ERIGERON PEREGRINUS AND *ERIGERON GLACIALIS* (ASTERACEAE: ASTEREAE)

Guy L. Nesom

Botanical Research Institute of Texas
509 Pecan Street
Fort Worth, Texas 76102-4060, U.S.A.
gnesom@brit.org

ABSTRACT

Erigeron glacialis (Nutt.) A. Nels. (= *E. callianthemus* Greene) is recognized as a species separate from *E. peregrinus* (Banks ex Pursh) Greene. It has most recently been treated as *E. peregrinus* subsp. *callianthemus*. Intermediates between *E. glacialis* and *E. peregrinus* do occur but the two species are mostly distinct even where in close contact in Washington and British Columbia; intermediates are uncommon or absent as *E. glacialis* at the western edge of its range is contiguous or perhaps intermittently sympatric with *E. peregrinus* northward into Alaska. **Erigeron glacialis** var. **hirsutus** (Cronq.) Nesom, comb. nov., is proposed in order to complete the alternate taxonomy. If Cronquist's recognition of two subspecies within *E. peregrinus* is to be followed, the name *E. peregrinus* subsp. *callianthemus* (1943) is incorrect, the precedent for a name at that rank set by *E. salsuginosus* subsp. *angustifolius* (1906).

RESUMEN

Erigeron glacialis (Nutt.) A. Nels. (= *E. callianthemus* Greene) se reconoce como una especie diferente de *E. peregrinus* (Banks ex Pursh) Greene. Ha sido tratada recientemente como *E. peregrinus* subsp. *callianthemus*. Se encuentran intermedios entre *E. glacialis* y *E. peregrinus* pero las dos especies son muy distintas incluso cuando están en contacto en Washington y en Columbia Británica; los intermedios son raros o ausentes ya que *E. glacialis* en el límite Oeste de su área vive contiguo o quizás intermitentemente simpátrico con *E. peregrinus* hacia el Norte hasta Alaska. Se propone **Erigeron glacialis** var. **hirsutus** (Cronq.) Nesom, comb. nov., para completar la taxonomía alternativa. Si se sigue el reconocimiento de Cronquist de dos subespecies en *E. peregrinus*, el nombre *E. peregrinus* subsp. *callianthemus* (1943) es incorrecto, el precedente de un nombre en ese rango está establecido por *E. salsuginosus* subsp. *angustifolius* (1906).

A taxon previously known as *Erigeron salsuginosus* (Richards. ex R. Br.) A. Gray was united by Cronquist (1943) at subspecific rank with *E. peregrinus* (Banks ex Pursh) Greene. Cronquist observed that *Erigeron* (*Aster*) *glacialis* (Nutt.) A. Nels. is the oldest name at specific rank to replace the misapplied *E. salsuginosus* but that the type of *E. callianthemus* Greene is more representative of the taxon, thus he used the latter for the name at subspecific rank (see nomenclatural summary below). He later (1947) recognized several varieties within each subspecies.

Erigeron peregrinus subsp. *callianthemus* is widely distributed in the mountains of the western U.S.A. and southwestern Canada, while *E. peregrinus* subsp. *peregrinus* occurs in coastal and near coastal habitats from southern Alaska to the northwestern conterminous U.S.A. Their ranges are largely dis-

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tinct (Fig. 1) but the occurrence of intermediates in Washington and British Columbia suggested to Cronquist (1947) that the two taxa were best treated within a single species, a taxonomic arrangement that has since been followed in accounts of North American *Erigeron*. Douglas et al. (1998, p. 252) also noted that the subspecies "intergrade" where ranges overlap. My observation, in contrast, is that intermediates do occur but that even where they overlap or are in close contact in Washington and British Columbia, populations of 'good' subsp. *peregrinus* (without signs of intermediacy) and 'good' subsp. *callianthemus* are more common.

The distribution of subsp. *peregrinus* runs from the Kamchatka area of the Russian Far East (Commander Islands: Botschantzev 1959; Czerepanov 1995) across the Aleutian Islands, southern-central Alaska, southwestern Yukon, and southward along the Alaskan-British Columbian archipelago into western Washington and northwest Oregon (Fig. 1; more detailed maps in Hultén 1950, 1968; Cody 2000). From the Yukon region, it trails southward in a relatively thin line along the Pacific; as noted by Douglas et al. (1998), it is "common in and west of the Coast-Cascade Mountains, rare east of the Coast-Cascade Mountains." Calder and Taylor (1968, p. 533) observed that in the Queen Charlotte Islands "a few collections [of subsp. *peregrinus* sensu stricto] show a tendency towards ssp. *callianthemus* as the involucral bracts are not conspicuously villous and tend to be slightly glandular."

Subspecies *callianthemus* is widely distributed and relatively abundant in montane regions throughout the western U.S.A. as well as in southwestern Alberta and British Columbia. At the western edge of its range from British Columbia northward into Alaska, it is contiguous and perhaps intermittently sympatric with subsp. *peregrinus*. Subsp. *callianthemus* is absent from the Queen Charlotte Islands (Calder & Taylor 1968) and absent or rare in other insular portions of the Alaskan-British Columbian archipelago. It is rare in southwestern Yukon and southeastern Alaska, apparently growing within the range of subsp. *peregrinus*. Scoggan (1979) recorded subsp. *peregrinus* for Alberta, but this probably is based on plants such as *Breitung 16978* (BRIT) from Waterton Lakes National Park, which have phyllaries stipitate-glandular and also sparsely villosulous on the proximal half, "determined by A. Cronquist" as *E. peregrinus* subsp. *callianthemus* var. *scaposus*. Typical subsp. *callianthemus* is the common form in the same region.

In the U.S.A., subsp. *peregrinus* occurs in Whatcom, Skagit, Snohomish, King, and Pacific counties, Washington, and Clatsop Co., Oregon. *Erigeron peregrinus* var. *thompsonii* occurs in Grays Harbor Co., Washington. Typical subsp. *callianthemus* is known from Whatcom, Snohomish, and King counties, and it also occurs in Clallam and Jefferson counties of the Olympic peninsula, Washington, immediately north of Grays Harbor Co. In Oregon, it occurs in Tillamook Co., immediately south of Clatsop Co.

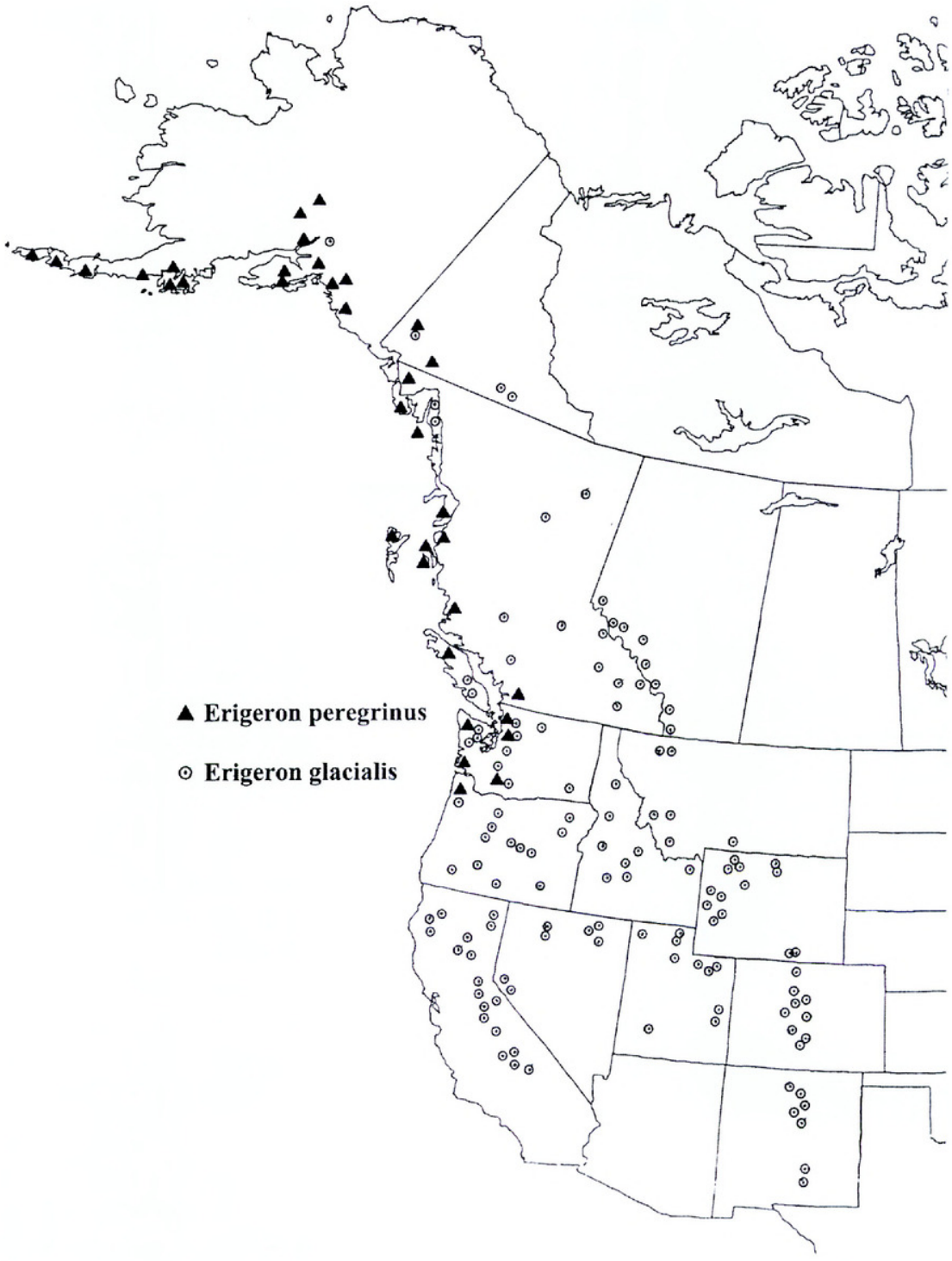

FIG. 1. Summary distribution of *Erigeron peregrinus* and *E. glacialis*. The distribution of *E. peregrinus* continues westward along the Aleutian Islands and into the Kamchatka region.

In the view here, subsp. *peregrinus* and subsp. *callianthemus* are reasonably treated as separate species, *E. peregrinus* and *E. glacialis*, apparently occasionally hybridizing but not intergrading in a sense that would imply the existence of a zone of intermediacy reflecting continuous gene exchange. The two species can be identified by the following morphological contrasts.

Phyllaries eglandular or sparsely sessile-glandular at the apices, rarely sparsely glandular over the surface, sparsely to moderately villous-hirsute on surfaces, margins usually ciliate _____ **Erigeron peregrinus**

Phyllaries densely and evenly stipitate-glandular, without other hairs or rarely sparsely villous on surfaces and margins of outer phyllaries _____ **Erigeron glacialis**

Cronquist (1955) noted other distinctions of *E. peregrinus* (vs. *E. glacialis*): leaves often toothed (vs. usually entire), often soft-pubescent (vs. usually glabrous), peduncular hairs rather loose (vs. close), but these are less diagnostic.

Choice of specific over infraspecific rank in this case emphasizes three factors:

(1) Reproductive isolation, although incomplete, apparently exists between *E. glacialis* and *E. peregrinus*, as noted above.

(2) The distinction between *E. glacialis* and *E. peregrinus* is analogous to that between other closely related species of *Erigeron*, where relatively small but consistent and conspicuous differences in vestiture are significant (e.g., *E. compactus-E. consimilis*; *E. ursinus-E. gracilis*; *E. caespitosus-E. abajoensis*; *E. tracyi* (*E. colomexicanus*)-*E. flagellaris*; *E. engelmannii-E. pumilus*; and *E. flettii-E. algidus-E. simplex/grandiflorus*).

(3) *Erigeron glacialis* may be as closely related to *E. howellii* (A. Gray) A. Gray as to *E. peregrinus*. These three species form a morphological unit and apparently are more closely related among themselves than to any other species. *Erigeron howellii*, which is essentially endemic to an area along the Columbia River in Oregon and Washington, differs from *E. glacialis* in its distally strigillose but otherwise glabrous stems (vs. stems strigillose, more densely so distally), more consistently spatulate basal and lower cauline leaves (vs. leaves linear-oblanceolate to broadly lanceolate or spatulate), consistently white rays (vs. rays blue to rose-purple or pink, less commonly white to pale blue), and habitats mostly at lower elevation. *Erigeron howellii* and *E. glacialis* are nearly identical in involucral vestiture, and a reasonable hypothesis is that the narrow endemic and *E. glacialis* are sister species. This is not intended as a "cladistic argument" for recognition of *E. glacialis* at specific rank, and it is clear that *E. glacialis* is more strongly differerentiated from *E. howellii* than from *E. peregrinus*, but it adds a line of evidence for consideration in this admittedly subjective decision concerning choice of rank.

Erigeron peregrinus (Banks ex Pursh) Greene, Pittonia 3:166. 1897. *Aster peregrinus* Banks ex Pursh, Fl. Amer. Septent. 2:556. 1814. TYPE: U.S.A. ALASKA. Unalaschka, *D. Nelson s.n.* (HOLOTYPE: BM).

Phyllaries moderately to densely hirsute to villous-hirsute on the surfaces, margins ciliate; ray corollas purplish to pink or white; upland habitats _____ **Erigeron peregrinus** var. **peregrinus**

Phyllaries very sparsely villous-hirsute to glabrous on the surfaces, margins ciliate; ray corollas white; sphagnum bogs _____ **Erigeron peregrinus** var. **thompsonii**

Erigeron peregrinus (Banks ex Pursh) Greene var. **peregrinus**

Erigeron unalaschkensis Less., Linnaea 6:122. 1831.
Erigeron peregrinus (Banks ex Pursh) Greene var. *dawsonii* Greene, Pittonia 3:166. 1897.

Erigeron peregrinus var. *dawsonii* was described from the Queen Charlotte Islands, where var. *peregrinus* is abundant. Calder and Taylor (1968) did not recognize var. *dawsonii*, noting that populational variants include plants of both varieties and numerous intermediates.

Cronquist (1955, p. 188) noted that "A phase of ssp. *peregrinus*, resembling var. *peregrinus* but perhaps properly to be segregated, occurs on Saddle Mt. in Clatsop Co., Oreg." Chambers (pers. comm.) observes that these plants "combine the genetic traits of *glacialis* and *peregrinus*," with villous hairs most abundant on the outer phyllaries, dense glandular indument on the inner phyllaries. They are perhaps "best interpreted as derived from a history of gene exchange between *E. peregrinus* and *E. glacialis*, along with segregation and recombination of the genes affecting the principal morphological differences in pubescence. 'Good' *peregrinus* has not yet been found in this part of the state, but 'good' *glacialis* is present nearby."

Erigeron peregrinus (Banks ex Pursh) Greene var. **thompsonii** (Blake ex J.W. Thompson) Cronquist, Brittonia 6:144. 1947. *Erigeron thompsonii* Blake ex J.W. Thompson, Rhodora 34:238. 1932. TYPE: U.S.A. WASHINGTON. GRAYS HARBOR CO.: open bog near Lake Quinault, 10 Jul 1931, *J.W. Thompson 7336* (HOLOTYPE: US!; ISOTYPES: GH!, K, MO!, UC). From details and wording of the protologue and description, it seems clear that Blake wrote both; he was not credited by Thompson, however, other than being cited as sole author of the name and the authorhip must be attributed to Thompson as "ex" rather than "in."

Cronquist (1947, p. 148) observed that var. *thompsonii* "is in a sense intermediate between [*E. glacialis* and *E. peregrinus*] and intergrades both ways." The taxonomic status and evolutionary relationships of this taxon, which is endemic to a small area of the Olympic peninsula in western Washington, need to be investigated in more detail.

Erigeron glacialis (Nutt.) A. Nels., Bot. Gaz. 37:270. 1904. *Aster glacialis* Nutt., Trans. Amer. Philos. Soc. n. ser. 7:291. 1840. *Erigeron salsuginosus* (Richards. ex R. Br.) A. Gray var. *glacialis* (Nutt.) A. Gray, Synopt. Fl. N. Amer. 1, pt. 2:209. 1884. TYPE: U.S.A. Nuttall's protologue observed that the habitat of *A. glacialis* was "with the preceding" species, *Aster andinus* Nutt. [=*Symphyotrichum spathulatum* (Lindl.) Nesom], which was noted to have been collected "on the highest summits of the Rocky Mountains, near the line of perpetual snow, in 42°. About ten thousand feet above the level of the sea. Near summit of Thornberg's Ridge, where we made an ineffectual attempt to cross the Northern Andes, in August, still deeply buried in snow." Gray saw the specimen—"Nutt.!" as indicated in Torrey and Gray (1841, p. 155) and later

noted (1884, p. 209) "first coll. by Nuttall in Wyoming." According to Graustein (1967), it is likely that Nuttall's group was on or near Hyndman Peak (Blaine Co., Idaho), at the place they called Thornberg's Ridge or Thornberg's Pass on 12–13 Aug 1834, this confirmed by the expedition narrative reproduced in McKelvey (1955). (HOLOTYPE: PH; HOLOTYPE fragment: CAS).

Stems densely strigillose with loosely appressed, slightly crinkled hairs, most densely strigillose close beneath the heads; leaves glabrous to short-villous on both surfaces
_____ **Erigeron glacialis** var. **glacialis**

Stems hirsute to hirsute-villous; leaves hirsute to hirsute-villous on both surfaces
_____ **Erigeron glacialis** var. **hirsutus**

Erigeron glacialis (Nutt.) A. Nels. var. **glacialis**

Erigeron callianthemus Greene, Leafl. Bot. Observ. Crit. 2:197. 1912. *Erigeron peregrinus* (Banks ex Pursh) Greene subsp. *callianthemus* (Greene) Cronq., Rhodora 45:264. 1943. *Erigeron peregrinus* (Banks ex Pursh) Greene var. *eucallianthemus* Cronq., Brittonia 6:145. 1947. *Erigeron peregrinus* (Banks ex Pursh) Greene var. *callianthemus* (Greene) Cronq., Univ. Wash. Publ. Biol. 17(5):188. 1955 (in clave).

Aster salsuginosus Richards. ex R. Br. var. *angustifolius* A. Gray, Bot. Calif. 1:325. 1876. *Erigeron salsuginosus* (Richards. ex R. Br.) A. Gray var. *angustifolius* (A. Gray) A. Gray, Proc. Amer. Acad. Arts 16:93. 1880. *Erigeron angustifolius* (A. Gray) Rydb., Bull. Torrey Bot. Club 24:295. 1897. *Erigeron salsuginosus* (Richards. ex R. Br.) A. Gray subsp. *angustifolius* (A. Gray) Piper, Contr. U.S. Natl. Herb. 11:565. 1906. *Erigeron peregrinus* (Banks ex Pursh) Greene var. *angustifolius* (A. Gray) Cronq., Brittonia 6:147. 1947.

Aster salsuginosus Richards. ex R. Br. var. *scaposus* Torr. & A. Gray, Fl. N. Amer. 2:503. 1841. *Erigeron peregrinus* (Banks ex Pursh) Greene var. *scaposus* (Torr. & A. Gray) Cronq., Brittonia 6: 146. 1947. *Erigeron callianthemus* Greene var. *scaposus* (Torr. & A. Gray) Breitung, Canad. Field-Naturalist 71:69. 1957.

As earlier observed (Nesom 1992, p. 190), within *Erigeron peregrinus* subsp. *callianthemus*, var. *scaposus* and var. *angustifolius* can be recognized apart from var. *callianthemus* "only as arbitrarily distinguished and intergrading populations." Douglas et al. (1998) also noted that the varieties "often grow together and show a continuous variation." Cronquist (1947, p. 148) regarded var. *scaposus* as a "reduced alpine phase" with the dwarfing "probably genetically controlled," but he observed that it "intergrades profusely with var. *eucallianthemus* ... and both are often present in the same collection." Var. *angustifolius*, also, was seen by Cronquist to be strongly intergrading with other expressions of the species.

If *Erigeron glacialis* is maintained at infraspecific rank within *E. peregrinus*, the taxon *E. peregrinus* subsp. *callianthemus* (sensu Cronquist) includes all varietal taxa, but if the widespread entity identified by Cronquist as *E. peregrinus* var. *callianthemus* is interpreted to include either var. *scaposus* or var. *angustifolius* or both, it should be recognized that both latter names at varietal rank have precedence over var. *callianthemus* (var. *scaposus* the oldest). If any of these varieties are to be recognized within *E. glacialis*, the type of *E. glacialis* represents the alpine form treated as var. *scaposus*. In the taxonomic alternative proposed here, all three of these taxa are included within *Erigeron glacialis* var. *glacialis*.

Further complicating the nomenclature is the observation that the earliest name at subspecific rank in this whole complex is *Erigeron salsuginosus* subsp. *angustifolius* (A. Gray) Piper, from 1915, rendering Cronquist's combination in 1943 based on *E. callianthemus* incorrect (superfluous, because it included the type of "subsp. *angustifolius*"). Thus, if one desires to follow Cronquist's concept of recognizing two subspecies within *E. peregrinus*, the one he treated as "subsp. *callianthemus*" requires a new combination, based on Gray's original *Aster salsuginosus* var. *angustifolius*.

Erigeron glacialis (Nutt.) A. Nels. var. **hirsutus** (Cronq.) Nesom, comb. nov. *Erigeron peregrinus* (Banks ex Pursh) Greene var. *hirsutus* Cronq., Brittonia 6:147. 1947. TYPE: U.S.A. CALIFORNIA. [TUOLUMNE CO.]: Yosemite National Park, vicinity of Lake Tenaya, 8300 ft, Jun 1902, *H.M. Hall and E.C. Babcock 3506B* (HOLOTYPE: UC).

Variety *hirsutus* is restricted to the seven southernmost counties in the range of the species in California (Fresno, Inyo, Madera, Mariposa, Mono, Tulare, and Tuolumne cos.) and in Mineral Co., Nevada. I also have seen plants of typical *E. glacialis* and intergrades toward var. *hirsutus* from Mono, Tulare, Fresno, and Inyo cos., but they apparently are less common than those identified as typical var. *hirsutus*.

ACKNOWLEDGMENTS

I thank Bob Kiger for pointing out that *Erigeron peregrinus* var. *callianthus* is not the correct name when it includes var. *scaposus* and var. *angustifolius* (as I have used it in the past). His comments precipitated the presentation of this taxonomic alternative, which I have anticipated for more than a decade. Ken Chambers further pointed out that the name *E. peregrinus* subsp. *callianthemus* is incorrect, as it was preceded at that rank by "subsp. *angustifolius*." Ron Hartman gave advice on geography of the *E. glacialis* type collection, Kanchi Gandhi reviewed aspects of the nomenclature, James Macklin provided information on the type collection at PH, and Ken Chambers reviewed the whole manuscript and arranged a loan of pertinent specimens from OSU. Review comments by David Murray also were very helpful.

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