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# Transfer of *Dodecatheon* to *Primula* (Primulaceae)

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**Abstract.** Phylogenies inferred from both chloroplast and nuclear DNA regions have placed the small genus *Dodecatheon* (the shooting stars; 17 spp.) among the descendants of the most recent common ancestor of *Primula* (the primroses; ca. 430 spp.). This is congruent with conclusions previously derived from morphology and cytology. We illustrate how failure to formalize this information in the circumscription of *Primula* might have impeded understanding of the evolution of distyly (as seen in *Primula*) and buzz-pollination (as seen in *Dodecatheon*). To avoid future confusion, we make new combinations for *Dodecatheon* in *Primula*, and erect ***Primula* sect. *Dodecatheon*** in *Primula* subgenus *Auriculastrum* for the taxa from *Dodecatheon*.

**Key words:** Buzz-pollination, distyly, *Dodecatheon*, heterostyly, *Primula*, Primulaceae.

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Recent molecular evidence from both the chloroplast (cpDNA; Källersjö et al., 2000; Mast et al., 2001, 2004, 2006; Trift et al., 2002) and nuclear (Martins et al., 2003) genomes is congruent with prior hypotheses based on morphological and cytological evidence (Thompson, 1953; Wendelbo, 1961; Richards, 1993; Holmgren, 1994) that *Dodecatheon* L. (17 spp.) is most closely related to one of the seven subgenera of *Primula* L. (ca. 430 spp.; Primulaceae). The study by Mast et al. (2004) represents the most extensive sampling of cpDNA characters (seven regions) and taxa within *Dodecatheon* (16 of the 17 spp. recognized here) and the closely related *Primula* subgen. *Auriculastrum* Schott (all four sections sampled, three of them exhaustively) to date. In the cpDNA phylogeny inferred in that study, sampled members of *Dodecatheon* form a monophyletic group (97% bootstrap frequency) that is sister to the only species of *Primula* sect. *Suffrutescens* A. J. Richards (100% bootstrap frequency) of *P.* subgen. *Auriculastrum*. The study by Martins

et al. (2003) represents the most complete sampling of nuclear DNA (in this case, the two internal transcribed spacers of the nuclear ribosomal DNA) and subgenera of *Primula* (five of seven) to date. In the nuclear DNA phylogeny inferred in that study, the single sampled species of *Dodecatheon* is sister to the single sampled species of *P.* subgen. *Auriculastrum* (100% bootstrap frequency). Thus, DNA sampling of two independent 'linkage partitions' (sensu Slowinski & Page, 1999) is congruent in support of the conclusion that *Primula* is paraphyletic with respect to *Dodecatheon*.

While the buzz-pollinated flowers of *Dodecatheon* distinguish the lineage from others in *Primula*, individuals of *Dodecatheon* in sterile, pre-anthetic, and fruiting stages are strikingly similar to members of *P.* subgen. *Auriculastrum*. Both groups have members that grow in moist alpine meadows and along streamsides, have chromosome numbers of  $2n = 44$ , and produce valvate capsules on long scapes arising from a rosette of fleshy, lance-

shaped leaves with involute veneration (Thompson, 1953). Furthermore, Thompson (p. 75) noted that *D. jeffreyi* Van Houtte and *P. parryi* A. Gray (a member of *P.* subgen. *Auriculastrum*) are “virtually indistinguishable when the corollas and inserted anthers are removed.” Both *Dodecatheon* and *P.* subgen. *Auriculastrum* occur in western North America, though each is also found elsewhere (one sp. of *Dodecatheon* extends across the Bering Strait; *P.* subgen. *Auriculastrum* is also found in Pacific coastal Asia and in Europe). Some previous authors (e.g., Pax, 1889) grouped *Dodecatheon* at the tribal rank (as *Cyclameae* Dumort.) with another buzz-pollinated genus, the Mediterranean genus *Cyclamen* L., which was still then considered part of the family (c.f., Källersjö et al., 2000). However, recent authors (Thompson, 1953; Wendelbo, 1961; Richards, 1993, 2002; Holmgren, 1994) have taken the geographical, morphological, and cytological similarities as evidence for a close phylogenetic relationship between *Dodecatheon* and *Primula*, and interpreted floral similarities between *Dodecatheon* and *Cyclamen* as due to convergence on buzz-pollination.

*Dodecatheon* is one of four genera composed of species that have been segregated from *Primula* but that are inferred to be descended from the most recent common ancestor (MRCA) of *Primula* using morphological and cytological (Wendelbo, 1961), cpDNA (Källersjö et al., 2000; Mast et al., 2001, 2004, 2006; Trift et al., 2002), and nuclear DNA (Martins et al., 2003) evidence. Like 92% of species in *Primula*, one of the four segregated genera, *Dionysia* Fenzl (ca. 50 spp. of mostly cushion plants from the Middle East; Grey-Wilson, 1989; Trift et al., 2004), is distylous. In distylous plants, a genetic polymorphism produces two floral types: the “pin” morph has stigmas high and anthers low in the corolla tube and small pollen; the “thrum” morph has stigmas low and anthers high in the corolla tube and large pollen (Darwin, 1877; Ganders, 1979; Barrett, 1992, 2002; Richards, 2002). Like the remaining 8% of species in *Primula*, the three other segregated genera, *Dodecatheon*, *Cortusa* L. (1[–3] spp. from Asia), and *Sredinskya* (Stein) Fedorov (1 sp. from the Caucasus; most recently recognized as *Prim-*

*ula grandis* Trautv. by Richards [2002]), are monomorphic. That is, they have a single floral morphology within each species. Most monomorphic lineages in *Primula* are thought to arise by a recombination of the “heterostyly supergene” that is later fixed in a population and produces flowers in which the anthers and stigma are both high in the corolla tube and pollen is large (see Mast et al. [2006] for a recent review). However, flowers of *Dodecatheon*, *Cortusa*, and *Sredinskya* have their stigmas positioned well above their anthers (by virtue of long styles and filaments adnate low in the corolla tube), differing in the phenotype expected after the typical recombinational route to monomorphy. Mast et al. (2004) marshaled evidence to suggest that *Dodecatheon*, and perhaps *Cortusa* and *Sredinskya* as well, represent an alternate route to monomorphy in the descendants of the MRCA of *Primula*: the fixation of the recessive alleles of the heterostyly supergene and thus the “pin” morphology.

The alternate route to monomorphy proposed by Mast et al. (2004) for descendants of the MRCA of *Primula* was not previously suggested, in part, because comparative biologists thinking about the function, genetics, and evolution of distyly confined their attention to monomorphic species in genera that also contained distylous members. Thus, they were not making potentially informative morphological comparisons involving *Dodecatheon* (e.g., pollen size between *Dodecatheon* and *P.* subgen. *Auriculastrum*; Mast et al., 2004). By making these comparisons, Mast et al. (2004) placed the floral variation seen between these groups into an evolutionary scenario that involves the co-opting of pre-existing features from the distylous ancestor (e.g., the “pin” positioning of stigma and anthers), the genesis of new features with the origin of *Dodecatheon* (e.g., the enlargement of the anthers and delayed longitudinal dehiscence to produce “poricidal” anthers in the first days of anthesis), and the later fine-tuning of the buzz pollination syndrome (development of rugosity on the anther connectives). The study of Mast et al. (2004) clearly illustrates both the utility of recognizing phylogenetic relationships in comparative biology, and the importance of maintaining monophyly in our currently recognized taxa.

In this paper, we make new combinations for the currently accepted entities of *Dodecatheon* in *Primula*, and establish *Primula* sect. *Dodecatheon* (L.) A. R. Mast & Reveal as a member of *P.* subgen. *Auriculastrum*. This is a necessary step in making *Primula* monophyletic and produces a monophyletic *P.* subgen. *Auriculastrum*. Although both *Primula* and *Dodecatheon* were proposed by Linnaeus in 1753, we choose to retain *Primula*, since it represents a far larger and more widespread group.

- Primula** L. sect. **Dodecatheon** (L.) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon* L., Sp. Pl.: 144. 1753 - Type species: *D. meadia* L. ≡ *P. meadia* (L.) A. R. Mast & Reveal.
- Primula austrofrigida** (K. L. Chambers) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon austrofrigidum* K. L. Chambers, Sida 22: 462. 2006.
- Primula clevelandii** (Greene) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon clevelandii* Greene, Pittonia 1: 213. 1888. [as clevelandii].
- Primula clevelandii** var. **gracilis** (Greene) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon patulum* var. *gracile* Greene, Erythea 3: 72. 1895.
- Primula clevelandii** var. **insularis** (H. J. Thoms.) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon clevelandii* subsp. *insulare* H. J. Thoms., Contr. Dudley Herb. 4: 134. 1953 [as *insularis*].
- Primula clevelandii** var. **patula** (Kuntze) A. R. Mast & Reveal, **comb. nov.**, *Meadia patula* Kuntze, Revis. Gen.: 398. 1891.
- Primula conjugens** (Greene) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon conjugens* Greene, Erythea 3: 40. 1895.
- Primula conjugens** var. **viscida** (Piper) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon viscidum* Piper, Bull. Torrey Bot. Club 28: 43. 1901.
- Primula fassettii** A. R. Mast & Reveal, **nom. nov.**, *Dodecatheon meadia* var. *amethystinum* Fassett, Rhodora 31: 52. 1929, non *P. amethystina* Franch., 1885. Replaces *D. amethystinum* (Fassett) Fassett, Rhodora 33: 224. 1931.
- Primula fragrans** A. R. Mast & Reveal, **nom. nov.**, *Dodecatheon jeffreyi* var. *redolens* H. M. Hall, Bot. Gaz. 31: 392. 1901, non *P. redolens* Balf. f. & Kingdon-Ward, 1916. Replaces *D. redolens* (H. M. Hall) H. J. Thoms., Contr. Dudley Herb. 4: 143. 1953.
- Primula frenchii** (Vasey) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon meadia* var. *frenchii* Vasey, Gray's Manual, ed. 6. 735b. 1891.
- Primula frigida** (Cham. & Schltdl.) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon frigidum* Cham. & Schltdl., Linnaea 1: 222. 1826.
- Primula hendersonii** (A. Gray) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon hendersonii* A. Gray, Bot. Gaz. 11: 233. 1886.
- Primula jeffreyi** (Van Houtte) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon jeffreyi* Van Houtte, Fl. Serres Jard. Eur. 16: 99, t. 1662. 1867. The name *Dodecatheon jeffreyi* has been proposed for conservation against the earlier *D. jeffreyanum* K. Koch (1866) in a paper by Veldkamp, Reveal and Gandhi that has yet to appear in Taxon.
- Primula latiloba** (A. Gray) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon meadia* var. *latilobum* A. Gray, Syn. Fl. N. Amer. 2(1): 58. 1878. Replaces *D. dentatum* Hook., Fl. Bor.-Amer. 2: 119. 1838, non *P. dentata* Donn ex Roem. & Schult., 1819. The epithet *latilobum* has priority by virtue of the combination *D. latilobum* (A. Gray) Elmer ex R. Knuth, Pflanzenr. (Engler) IV, 237 (22): 239. 1905.
- Primula meadia** (L.) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon meadia* L., Sp. Pl. 144. 1753.
- Primula pauciflora** (Greene) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon pauciflorum* Greene, Pittonia 2: 72. 1890. Replaces *D. pulchellum* (Raf.) Merr., J. Arnold Arbor. 29: 212. 1948, non *P. pulchella* Franch., 1888.
- Primula pauciflora** var. **cusickii** (Greene) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon cusickii* Greene, Pittonia 2: 73. 1890.
- Primula pauciflora** var. **distola** (Reveal) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon pulchellum* (Raf.) Merr. var. *distolum* Reveal, Phytologia 88: 294. 2006.

- Primula pauciflora** var. **macrocarpa** (A. Gray) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon meadia* var. *macrocarpum* A. Gray, Bot. Calif. 1: 467. 1876.
- Primula pauciflora** var. **monantha** (Greene) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon pauciflorum* Greene var. *monanthum* Greene, Pittonia 2: 73. 1890.
- Primula pauciflora** var. **shoshonensis** (A. Nelson) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon pauciflorum* Greene var. *shoshonense* A. Nelson, Bot. Gaz. 54: 143. 1912.
- Primula pauciflora** var. **zionensis** (Eastw.) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon zionense* Eastw., Leafl. W. Bot. 2: 37. 1937.
- Primula poetica** (L. F. Hend.) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon poeticum* L. F. Hend., Rhodora 32: 27. 1930.
- Primula standleyana** A. R. Mast & Reveal, **nom. nov.**, *Dodecatheon ellisiae* Standl., Proc. Biol. Soc. Wash. 26: 195. 1913, non *P. ellisiae* Pollard & Cockerell, 1902.
- Primula subalpina** (Eastw.) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon subalpinum* Eastw., Leafl. W. Bot. 2: 37. 1937.
- Primula tetrandra** (Suksd. ex Greene) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon tetrandrum* Suksd. ex Greene, Erythea 3: 40. 1895. Replaces *D. alpinum* (A. Gray) Greene, Erythea 3: 39. 1895, non *P. alpina* Salisb., 1796.
- Primula utahensis** (N. H. Holmgren) A. R. Mast & Reveal, **comb. nov.**, *Dodecatheon dentatum* var. *utahense* N. H. Holmgren, Brittonia 46: 91. 1994.

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