

**NEW NOMENCLATURAL COMBINATIONS FOR BLUE DICKS
(DIPTEROSTEMON CAPITATUS; ASPARAGACEAE: BRODIAEOIDEAE)**

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ABSTRACT

Dichelostemma capitatum (Benth.) Alph.Wood, traditionally treated as one of five geophyte species included in *Dichelostemma* Kunth, a genus endemic to the western USA and northern Mexico, has been the subject of nearly perpetual taxonomic confusion since the early 19th century. In this paper, I review the errors that perpetuated the misapplication of names to *D. capitatum*, resurrect *Dipterostemon* Rydb. as the alternative genus for *D. capitatum*, and propose new infraspecific combinations. *Dichelostemma pulchellum* (Salisb.) A. Heller, a name persistently misapplied to *D. capitatum*, is a confused name that is synonymous with *D. congestum* (Sm.) Kunth. **Dipterostemon capitatus** (Benth.) Rydb. subsp. **pauciflorus** (Torr.) R.E. Preston, **comb. nov.**, and **D. capitatus** (Benth.) Rydb. subsp. **lacuna-vernalis** (L.W. Lenz) R.E. Preston, **comb. nov.**, are proposed.

The genus *Dichelostemma* traditionally has consisted of five geophyte species endemic to the western USA and northern Mexico (Pires 2002; Pires & Keator 2012). Phylogenetic studies place *Dichelostemma* in the Themidaceae (Fay & Chase 1996; Fay et al. 2000; Pires et al. 2001; Pires & Sytsma 2002) and more recently in the subfamily Brodiaeoidae of the Asparagaceae (Chase et al. 2009; Steele et al. 2012; Chen et al. 2013). These studies also indicate that *Dichelostemma* is not monophyletic; *Dichelostemma capitatum* (Benth.) Alph.Wood is sister to the clade that includes *Brodiaea* and the other four species of *Dichelostemma*. *Dichelostemma capitatum* has been the subject of nearly perpetual taxonomic confusion since the early 19th century, so much so that Keator (1992) dubbed it a “problematic” species. In this paper, I review the errors that perpetuated the misapplication of names to *D. capitatum*, resurrect an alternative name for *D. capitatum*, and propose new infraspecific combinations.

The source of the taxonomic confusion stems from a botanical rivalry between Richard Salisbury and James Smith that took place in the early part of the 19th Century (Britten 1886; Mabblerly 1985; Preston 2013). Salisbury (1808a) described a new genus, *Hookera* Salisb., with two new species, *H. coronaria* Salisb. and *H. pulchella* Salisb., based on specimens collected in 1792 by Archibald Menzies, naturalist aboard the H.M.S. Discovery during Vancouver’s explorations in the vicinity of Puget Sound and the San Juan Islands. Salisbury provided a diagnosis for *H. pulchella* but did not publish a full description until later that year (Salisbury 1808b). Shortly after Salisbury’s initial publication, James Smith completed his own alternative treatment of these taxa, based on the same specimens but also on Menzies’ field notes. Smith presented his description of *Brodiaea* Sm., with two species, *B. grandiflora* Sm. and *B. congesta* Sm., in a paper read before the Linnean Society on April 19, 1808, but his description of *Brodiaea* did not make it into print until two years later (Smith 1810). Despite having priority of publication, *Hookera* appears to have been suppressed in favor of *Brodiaea*, apparently for various personal and social reasons. When Kunth (1843) later proposed the segregate genus *Dichelostemma* (Greek, “bifid corona”), based on the densely clustered inflorescence and the shape of the perianth appendages, he cited *B. congesta* as the basionym, not *H. pulchella*, which he cited as a synonym.

Salisbury made several errors in his description of *Hookera pulchella*, which suggests that he rushed his species description into print in an effort to upstage Smith and to further his own botanical legacy (Preston 2013). Salisbury's initial error was to state that Menzies had collected the specimens in California, whereas Menzies (1923, p. 42) explicitly described collecting the specimens at Restoration Point, which is located on what is now Bainbridge Island in the state of Washington. Because *D. capitatum* and *D. congestum* (Sm.) Kunth both occur in California but *D. capitatum* does not occur in the Pacific Northwest, the incorrect collection locality appears to have led others to believe that Menzies had collected the two species growing together in California (Greene 1886; Hoover 1940). Although the Vancouver expedition overwintered in California, most of Menzies' collecting was done during the spring and summer in the Pacific Northwest.

Salisbury's second error was his claim that *Hookera pulchella* flowers are hexandrous. Salisbury provided a detailed description of *H. pulchella* and precisely described the three appendages that occur on the outer perianth lobes, but he interpreted them as three "emarginate" (i.e., with a bifid apex) filaments that had lost their anthers. Salisbury was adamant that the flowers were hexandrous and suggested that Menzies' field notes and Smith's description of flowers as triandrous were incorrect because the anthers of three stamens had fallen off before Menzies and Smith had noticed them. Salisbury reinforced his mistaken belief that *H. pulchella* was hexandrous when he and several others examined what he believed to be that species blooming in the garden of an acquaintance, and all had noticed that the plants possessed six anthers. The origin and identity of the garden plants Salisbury cited are unknown.

Salisbury's claim seems dubious, because the anthers of *Brodiaea* and *Dichelostemma* are basifixed and not deciduous. How could he have made this mistake? The first clue comes from the herbarium sheet at the British Museum bearing part of Menzies' type collection. One of the four specimens is not actually *D. congestum*; it was annotated "distinct and hexandrous" by Robert Brown, and later annotated to "*Triteleia howellii*" by James Dandy (botanist and Keeper of the Herbarium at the British Museum). It appears that Menzies collected two species growing together, just not *D. congestum* and *D. capitatum*.

Salisbury's illustration of a dissected flower of *Hookera pulchella* (Figures 1 and 2) shows six stamens clearly placed at two levels on the perianth tube, with the appendages opposite the outer perianth lobes. Because the stamens of *D. capitatum* are on the same level on the perianth tube, the appendages are opposite the inner perianth lobes, and the perianth lobes are longer than the tube, the illustration does not represent that species. Instead, the drawing appears to be a composite of *D. congestum* and at least one species of *Triteleia*. Some *Triteleia* species, including *Triteleia grandiflora* Lindl. var. *howellii* (S. Wats.) Hoover, have stamens that are inserted at two levels on the perianth, as in Salisbury's figure. Undoubtedly, Salisbury applied the name *H. pulchella* to the same specimens to which Smith had applied the name *B. congestum*, but Salisbury's description and illustration combined details of two different species.

Salisbury's errors might have had little impact, except for the subsequent discovery of a new species from California superficially resembling *D. congestum* but possessing six stamens. Theodor Hartweg, collecting in the vicinity of Monterey Bay in 1848, returned with specimens that were the type of the species *Brodiaea capitata* Benth. In the protologue, Bentham (1857) cited several other collections of the species from California by David Douglas, Thomas Coulter, and John Bigelow, and from Oregon by John Jeffrey. Additional collections from California were made during the Pacific Railroad surveys. Torrey (1856a, 1856b) contributed to the confusion by initially misapplying the name *Brodiaea congesta* to collections of hexandrous specimens from southern California. Subsequent generations of botanists weighed in with different opinions over the taxonomic distinction between *Brodiaea* and *Dichelostemma* and whether *pulchellum* or *capitatum* was the correct epithet for the hexandrous species, resulting in a tangle of nomenclature.

Although the debate over recognizing a broadly circumscribed *Brodiaea* vs. recognizing several smaller segregate genera continued for many years, many botanists accepted *Dichelostemma capitatum* as the hexandrous species from California, albeit under several generic names and with continued uncertainty as to the species with which to place *H. pulchella* in synonymy (Bentham 1857; Torrey 1859; Wood 1869; Baker 1871; Watson 1879; Britten 1886; Jepson 1922; Abrams 1923). A notable exception was E.L. Greene, the first California botanist to contribute to the discussion and whose views greatly added to the confusion. Greene (1886) proposed that three segregate genera, *Hookera*, *Brodiaea*, and *Triteleia* be recognized, but based on his interpretation of the rule of priority (see Article 11.3 of the International Code of Botanical Nomenclature [ICBN]; McNeill et al. 2012), he applied the genus name *Hookera* to the species currently placed in *Brodiaea* (based on *Brodiaea grandiflora*) and the genus name *Brodiaea* to the species currently placed in *Dichelostemma* (based on *Brodiaea congesta*). Greene interpreted Salisbury's statements about *H. pulchella* having six stamens at face value, i.e., that *D. pulchellum* and *D. congestum* were not the same taxon. This was based on his having observed *D. capitatum* and *D. congestum* growing sympatrically, coupled with his presumption that Menzies had collected his specimens under similar circumstances. Greene further muddied the waters when he proposed that *B. pulchella* (Salisb.) Greene and *B. capitata* were separate hexandrous species. After *Brodiaea* was proposed as a conserved name (Harms 1904) and accepted as such by the International Botanical Congress at Vienna in 1905, Heller (1906) contributed the new combination, *Dichelostemma pulchellum* (Salisb.) A. Heller.

Although Jepson (1922) and Abrams (1923) took different positions on the generic circumscription of *Brodiaea*, both rejected Greene's interpretation of *Dichelostemma pulchellum* and treated it synonymously with *D. congestum*. As these were the early major floristic works for the Pacific Coast states, the issue should have been settled. However, in his monograph of *Dichelostemma*, Hoover (1940) unfortunately resurrected Salisbury's erroneous figure of *H. pulchella* as the basis for recognizing *D. pulchellum* as the correct name for the hexandrous species, with *D. capitatum* in synonymy. Subsequently, later regional floras (Kearney & Peebles 1951; Munz 1959; Shreve & Wiggins 1964; Reveal 1977) as well as many local floras followed Hoover in misapplying the name *D. pulchellum* to the hexandrous species.

It required another monograph of *Dichelostemma* (Keator 1968, 1991) to point out Salisbury's errors and clarify that *D. capitatum* was the correct name for the hexandrous species and that *D. pulchellum* and *D. congestum* are synonymous. Because *Hookera pulchella* was published before *Brodiaea congesta*, the name *Dichelostemma pulchellum* would have priority over *Dichelostemma congestum* (Article 11.4 of the ICBN). However, because *Brodiaea pulchellum* and *Dichelostemma pulchellum* have been widely and persistently misapplied to the hexandrous species *D. capitatum*, they are to be maintained in current usage until a proposal to deal with the situation under Art. 14.1 or 56.1 has been submitted and rejected (following ICBN Article 57.1). Both *The Jepson Manual* (Keator 1993; Pires & Keator 2012) and the *Flora of North America* (Pires 2002) treatments of *Dichelostemma* have followed Keator's monograph.

Because *Dichelostemma capitatum* is the only hexandrous species in the genus, Baker (1871) proposed moving it to the hexandrous genus *Muilla*. On the same basis, Rydberg (1912) proposed placing the species in its own genus, *Dipterostemon*, into which he also placed three other taxa now treated as synonyms or subspecies of *Dichelostemma capitatum*. Rydberg's argument that the possession of six stamens was sufficiently diagnostic to warrant segregation of this new genus may seem weakly justified. However, *D. capitatum* possesses multiple other characters that further differentiate it from other *Dichelostemma* species. Hoover (1940) observed that *D. capitatum* produces cormlets at the base of the corms and at the ends of short stalks, whereas all other species of *Dichelostemma* produce cormlets only at the base of the corm. Keator (1968) noted additional differences between *D. capitatum* and the other species of *Dichelostemma* in leaf width, pubescence

of the scape, arrangement of tracheids in the stem, shape of the seed coat cells, and seed germination pattern. Keator (1991) also noted that *D. capitatum* does not hybridize with other *Dichelostemma* species, whereas the other species do hybridize with each other. In *D. capitatum*, the six stamens are united at the base of the filaments into a short staminal tube via fusion of the connective tissue, a feature not present in the other species of *Dichelostemma* (Lenz 1976). Moreover, the staminal tube possesses six lanceolate appendages that extend upward and cover the anthers and style, similar to but not homologous to the corona found in other species of *Dichelostemma*, which is an extension of the perianth (Lenz 1976).

Berg (1996) proposed resurrecting *Dipterostemon* on the basis of embryology. Although the embryology of *Brodiaea* and *Dichelostemma* is quite similar, the inner integument of the ovule of *D. capitatum* consists of two cell layers, similar to that of *Muilla* and *Triteleia* but different from the multilayered inner integument that represents a synapomorphy of *Brodiaea* and the other *Dichelostemma* species (Berg 1978, 1996, 2003).

Morphological evidence for recognizing *Dipterostemon* is fully supported by molecular data, which show that *D. capitatum* is sister to a clade composed of *Brodiaea* and the other species of *Dichelostemma* and that *Dichelostemma* is only monophyletic if *D. capitatum* is excluded (Pires et al. 2001; Pires & Sytsma 2002; Nguyen et al. 2008; Steele et al. 2012). Accordingly, a revised treatment of *Dichelostemma capitatum* is presented here that treats the species and its infraspecific taxa under the genus *Dipterostemon*.

TAXONOMIC TREATMENT

DIPTEROSTEMON Rydb., Bull. Torrey Bot. Club 12: 110. 1912. **TYPE:** *Brodiaea capitata* Benth., Pl. Hartw. 339. 1857.

DIPTEROSTEMON CAPITATUS (Benth.) Rydb., Bull. Torrey Bot. Club 12: 111. 1912. *Brodiaea capitata* Benth., Pl. Hartw. 339. 1857. *Dichelostemma capitatum* (Benth.) Alph.Wood, Proc. Acad. Nat. Sci. Philadelphia 20: 173. 1868. *Milla capitata* (Benth.) Baker, J. Linn. Soc., Bot. 11: 381. 1870. *Hookera capitata* (Benth.) Kuntze, Revis. Gen. Pl. 2: 712. 1891. **TYPE:** **USA. California.** “In silvis prope Monterey,” Hartweg 2000 (holotype: K000802775[digital image!]).

Brodiaea insularis Greene, Bull. Calif. Acad. Sci. 2: 134. 1886. *Dichelostemma insulare* (Greene) Burnham, Muhlenbergia 3: 74. 1907. *Dipterostemon insularis* (Greene) Rydb., Bull. Torrey Bot. Club 12: 110. 1912. *Brodiaea capitata* Benth. var. *insularis* (Greene) J.F. Macbr., Contr. Gray Herb. 56: 9. 1918. **TYPE.** Not located. (Note: Greene [1886] cited his earlier observation of *B. capitata* on Guadalupe Island in April, 1885, as the basis of his description, but although Greene reports having collected corms from there and growing them out at Berkeley, no record of a specimen could be found at CAS, NDG, or UC.)

“*Hookera pulchella*” auct. non Salisb.: Greene, Bull. Calif. Acad. Sci. 2: 133. 1886; A.Heller, Muhlenbergia 1: 132. 1906; Rydb., Bull. Torrey Bot. Club 12: 111. 1912; Hoover, Amer. Midl. Naturalist 24: 471. 1940; C.V. Morton, Herbertia 7: 81. 1941; Reveal, Taxon 32: 294. 1983.

DIPTEROSTEMON CAPITATUS (Benth.) Rydb. subsp. **CAPITATUS**

Dipterostemon capitatus subsp. *capitatus* (Fig. 3) is widespread throughout the California Floristic Province in California and Oregon. The populations are highly variable, and further study is needed to determine whether additional taxa can be distinguished morphologically and geographically (Preston 2014).

Dipterostemon capitatus (Benth.) Rydb. subsp. **pauciflorus** (Torr.) R.E. Preston, **comb. nov.** *Brodiaea capitata* Benth. var. *pauciflora* Torr., Rep. U.S. Mex. Bound., Bot. 218. 1858. *Milla capitata* Baker var. *pauciflora* (Torr.) Baker, J. Linn. Soc., Bot. 11: 381. 1870. *Dichelostemma pauciflorum* Standl., Contr. U.S. Natl. Herb. 13: 179, 227. 1910. *Dipterostemon pauciflorus* (Torr.) Rydb., Bull. Torrey Bot. Club 12: 110. 1912. *Hookera pauciflora* (Torr.) Tidestr. Contr. U.S. Natl. Herb. 25: 123. 1925. *Dichelostemma capitatum* (Benth.) Alph. Wood subsp. *pauciflorum* (Torr.) Keator, Four Seasons 9: 30. 1992. **SYNTYPES. USA. New Mexico.** Near the copper mines, *Bigelow s.n.* (NY [digital image!]); **Arizona.** on the Gila River, *Parry s.n.* (NY [digital image!]). **Mexico. Sonora.** San Francisco Spring, *Capt. E.K. Smith s.n.* (NY [digital image!]).

Dipterostemon capitatus subsp. *pauciflorus* (Fig. 4) occurs in desert habitats of the southwestern USA and northern Mexico. Although the distinctiveness of this taxon has been questioned, both Hoover (1940) and Keator (1968, 1991, 1993) recognized it on the basis of morphological differences and its occurrence in desert habitats.

Dipterostemon capitatus (Benth.) Rydb. subsp. **lacuna-vernalis** (L.W. Lenz) R.E. Preston, **comb. nov.** *Dichelostemma lacuna-vernalis* L.W. Lenz, Aliso 8: 129. 1974. *Dichelostemma capitatum* (Benth.) Alph. Wood subsp. *lacuna-vernalis* (L.W. Lenz) D.W. Taylor, Fl. Yosemite Sierra 373. 2010. **TYPE. USA. California.** Sacramento Co.: Orangevale, 12 Apr 1967, *L.W. Lenz 24671a* (holotype: RSA 235779 [digital image!]; isotypes: RSA 235800, RSA 457167, RSA 457168, RSA 457169, RSA 457170, RSA 457171 [digital images!]).

Dipterostemon capitatus subsp. *lacuna-vernalis* (Fig. 5) is endemic to the western base of the Sierra Nevada foothills and adjacent Great Valley, ranging from Butte County south to Merced County (Preston 2014). The populations are restricted to a narrow elevation band between 30 and 270 m.

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Figure 1. *Hookera pulchellum*. Illustrated by William Hooker in the *Paradisus Londinensis*, 1808. The insets illustrate the open corolla, pistil, and a transverse section of the young fruit.

Figure 2. Enlargement of floral dissection in Figure 1. The illustration shows six stamens, the longer stamens opposite the inner perianth lobes and the shorter stamens opposite the outer perianth lobes, with appendages on the shorter stamens, and the perianth tube longer than the tepals.

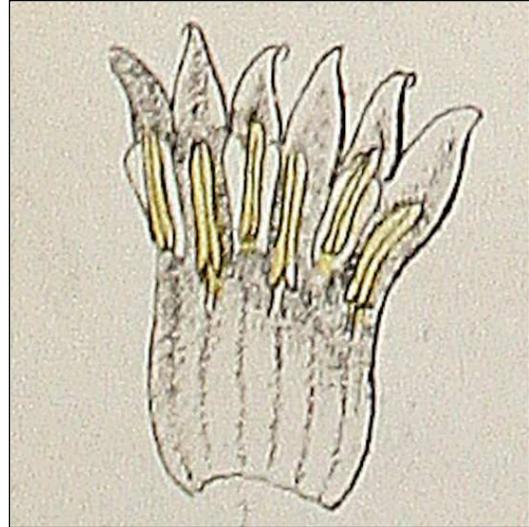


Figure 3. *Dipterostemon capitatus* subsp. *capitatus*. The inflorescences are characterized by dark bracts and short pedicels. Photo by Steve Matson.



Figure 4. *Dipterostemon capitatus* subsp. *pauciflorus*. The inflorescences are characterized by pale bracts and long pedicels. Photo by R. Preston.



Figure 5. *Dipterostemon capitatum* subsp. *lacuna-vernalis*. The flowers are characterized by broadly ovate outer perianth lobes and very short perianth tubes (less than or equal to 4 mm). Photo by R. Preston.