennials in Madiinae that combine phyllaries each about half-enclosing a ray ovary, receptacular bracts usually restricted to a peripheral ring, yellow ray corollas, beaked ray cypselae, and leaves lacking apical spines or large tack or pit glands. The names *Deinandra* Greene [type: *D. fasciculata* (DC.) Greene] and *Zonanthemis* Greene [type: *Z. corymbosa* (DC.) Greene, designated by Tanowitz (1982)] were published simultaneously. Their types fall within *H.* sect. *Madiomeris* sensu Tanowitz (1982); both names are available at the generic rank for the taxon comprising *H.* sect. *Madiomeris* sensu Tanowitz (1982) plus "Fruticosae" or "Zonamra" [the older generic name *Hartmannia* DC. is a later homonym of *Hartmannia* Spach]. I have chosen to use *Deinandra* to minimize the number of new combinations necessary to institute the revised taxonomy of *Hemizonia* sensu Keck (1959). New infraspecific combinations in *Deinandra* are provided for practical convenience, prior to critical systematic re-evaluation of the infraspecific taxa.

*Deinandra* in the new sense is nearly endemic to the California Floristic Province, with the exceptions of one species in the San Benito Islands of central Baja California (*D. streetsii*) and two species in the Mojave Desert of California (*D. arida* and *D. mohavensis*). Members of *Deinandra* usually occur in exposed, low- to mid-elevational habitats, mostly in seasonally dry sites. Based on results of phylogenetic analyses, *Deinandra* is apparently more closely related to the distinctive and reproductively isolated genus *Holocarpa* Greene than to the spikeweeds (*Centromadia*) (Baldwin, unpublished), despite crossability and partial interfertility between some members of *Centromadia* and *Deinandra* (Clausen, 1951; Tanowitz, 1977).

**Deinandra arida** (D. D. Keck) B. G. Baldwin, comb. nov. Basionym: *Hemizonia arida* D. D. Keck, Aliso 4: 109. 1958. TYPE: U.S.A. California: Kern County, Mojave Desert, mouth of Red Rock Canyon, 2300 ft., 11 May 1935, *D. D. Keck & P. Stockwell 3279* (holotype, DS; isotypes, CAS, UC; also ARIZ, B, BKL, BM, BR, BRY, C, CAN, CI, COLO, CU, E, F, G, GH, HEL, IA, ILL, IND, K, L, LA, LD, MICH, MIN, MO, MT, NY, OC, OKL, ORE, OS, OSC, P, PENN, PH, POM, RM, S, SBBG, TEX, U, UPS, US, UTC, WIS, WS, WTU, not seen).

- Deinandra clementina** (Brandege) B. G. Baldwin, comb. nov. Basionym: *Hemizonia clementina* Brandege, *Erythea* 7: 70. 1899. *Zonanthemis clementina* (Brandege) Davidson & Moxley, *Fl. S. Calif.* 401. 1923. TYPE: U.S.A. California: San Clemente Island, 25 Aug. 1894, *T. S. Brandege s.n.* (lectotype, selected here, UC 174175). Type not designated by Brandege.
- Deinandra conjugens** (D. D. Keck) B. G. Baldwin, comb. nov. Basionym: *Hemizonia conjugens* D. D. Keck, *Aliso* 4: 109. 1958. TYPE: U.S.A. California: San Diego County, "river bottom land near Otay," 16 May 1903, *L. Abrams 3521* (holotype, UC 407335; isotypes, CAS; also NY, POM, not seen).
- Deinandra corymbosa** (DC.) B. G. Baldwin, comb. nov. Basionym: *Hartmannia corymbosa* DC., *Prodr.* 5: 694. 1836. *Hemizonia corymbosa* (DC.) Torrey & A. Gray, *Fl. N. Amer.* 2: 398. 1843. *Zonanthemis corymbosa* (DC.) Greene, *Fl. Fran.* 425. 1897. TYPE: U.S.A. California: "Nova California," 1833, *Douglas 2* (holotype, G-DC not seen; photograph and fragments, UC; isotypes [fide Tanowitz (1982)], BM, K, not seen).
- Deinandra corymbosa** (DC.) B. G. Baldwin subsp. **macrocephala** (Nuttall) B. G. Baldwin, comb. nov. Basionym: *Hemizonia macrocephala* Nuttall, *J. Acad. Nat. Sci. Philadelphia II* 1: 175. 1848. *Hemizonia angustifolia* DC. subsp. *macrocephala* (Nuttall) D. D. Keck, *Madroño* 3: 12. 1935. *Hemizonia corymbosa* (DC.) Torrey & A. Gray subsp. *macrocephala* (Nuttall) D. D. Keck, *Aliso* 4: 109. 1958. TYPE: U.S.A. California: "At St. Simeon, Upper California," *W. Gambel* (holotype, PH not seen). Tanowitz (1982), who reported seeing the type, indicated the type locality as "in the vicinity of Monterey" and the collector as Nuttall.
- Deinandra frutescens** (A. Gray) B. G. Baldwin, comb. nov. Basionym: *Hemizonia frutescens* A. Gray, *Proc. Amer. Acad. Arts* 11: 79. 1876. TYPE: Mexico. Baja California: "the interior of Guadalupe Island," 1875, *E. Palmer s.n.* (holotype, GH).
- Deinandra greeneana** (Rose) B. G. Baldwin, comb. nov. Basionym: *Hemizonia greeneana* Rose, *Contr. U.S. Natl. Herb.* 1: 24. 1890. TYPE: Mexico. Baja California: Guadalupe Island, "south end" (on label), 29 Mar. 1889, *E. Palmer 865* (holotype, US; isotype, CAS).
- Deinandra greeneana** (Rose) B. G. Baldwin subsp. **peninsularis** (Moran) B. G. Baldwin, comb. nov. Basionym: *Hemizonia greeneana* Rose subsp. *peninsularis* Moran, *Trans. San Diego Soc. Nat. Hist.* 15: 286. 1969. *Hemizonia greeneana* Rose var. *peninsularis* (Moran) B. L. Turner, *Phytologia* 69: 15. 1990. TYPE: Mexico. Baja California: Punta Banda, Banda Peak, 27 Aug. 1966, *Moran 13437* (holotype, SD not seen; isotypes, CAS, UC; also K, MEXU, US, "etc.," not seen).
- Deinandra halliana** (D. D. Keck) B. G. Baldwin, comb. nov. Basionym: *Hemizonia halliana* D. D. Keck, *Madroño* 3: 12. 1935. TYPE: U.S.A. California: San Luis Obispo County, 1.5 mi. E of Cholame, dry flood plain of Cholame Creek, 1200 ft., 4 May 1933, *D. D. Keck & W. M. Heusi 2170* (holotype, DS; isotypes, DS, UC; also [fide Tanowitz (1982)] MO, NY, US, not seen).
- Deinandra increscens** (H. M. Hall ex D. D. Keck) B. G. Baldwin, comb. nov. Basionym: *Hemizonia paniculata* A. Gray subsp. *increscens* H. M. Hall ex D. D. Keck, *Madroño* 3: 11. 1935. *Hemizonia increscens* (H. M. Hall ex D. D. Keck) Tanowitz, *Syst. Bot.* 7: 328. 1982. TYPE: U.S.A. California: San Luis Obispo County, 7.5 mi. SW of Arroyo Grande, 7 June 1931, *H. M. Hall 13136* (holotype, DS; isotype, DS).
- Deinandra increscens** (H. M. Hall ex D. D. Keck) B. G. Baldwin subsp. **foliosa** (Hoover) B. G. Baldwin, comb. nov. Basionym: *Hemizonia paniculata* A. Gray subsp. *foliosa* Hoover, *Fl. Vasc. Pl. San Luis Obispo Co., Calif.* 288. 1970. *Hemizonia increscens* (H. M. Hall ex D. D. Keck) Tanowitz subsp. *foliosa* (Hoover) Tanowitz, *Syst. Bot.* 7: 330. 1982. TYPE: U.S.A. California: San Luis Obispo County, sand hills N of Pozo, 6 Oct. 1965, *Hoover 9715* (lectotype, designated by Tanowitz (1982), OBI not seen; isolectotypes, CAS, UC; also OBI, RSA, not seen).

**Deinandra increscens** (H. M. Hall ex D. D. Keck) B. G. Baldwin subsp. **villosa** (Tanowitz) B. G. Baldwin, comb. nov. Basionym: *Hemizonia increscens* (H. M. Hall ex D. D. Keck) Tanowitz subsp. *villosa* Tanowitz, Syst. Bot. 7: 331. 1982. TYPE: U.S.A. California: Santa Barbara County, Gaviota, *Tanowitz 1650* (holotype, UCSB; isotypes (2), JEPS).

**Deinandra martirensis** (D. D. Keck) B. G. Baldwin, comb. nov. Basionym: *Hemizonia martirensis* D. D. Keck, Madroño 3: 12. 1935. TYPE: Mexico. Baja California: 25 mi. E of San Telmo, in immediate vicinity of San Jose, foothill region at base of San Pedro Martir Mountains, 23 Feb. 1931, *A. Meling 2* (holotype, DS; isotypes, DS, UC; also [fide Tanowitz (1982)] C, GH, US, not seen).

**Deinandra minthornii** (Jepson) B. G. Baldwin, comb. nov. Basionym: *Hemizonia minthornii* Jepson, Man. Fl. Pl. Calif. 1092. 1925. TYPE: U.S.A. California: Ventura County, Santa Susana Mountains, 15 Nov. 1923, *T. W. Minthorn s.n.* (holotype, JEPS 2628).

**Deinandra mohavensis** (D. D. Keck) B. G. Baldwin, comb. nov. Basionym: *Hemizonia mohavensis* D. D. Keck, Madroño 3: 9. 1935. TYPE: U.S.A. California: San Bernardino County, "Mohave River, at confluence with Deep Creek, Mohave Desert," 900 m, 17 Sep. 1933, *D. D. Keck 2531* (holotype, DS; isotype, DS).

**Deinandra pallida** (D. D. Keck) B. G. Baldwin, comb. nov. Basionym: *Hemizonia pallida* D. D. Keck, Madroño 3: 8. 1935. TYPE: U.S.A. California: Kern County, 5.3 mi. N of Grapevine, "Head of the San Joaquin Valley," 6 May 1933, *D. D. Keck & W. M. Heusi 2255* (holotype, DS; isotypes, CAS, UC; also B, C, FM, GH, K, MO, NY, PH, POM, US, not seen).

**Deinandra palmeri** (Rose) B. G. Baldwin, comb. nov. Basionym: *Hemizonia palmeri* Rose, Contr. U.S. Natl. Herb. 1: 24. 1890. TYPE: Mexico. Baja California: Guadalupe Island, Mar. 1889, *E. Palmer 874* (holotype, US).

**Deinandra pentactis** (D. D. Keck) B. G. Baldwin, comb. nov. Basionym: *Hemizonia lobbii* Greene subsp. *pentactis* D. D. Keck, Madroño 3: 8. 1935. *Hemizonia pentactis* (D. D. Keck) D. D. Keck, Aliso 4: 109. 1958. TYPE: U.S.A. California: San Luis Obispo County, "East side of the Salinas River, opposite San Miguel," 27 Apr. 1934, *D. D. Keck & J. Clausen 2836* (holotype, DS; isotypes, DS; also GH, K, not seen).

**Deinandra streetsii** (A. Gray) B. G. Baldwin, comb. nov. Basionym: *Hemizonia streetsii* A. Gray, Proc. Amer. Acad. Arts 12: 162. 1877. TYPE: Mexico. Baja California: "San Benito Island," *T. H. Streets* (holotype, GH).

The following key institutes a new taxonomy of Madiinae. The key was constructed for convenience of identification rather than to reflect phylogenetic relationships and does not list all distinguishing characteristics of the taxa or groups of taxa.

KEY TO GENERA OF MADIINAE

- 1a. Ray cypselae strongly obcompressed; if rays lacking, plants pappose annuals.
  - 2a. Disc florets 1(-2); minute annuals . . . . . *Hemizonella* A. Gray
  - 2b. Disc florets 3 or more; annuals or perennials.
    - 3a. Plants rhizomatous perennials . . . . . *Holozonia* Greene
    - 3b. Plants annuals.
      - 4a. Pappi of 10 broad, apically obtuse scales . . . . . *Achyrrachaena* Schauer
      - 4b. Pappi absent or of elements with acute apex.
        - 5a. Heads calyculate; ray florets 5; disc florets 6, functionally staminate; disc pappus absent . . . . . *Lagophylla* Nuttall
        - 5b. Heads not calyculate; ray florets 0 or 3-27; disc florets 5-100+, bisexual; disc pappi usually present . . . . . *Layia* Hooker & Arnott
- 1b. Ray cypselae compressed or ± terete or somewhat triangular in cross section; if rays lacking, plants perennials or epappose annuals.
  - 6a. Styles of disc florets hairy proximal to minute branches; annuals . . . . . *Blepharipappus* Hooker
  - 6b. Styles of disc florets glabrous proximal to branches; annuals or perennials.
    - 7a. Plants perennial herbs, ± scapose; disc pappi of ciliate-plumose, subulate scales . . . . . *Raillardella* A. Gray
    - 7b. Plants annuals, leafy-stemmed perennial herbs, perennial rosette plants, or of woody growth form; disc pappi absent or various.



- 8a. Heads radiate or discoid; each ray cypsela usually compressed (to 3-angled with broad, rounded abaxial surface) and completely or mostly enclosed within a phyllary (if ray cypsela terete with phyllary only enclosing abaxial surface of cypsela, plants high-montane annuals or perennials).
- 9a. Plants woody or semi-woody, evergreen; Hawaiian.
- 10a. Ray florets present; rosette plants . . . . . *Argyroxiphium* DC.
- 10b. Ray florets absent; habits various.
- 11a. Leaves 1–4 per node, free or weakly united; trees, (sub)shrubs, mat-plants, cushion-plants, vines . . . . . *Dubautia* Gaudichaud-Beaupré
- 11b. Leaves 5 or more per node, strongly coalescent at base; rosette plants . . . . . *Wilkesia* A. Gray
- 9b. Plants herbaceous (aerial stems rarely semi-woody), seasonal; North American or South American.
- 12a. Disc pappi absent . . . . . *Madia* Molina
- 12b. Disc pappi present.
- 13a. Heads all discoid . . . . . *Carlquistia* B. G. Baldwin
- 13b. Heads radiate on at least part of plant.
- 14a. Plants perennials.
- 15a. Involucres campanulate to hemispheric; anthers dark purple . . . . . *Kyhosia* B. G. Baldwin
- 15b. Involucres elliptic or rounded in silhouette; anthers yellow . . . . . *Anisocarpus* Nuttall
- 14b. Plants annuals.
- 16a. Anthers yellow . . . . . *Harmonia* B. G. Baldwin
- 16b. Anthers dark purple . . . . . *Jensia* B. G. Baldwin
- 8b. Heads radiate; each ray cypsela terete to slightly obcompressed with adaxial surface flattened, slightly bulging, or low-keeled and only abaxial surface enclosed within a phyllary; plants low- to mid-elevation annuals, perennial herbs, and (sub)shrubs.
- 17a. Annuals; leaves filiform to narrowly linear and often strongly revolute; mostly with tack glands; ray corolla lobes often more than half the total length of the limb, the lateral lobes often spreading.
- 18a. Ray cypselae beaked; tack glands absent . . . . . *Osmadenia* Nuttall
- 18b. Ray cypselae not beaked; tack glands present . . . . . *Calycadenia* DC.
- 17b. Annuals, perennial herbs, or (sub)shrubs; leaves linear or broader and usually not strongly revolute; mostly without tack glands; ray corolla lobes usually less than half the total length of the limb, the lobes  $\pm$  parallel.
- 19a. Ray cypselae not beaked; corollas white or, less commonly, yellow.
- 20a. Disc florets bisexual; ray and disc cypselae hairy, often with pappus . . . . . *Blepharizonia* Greene
- 20b. Disc florets functionally staminate; ray cypselae glabrous, without pappus . . . . . *Hemizonia* DC.
- 19b. Ray cypselae beaked; corollas yellow.
- 21a. Leaves each with an apical spine . . . . . *Centromadia* Greene
- 21b. Leaves each without an apical spine.
- 22a. Bracts each with large apical pit gland; receptacles with paleae throughout . . . . . *Holocarpa* (DC.) Greene
- 22b. Bracts without large pit glands; receptacles with paleae usually restricted to bases of outermost disc florets . . . . . *Deinandra* Greene

*Acknowledgments.* I thank Gerald D. Carr, David J. Keil, and John L. Strother for helpful reviews of the manuscript; JLS for his advice and encouragement during the study; JLS and Alan R. Smith for assistance with the Latin diagnoses; and Victoria C. Hollowell and Roy Gereau for careful editing of the paper. I also thank the curators of GH, HSC, NDG, and US for loans. This paper is based on research supported by the National Science Foundation (DEB-9458237), and by Roderick Park and other generous Friends of the Jepson Herbarium.

#### Literature Cited

Baldwin, B. G. 1992. Phylogenetic utility of the internal transcribed spacers of nuclear ribosomal DNA in

plants: An example from the Compositae. *Molec. Phylogenetics Evol.* 1: 3–16.

———. 1993. Molecular phylogenetics of *Madia* (Compositae–Madiinae) based on ITS sequences of 18–26S nuclear ribosomal DNA. *Amer. J. Bot.* 80 (6, suppl.): 130.

———. 1996. Phylogenetics of the California tarweeds and the Hawaiian silversword alliance (Madiinae; Heliantheae *sensu lato*). Pp. 377–391 in D. J. N. Hind & H. J. Beentje (editors), *Compositae: Systematics. Proceedings of the International Compositae Conference, Kew, 1994*, vol. 1. Royal Botanic Gardens, Kew.

———. 1997. Adaptive radiation of the Hawaiian silversword alliance: Congruence and conflict of phylogenetic evidence from molecular and non-molecular investigations. Pp. 103–128 in T. J. Givnish & K. J.

- Sytsma (editors), *Molecular Evolution and Adaptive Radiation*. Cambridge Univ. Press, Cambridge, U.K.
- & R. H. Robichaux. 1995. Historical biogeography and ecology of the Hawaiian silversword alliance (Asteraceae): New molecular phylogenetic perspectives. Pp. 259–287 in W. L. Wagner & V. A. Funk (editors), *Hawaiian Biogeography: Evolution on a Hot Spot Archipelago*. Smithsonian Institution Press, Washington, D.C.
- , D. W. Kyhos, J. Dvorak & G. D. Carr. 1991. Chloroplast DNA evidence for a North American origin of the Hawaiian silversword alliance (Asteraceae). *Proc. Natl. Acad. U.S.A.* 88: 1840–1843.
- Carlquist, S. 1959. Studies on Madinae: Anatomy, cytology, and evolutionary relationships. *Aliso* 4: 171–236.
- Carr, G. D. 1985. Monograph of the Hawaiian Madiinae (Asteraceae): *Argyroxiphium*, *Dubautia*, and *Wilkesia*. *Allertonia* 4: 1–123.
- , B. G. Baldwin & D. W. Kyhos. 1996. Cytogenetic implications of artificial hybrids between the Hawaiian silversword alliance and North American tarweeds (Asteraceae: Heliantheae–Madiinae). *Amer. J. Bot.* 83: 653–660.
- Clausen, J. 1951. *Stages in the Evolution of Plant Species*. Hafner, New York.
- Keck, D. D. 1935. Studies upon the taxonomy of the Madinae. *Madroño* 3: 4–18.
- . 1959. Subtribe Madiinae. Pp. 1106–1129 in P. A. Munz, *A California Flora*. Univ. California Press, Berkeley.
- Kyhos, D. W., G. D. Carr & B. G. Baldwin. 1990. Biodiversity and cytogenetics of the tarweeds (Asteraceae: Heliantheae–Madiinae). *Ann. Missouri Bot. Gard.* 77: 84–95.
- Tanowitz, B. D. 1977. An intersectional hybrid in *Hemizonia* (Compositae: Madiinae). *Madroño* 24: 55–61.
- . 1982. Taxonomy of *Hemizonia* sect. *Madiomeris* (Asteraceae: Madiinae). *Syst. Bot.* 7: 314–339.