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TAXONOMY OF *DOELLINGERIA* (ASTERACEAE: ASTEREAE)

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ABSTRACT

Doellingeria has most recently been treated within *Aster*, but it is here regarded as a distinct genus comprising eleven species. The five species of sect. *Doellingeria* are divided between eastern Asia (two species) and eastern North America (three species), while the six species of sect. *Cordifolium* are restricted to eastern Asia. The genus is hypothesized to be as closely related to *Solidago* and its relatives as to *Aster*.

KEY WORDS: *Doellingeria*, *Aster*, Astereae, Asteraceae

The genus *Doellingeria* was established by Nees (1832) and recognized by him as a group divided between North America and Asia. DeCandolle (1836) accepted *Doellingeria* as a distinct genus but restricted it to Asian species, inexplicably relegating the type (*D. umbellata* [Mill.] Nees) and other North American species to the genus *Diplostephium* Kunth. *Doellingeria* was accepted for a period during the 19th century, until Bentham (in Bentham & Hooker 1873) included it within a greatly expanded, heterogeneous *Aster*. Asa Gray maintained *Doellingeria* as a distinct genus in various treatments but finally submerged it within *Aster* in his *Synoptical Flora* (1884), deciding to adopt Bentham's view. Most North American botanists subsequently have subscribed in some degree to the concept of a conglomerated *Aster* advocated by Bentham and Gray, but some have continued to recognize *Doellingeria* as distinct (*e.g.*, Greene 1896; Rydberg 1917; Small 1933; Correll & Johnston 1970). Two recent studies of *Aster* in a relatively broad perspective (Jones 1980; Semple & Brouillet 1980) retained *Doellingeria* within *Aster*, although their justification for including it was not explicit.

The revisional study of *Aster* subg. *Doellingeria* (Semple *et al.* 1991) clarified the variation patterns of the North American taxa and their corresponding taxonomy, but the Old World taxa were not considered. Following an early judgment by Asa Gray (1884), recent treatments by Jones (1980), Semple &

Brouillet (1980), and Semple *et al.* (1983) have included *A. reticulatus* Pursh in subg. *Doellingeria*, but that species is here considered to lie outside the bounds of *Doellingeria* (see comments below).

Some Asian taxonomists have recently recognized the distinctiveness of *Doellingeria* (*e.g.*, Ling *et al.* 1985), but a number of "doellingerioid" Asian species have been retained within *Aster*. Tamamschyan (1959), apparently following DeCandolle, regarded the genus as monotypic, comprising only the Old World *D. scabra* (Thunb.) Nees. In China and Japan, where the greatest number of *Doellingeria* species occur, they have been treated either as *Aster* or *Kalimeris* Cass. (Kitamura 1936, 1937; Ohwi 1965; and literature citations below). Thus, *Doellingeria* as a genus has never been consolidated. The nature of the relationship between the Asian and American species of the genus apparently has only been considered by Bentham (in Bentham & Hooker 1873), who observed a strong relationship between the Asian *D. scabra* and the American *D. infirma* (Michx.) E. Greene.

As interpreted here, the boundaries of *Aster* do not encompass *Doellingeria*, which has ancestry closer to *Solidago* and related genera (comments below). *Doellingeria* comprises eleven species in two main groups: those of sect. *Doellingeria* have lanceolate, entire to serrulate, essentially epetiolate leaves, while those of sect. *Cordifolium* have ovate, coarsely toothed leaves with a distinct, narrowly winged petiole. There is a named hybrid (see below) between species of the two sections. Three species of sect. *Cordifolium* ser. *Cordifolium* have strongly foreshortened pappus and have been treated within the genus *Kalimeris*. Gu (1987, in press) excluded these species from *Kalimeris* but has not suggested an alternate placement for the group.

The five species of sect. *Doellingeria* are divided between eastern Asia and eastern North America, while the six of sect. *Cordifolium* are restricted to eastern Asia. *Doellingeria scabra* (sect. *Cordifolium*) occurs widely in eastern China, Japan, Korea, and northward into the Manchurian region of China and Russia; *D. marchandii* (Levl.) Ling and *D. longipetiolata* (Chang) Nesom (sect. *Cordifolium*) are endemic to southeastern China; and all of the other Old World species are restricted to Japan.

TAXONOMY OF *DOELLINGERIA*

Complete synonymy for the New World species is found in Semple *et al.* (1991); also see comments on nomenclature and typification in Jones (1980) and Reveal (1991).

Doellingeria Nees, *Gen. Sp. Aster.* 177. 1832. (TYPE: *Doellingeria umbellata* [Mill.] Nees).

Perennial, rhizomatous herbs, glabrous to sparsely strigose, eglandular. Leaves elliptic-oblanceolate or oblong-oblanceolate without an evident petiole to ovate-cordate with a long petiole, margins entire to coarsely toothed. Heads solitary on leafy peduncles, borne in a corymboid capitulescence; phyllaries in 2-4 weakly to strongly graduated series, broadly elliptic-oblong to ovate with a blunt or rounded apex, without a distinctly differentiated herbaceous tip, the midvein commonly slightly raised and resinous, often with conspicuous lateral nerves. Disc corollas abruptly broadened at the tube-throat junction, with long, reflexing-coiling lobes. Ray flowers few, the ligules white, not coiling with maturity. Achenes eglandular, otherwise sparsely strigose to glabrous, obovoid with 5-9, raised, broad, sometimes orange-resinous, equally spaced nerves or ribs, the achenes elongating at maturity to 3-4 mm long, nearly the length of the involucral bracts, raising the pappus almost completely above the involucre. Pappus 2-3-seriate, an outer series of setae or slender bristles much shorter than the inner, and much longer bristles in one or two inner series, all elements highly reduced in length in the three species of ser. *Cordifolium*; inner bristles with dilated apices. Chromosome number in all reported species of *Doellingeria*, $n=9$; secondary constriction of NOR chromosome in the middle of the short arm, the "primitive" type among various groups of *Aster* sensu lato according to Semple *et al.* (1983).

Key to the sections of *Doellingeria*

Pappus 3-seriate or 2(-3)-seriate; leaves entire, lanceolate, epetiolate or nearly so; eastern North America and eastern Asia. ..... sect. *Doellingeria*

Pappus 2(-3)-seriate, sometimes prominently reduced in length; leaves coarsely toothed, ovate with relatively long, winged petioles; eastern Asia. ..... sect. *Cordifolium*

A. *Doellingeria* sect. *Doellingeria*

Aster subg. *Doellingeria* (Nees) A. Gray, *Synopt. Fl. N. Amer.* 1(2):196. 1884. *Aster* sect. *Doellingeria* (Nees) Kitamura, J. Jap. Bot. 12:721. 1936.

Diplopappus sect. *Triplopappus* Torr. & Gray, *Fl. N. Amer.* 2:182. 1841. (TYPE: *Aster umbellatus* Mill.). *Aster* subg. *Doellingeria* sect. *Triplopappus* (Torr. & Gray) A.G. Jones, Brittonia 32:237. 1980.

Aster ser. *Sohayakienses* Kitamura, J. Jap. Bot. 12:722. 1936. (TYPE: *Aster sohayakiensis* Koidzumi).

a. *Doellingeria* ser. *Doellingeria*

1. *Doellingeria infirma* (Michx.) E. Greene, Pittonia 3:52. 1896. BASIONYM: *Aster infirmus* Michx., *Fl. Bor.-Amer.* 2:109. 1803.

   Doellingeria humilis (Willd.) Britt., *Britt. & Br. Illus. Fl.* 3:392. 1898.

   Aster cornifolius Muhl. *ex* Willd., *Sp. Pl.* 3:2039. 1803.

   Appalachian Mountains in eastern United States, northern Florida to New York and Massachusetts (see Semple *et al.* 1991, Fig. 16).

2. *Doellingeria sericocarpoides* Small, Bull. Torrey Bot. Club 25:620. 1898. *Aster sericocarpoides* (Small) K. Schum., Just. Bot. Jahresb. 26(1):375. 1900.

   Southeastern to south-central United States, North Carolina to Arkansas, southeastern Oklahoma, and east Texas (see Semple *et al.* 1991, Fig. 15).

3. *Doellingeria umbellata* (Miller) Nees, *Gen. Sp. Aster.* 178. 1832. BASIONYM: *Aster umbellatus* Miller, *Gard. Dict.*, ed. 8, no. 22. 1768.

   Aster amygdalinus Lam., *Encycl. Meth.* 1:305. 1783. *Doellingeria amygdalina* (Lam.) Nees, *Gen. Sp. Aster.* 179. 1832.

   Doellingeria umbellata (Miller) Nees var. *umbellata*

   Northeastern to east-central United States and immediately adjacent Canada (see Semple *et al.* 1991, Fig. 13).

   Doellingeria umbellata (Miller) Nees var. *pubens* (A. Gray) Britt., *Britt. & Br. Illus. Fl.* 3:392. 1898. BASIONYM: *Aster umbellatus* Miller var. *pubens* A. Gray, *Synopt. Fl. N. Amer.* 1(2):197. 1884. *Doellingeria pubens* (A. Gray) Rydb., Bull. Torrey Bot. Club 37:147. 1910. *Doellingeria umbellata* (Miller) Nees subsp. *pubens* (A. Gray) Löve & Löve, Taxon 31:357. 1982.

   Aster pubentior Cronq., Bull. Torrey Bot. Club 74:147. 1947.

   Northeast-central United States and immediately adjacent Canada, completely sympatric with var. *umbellata* (see Semple *et al.* 1991, Figs. 13 and 14).

4. **Doellingeria sohayakiensis** (Koidzumi) Nesom, *comb. nov.* BASIONYM: *Aster sohayakiensis* Koidzumi, Tokyo Bot. Mag. 37:56. 1923.

Japan.

5. **Doellingeria rugulosa** (Maxim.) Nesom, *comb. nov.* BASIONYM: *Aster rugulosus* Maxim., *Mel. Biol.* 7:333. 1870.

Japan.

B. **Doellingeria** sect. **Cordifolium** (Kitamura) Nesom, *comb. nov.* BASIONYM: *Kalimeris* sect. *Cordifolium* Kitamura, Mem. Coll. Sci. Kyoto Univ., ser. B. 8:312. 1937. (LECTOTYPE, designated here: *Biotia japonica* Miq.).

Aster sect. *Teretiachaenium* Kitamura, Mem. Coll. Sci. Kyoto Univ., ser. B. 8:357. 1937. (LECTOTYPE, designated here: *Aster scaber* Thunb.).

b. **Doellingeria** ser. **Cordifolium** (Kitamura) Nesom, *comb. et stat. nov.* BASIONYM: *Kalimeris* sect. *Cordifolium* Kitamura, Mem. Coll. Sci. Kyoto Univ., ser. B. 8:312. 1937. LECTOTYPE: *Doellingeria japonica* (Miq.) Nesom.

6. **Doellingeria japonica** (Miq.) Nesom, *comb. nov.* BASIONYM: *Biotia japonica* Miq., Ann. Mus. Bot. Lugduno-Batavum 2:170. 1866. *Boltonia japonica* (Miq.) Franch. & Sav., *Enum. Pl. Japon.* 1:226. 1875. *Asteromoea japonica* (Miq.) Matsum., *Shokub. Mei-i* ed. 2:41. 1895. *Aster japonicus* (Miq.) Franch. & Sav., *Enum. Pl. Japon.* 2:398. 1876. Not Less. *ex* Nees 1832. *Aster miquelianus* Hara [*nom. nov.*], J. Jap. Bot. 12:338. 1936. *Kalimeris miqueliana* (Hara) Kitamura, Mem. Coll. Sci. Kyoto Univ., ser. B. 8:312. 1937.

Japan.

7. *Doellingeria marchandii* (Levl.) Ling, *Icon. Cormorph. Sin.* 4:423. 1975. BASIONYM: *Aster marchandii* Levl., Fedde Repert. Sp. Nov. 11:306. 1912. *Kalimeris marchandii* (Levl.) Kitamura, Acta Phytotax. Geobot. 33:195. 1982.

Widespread in southeastern China.

8. **Doellingeria longipetiolata** (Chang) Nesom, *comb. nov.* BASIONYM: *Aster longipetiolatus* Chang, Sunyatsenia 6:22. 1941. *Kalimeris longipetiolata* (Chang) Ling, *Fl. Reipubl. Pop. Sin.* 74:108. 1985.

Aster trichanthus Hand.-Mazz., Oesterr. Bot. Zeit. 90:125. 1941.

China, Szechuan province.

c. **Doellingeria** ser. **Papposae** Nesom, *ser. nov.*

Setae pappi longitudine corollas disci aequantes.
TYPE: *Doellingeria scabra* (Thunb.) Nees.

9. *Doellingeria scabra* (Thunb.) Nees, *Gen. Sp. Aster.* 183. 1832. BASIONYM: *Aster scaber* Thunb., *Fl. Jap.* 316. 1784. *Eucephalus scaber* (Thunb.) Gandoger, Bull. Soc. Bot. France 65:40. 1918.

Biotia discolor Maxim., *Prim. Fl. Amur.* 146. 1859.

Widespread in eastern China, to Japan, Korea, and the Manchurian region of China and Russia.

10. **Doellingeria komonoensis** (Makino) Nesom, *comb. nov.* BASIONYM: *Aster komonoensis* Makino, Tokyo Bot. Mag. 12:65. 1898.

Japan.

11. **Doellingeria dimorphophylla** (Franch. & Sav.) Nesom, *comb. nov.* BASIONYM: *Aster dimorphophyllus* Franch. & Sav., *Enum. Pl. Japon.* 1:224. 1875.

Japan.

HYBRIDS:

Doellingeria sekimotoi (Makino) Nesom, *comb. nov.* BASIONYM: *Aster sekimotoi* Makino, J. Jap. Bot. 7:10. 1931. *Aster hashimotoi* Kitamura, Acta Phytotax. Geobot. 3:130. 1934. [*D. rugulosa* (Maxim.) Nesom × *D. scabra* (Thunb.) Nees; see Kitamura 1937, Ohwi 1965]

Japan.

EXCLUDED SPECIES:

1. *Doellingeria reticulata* (Pursh) E. Greene = *Aster reticulatus* Pursh.

2. *Doellingeria obovata* (Nutt.) Nees = *Aster reticulatus* Pursh.

   The alliance of *Aster reticulatus* with *Doellingeria* apparently has been on the basis of its corymboid capitulescence and other habital similarity and its tendency to produce a triseriate pappus. In *A. reticulatus*, however, the peduncles, phyllaries, and sometimes the leaves are glandular, the disc corolla lobes are erect and relatively more shallow, the achenes are fusiform and densely glandular, and the pappus bristles are apically acute. The species is an integral member of the group that includes *A. acuminatus* Michx. and *A. nemoralis* Sol. (Nesom in prep.).

3. *Doellingeria trichocarpa* DC., *Prodr.* 5:263. 1836. =? *Aster striatus* Champ. *ex* Benth. [*Fl. Hongkong.*], Hooker's J. Bot. Kew Gard. Misc. 4:233. 1852.

   Doellingeria trichocarpa was noted in *Index Kewensis* to be a synonym of *Aster striatus* Benth. The rationale for this is not clear, because Bentham (in Bentham & Hooker 1873) apparently accepted both species within the *Doellingeria* group of *Aster*. Judging from their descriptions, however, neither species can be interpreted as *Doellingeria* in the present view. Neither name has been included in *Aster* in relatively recent bibliographic and taxonomic accounts of the Chinese Compositae, but specimens at US originally identified as *A. striatus* have been annotated as *A. panduratus* Walp.

4. *Doellingeria ptarmicoides* Nees = *Oligoneuron album* (Nutt.) Nesom (Nesom 1993).

DEFINITION OF *DOELLINGERIA*

Doellingeria is recognized by its (1) corymboid capitulescence, (2) strongly graduated phyllaries with a blunt or rounded apex, without a distinctly differentiated herbaceous tip, with the midvein commonly raised and resinous, and often with conspicuous lateral nerves, (3) few ray flowers, the ligules not coiling with maturity, or at least coiling very little, (4) large, terete achenes with broad, often resinous ribs, and (5) a 2- or 3-seriate pappus of bristles with

dilated apices. The pappus in *Doellingeria* comprises one or two inner series of long bristles and an outer series of setae or slender bristles much shorter than the inner. The North American species have a consistently triseriate pappus, but within sect. *Doellingeria*, the pappus of the Asian *D. rugulosa* and *D. sohayakiensis* tends to be biseriate. The pappus in sect. *Cordifolium* also is mostly biseriate but the inner series tends to be congested or biseriate; the pappus is strongly reduced in length in ser. *Cordifolium*. The pappus bristles of the inner series in all species of both sections have dilated apices.

Doellingeria dimorphophylla and *D. japonica* differ between themselves primarily in relatively technical features of vestiture and the nature of their pappus. The pappus of the former (ser. *Papposae*) is composed of slender, apically dilated bristles 4-5 mm long in 2(-3) series; the pappus of *D. japonica* (ser. *Cordifolium*) is reduced to broad, flat, barbellate bristles 0.5-1.0 mm long, mostly lanceolate but sometimes with a distinctly clavellate apex. *Doellingeria marchandii* and *D. longipetiolata* have similarly reduced pappus, but the similarity between *D. japonica* and *D. dimorphophylla* in their particularly long stylar collecting appendages, which form 1/2-3/4 the length of the style branches, suggests that reduction of pappus may not be a reliable indicator of relationship among these species.

SUBTRIBAL PLACEMENT OF *DOELLINGERIA*

The phyletic position of *Doellingeria* is here hypothesized to lie near the base of the Solidagininae, near its point of divergence both from an Old World ancestor similar to *Aster* sensu stricto and from one group of New World *Aster* apparently closely related to the Solidagininae (*i.e.*, the "Biotian lineage", Nesom in prep.). The white rays and multiseriate pappus of *Doellingeria* are similar to true *Aster*, but the small number of ray flowers and eglandular, multinerved and more or less terete achenes are characteristic of the Solidagininae. White rays occur in other genera unequivocally placed among yellow-rayed Solidagininae (Nesom 1993) and they are invariably characteristic of the Biotian lineage. Disc corollas with deeply cut, reflexing-coiling lobes and pappus bristles with dilated apices occur in basal, yellow-rayed elements of the Solidagininae as well as the Biotian lineage. Correspondingly, the distinctive phyllaries of *Doellingeria* markedly resemble those of *Solidago* L., *Oligoneuron* Small, and the small group of species that has been treated as *Aster* sect. *Biotia* (DC.) Torr. & Gray (*e.g.*, Jones 1980).

Doellingeria was not included in the overview of the subtribe Solidagininae (Nesom 1993), but its morphology as well as its occurrence in eastern North America, with other primitive members of that subtribe, also suggest that the phyletic position of *Doellingeria* is in the same area. Although the radiation of the Solidagininae was primarily in North America, one of its most primitive

members (*Solidago*) has a distribution disjunct between North America and Asia. An analogous disjunction is hypothesized to occur between the southeast Asian endemic genus *Nannoglottis* Maxim., which also appears to be a primitive member of the Solidagininae, and the closely related, monotypic genus *Oreochrysum* Nutt. of the western United States (Nesom in prep.).

Jones & Young (1983, Figs. 4 and 5) placed *Doellingeria* as the sister group to the Eurasian genera *Galatella* DC. and *Crinitaria* Cass. (=*Linosyris* Cass.), but the latter two have glandular, flattened, primarily 2-ribbed, and obovate achenes and are more closely related to typical *Aster*. Plants of *Galatella* and *Crinitaria* also have a strong tendency to produce glandular-punctate leaves.

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