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DOELLINGERIA AND *EUCEPHALUS* (ASTERACEAE: ASTEREAE) AS DISTINCT GENERA

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ABSTRACT

Allen et al (2019) have treated *Doellingeria* (3 species, eastern USA and Canada) and *Eucephalus* (10 species, western USA and British Columbia) as congeneric, formally uniting them within *Doellingeria* -- based on ITS/ETS sequence data indicating that *Doellingeria* is sister to *E.elegans* and that these two are sister to the rest of *Eucephalus*. This mode of origin, however, requires a genetically complex and saltational leap in deriving the *Doellingeria* morphology directly from that of *Eucephalus*. Plastid sequences of Allen et al. suggest a more complex evolutionary history involving species of subtribe Baccharidinae (Nesom 2020). Until a more credible explanation might be found, two genera are justifiably recognized, each distinct and consistent in morphology and distantly separated from the other in geography.

A close evolutionary relationship between *Doellingeria* and *Eucephalus* has been shown by molecular data (Brouillet et al. 2009; Allen et al. 2019). Both genera are endemic to North America. Asian species sometimes placed in *Doellingeria* are not closely related to American *Doellingeria* and have been separated into the genus *Cardiagyris* Nesom (Nesom 2020a).

Relying primarily on molecular data, *Doellingeria* and *Eucephalus* have been recognized as Astereae subtribe Doellingeriinae (Nesom 2020b), and as supported by morphological characters noted here.

DOELLINGERIINAE Nesom, Phytoneuron 2020-53: 13. 2022. **TYPE**: *Doellingeria* Nees

Perennial herbs (fibrous-rooted [short rhizomes] in *Doellingeria*, long-rhizomatous in *Eucephalus*) with scale-like basal and lower cauline leaves; leaves eglandular; capitulescence corymbiform to paniculiform; phyllaries strongly graduate in length, midregion rounded (*Doellingeria*) or keeled (*Eucephalus*); rays absent or relatively few (2–20), white to bluish or violet; achenes eglandular, broadly columnar with 5–9 resinous veins (*Doelllingeria*) or strongly flattened and 2-nerved (*Eucephalus*); pappus bristles in 2–4 subequal series, apices clavate.

Doellingeria Nees, 1832 [3 species, eastern USA; type = *D. umbellata*]
Eucephalus Nutt., 1840, [10 species, western USA and British Columbia; type = *E. elegans*]

The two genera are allopatric and morphologically distinct and they were not suspected of being closely related until molecular data aligned them as sister taxa near the base of the North American lineage of Astereae (sensu Noyes & Reiseberg 1999). For Asteraceae in Flora of North America, *Doellingeria* (Semple & Chmielewski 2006) and *Eucephalus* (Allen 2006) were treated as separate genera.

All 13 species have been united as *Doellingeria* (Allen et al. 2019), based on analyses showing *Doellingeria* and *Eucephalus elegans* as sister to the rest of *Eucephalus* (ITS/ETS sequences; Fig. 1) or as more distantly related to the rest of *Eucephalus* (plastid sequences). The nuclear sequences suggest that species of *Doellingeria* arose as a derived lineage from within *Eucephalus*, while (as noted by Allen et al.) plastid sequences indicate a more complex evolutionary

history, involving species of subtribe Baccharidinae (Nesom 2020b). Their taxonomic option was based on the nuclear sequences.

Multivariate morphometric analyses by Allen et al. (2019) show that the three eastern species (*Doellingeria*) are distinct from all of the western species (*Eucephalus*) and that *E. glaucescens*, *E. gormanii*, and *E. paucicapitatus* are somewhat distinct (the 'Pacific Northwest Subgroup') from the other western species (the 'Rocky Mountain-Cascade Subgroup').

Nothing in the morphology of *Eucephalus elegans* suggests that it is more closely related to *Doellingeria* than to other *Eucephalus*. Although the nuclear molecular data can be construed to support the taxonomy proposed by Allen et. al., the hypothesis that species of *Doellingeria* arose as the evolutionary sister of *Eucephalus elegans* does not seem credible, as it requires a genetically complex and saltational leap in deriving the *Doellingeria* morphology directly from that of *Eucephalus*.

An alternative taxonomic solution, not considered by Allen et al. but based on their nuclear data, would be to transfer *Eucephalus elegans* to *Doellingeria*, thus maintaining two separate and monophyletic genera with only a single new combination. But such also requires the saltational leap noted above.

In any case, the gain in considering *Doellingeria* and *Eucephalus* congeneric is outweighed by evolutionary information conveyed by maintaining them as separate. Reticulate evolution and incongruence between nuclear and plastid phylogenies are known in many groups of plants (e.g., Morgan et al. 2009) and a more comprehensive explanation that might underlie the results of Allen et al. requires further study. Meanwhile, two genera of Doellingeriinae are justifiably recognized, each distinct and consistent in morphology and distantly separated from the other in geography.

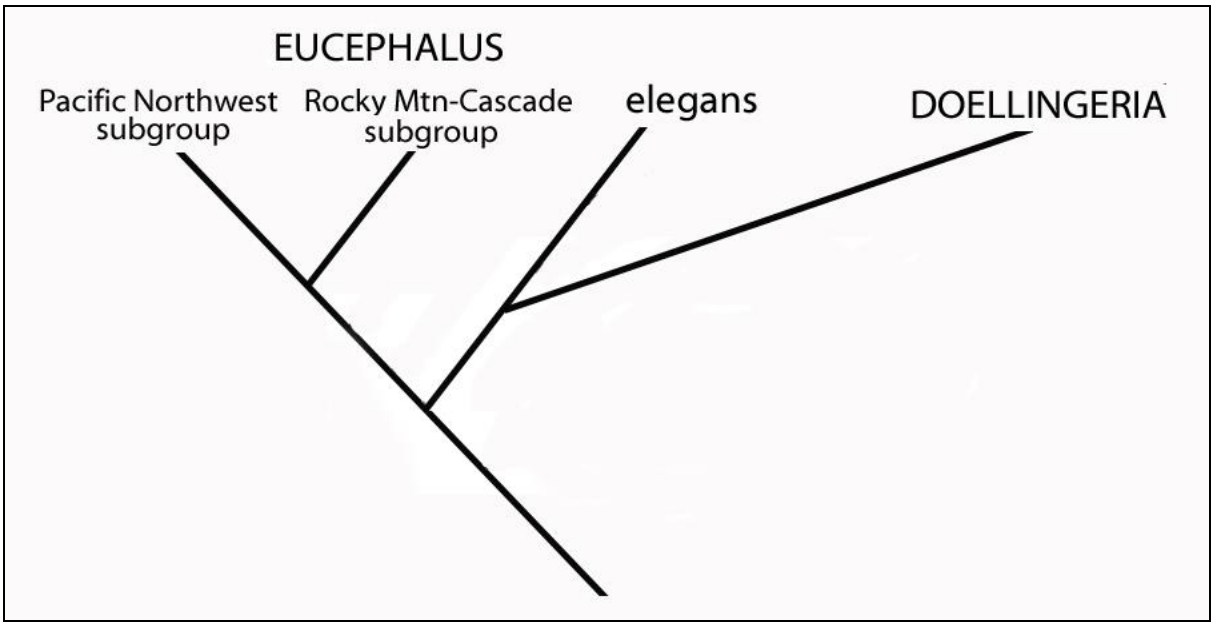

Figure 1. Cladistic relationships among *Doellingeria* and groups of *Eucephalus*, as inferred from nuclear sequence data of Allen et al. (2019).

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