CALIFORNIA, A NEW GENUS OF GERANIACEAE ENDEMIC TO THE SOUTHWEST OF NORTH AMERICA

by

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Resumen


Los datos morfológicos permiten distinguir, a nivel de género, Erodium macrophyllum Hook. & Arn. de las especies incluidas en Erodium y Monsonia (Geraniaceae). También los datos obtenidos de la secuencia de ADN cloroplásico (trnL-F) apoyan estas diferencias. Por lo tanto, proponemos un nuevo género monotípico, California Aldas., C. Navarro, P. Vargas, Ll. Sáez & Aedo, para que queden mejor reflejadas las relaciones filogenéticas en la clasificación de las Geraniaceae. Incluimos una diagnosis, ilustraciones, análisis comparativos de los caracteres diferenciales y una clave de géneros de Geraniaceae. Se propone una nueva combinación: California macrophylla (Hook. & Arn.) Aldas., C. Navarro, P. Vargas, Ll. Sáez & Aedo, comb. nov. [basion.: Erodium macrophyllum Hook. & Arn.]; y se designan dos lectótipos.

Palabras clave: taxonomía, morfología, Geraniaceae, Erodium, Monsonia, nuevo género, Norteamérica.

Abstract


Morphological data provide evidence for the separation of Erodium macrophyllum Hook. & Arn. in a new genus, different from either Erodium and Monsonia (Geraniaceae). Also cpDNA sequence data (trnL-F) support this view. Thus, we propose the recognition of a new monotypic genus, California Aldas., C. Navarro, P. Vargas, Ll. Sáez & Aedo, to better reflect phylogenetic relationships in Geraniaceae. We provide diagnosis, illustrations, comparative analysis of distinctive characters, and a key to genera of Geraniaceae. The new combination proposed is: California macrophylla (Hook. & Arn.) Aldas., C. Navarro, P. Vargas, Ll. Sáez & Aedo, comb. nov. [basion.: Erodium macrophyllum Hook. & Arn.]; and two lectotypes are designed.

Key words: taxonomy, morphology, Geraniaceae, Erodium, Monsonia, new genus, North America.

INTRODUCTION

Geraniaceae is a world-wide family comprising five genera: Erodium L'Her. ex Aiton, Geranium L., Monsonia L., Sarcocaulon (DC.) Sweet and Pelargonium L'Her. ex Aiton (HUTCHINSON, 1969; KNUTH, 1912). They have pentamorous flowers consisting
of five sepals; five petals; five antipetalous nectaries (Monsonia, Sarcocaulon, Erodium and Geranium), but only one nectary in Pelargonium; androecia with a variable number of stamens (15 in Monsonia and Sarcocaulon, 10 in Geranium, 2-7 in Pelargonium and 5 in Erodium), and consistently a gynoecium with 5 carpels in all genera (Hutchinson, 1969; Knuth, 1912). Staminodes are only present in two genera: 5 in Erodium and a variable number in Pelargonium, from 3 to 8 (Struck & Van der Walt, 1996). Most Geraniaceae studies have emphasized the importance of the androecium in family classifications, because it displays the main reliable characters (Knuth, 1912).

**Generic delimitation in the Geraniaceae**

Generic delimitation of Erodium has never seriously been questioned after it was segregated from Geranium as originally circumscribed by Linnaeus (Aiton, 1789; L'Heritier, 1792). The major difference between Erodium and Geranium is the fertile stamen number, ten forming two whorls in Geranium and five in a whorl plus a second whorl of five staminodes in Erodium. In both cases, stamens and staminodes are free. However, an exception is Geranium pusillum L., which lacks one whorl of fertile stamens (Aedo & al., 1998). The other Geraniaceae genera (Monsonia and Sarcocaulon) have a whorl of 15 stamens fused in the base (monadelphous) or fused in five groups of three (pentadelphous), whereas Pelargonium has 2-7 monadelphous stamens. An exception is also found in Monsonia brevirostrata Knuth, which has only five fertile stamens (Aldasoro & al., 2001). The androecium structure of Erodium could be related to that of Geranium due to a likely substitution of a whorl of fertile stamens by staminodes.

The protologue of Erodium macrophyllum Hook. & Arn. is somewhat misleading, not allowing one to know the number of sterile and fertile stamens: "This is a true Erodium, having the five sterile stamens in the flower..." (Hooker & Arnott, 1838). Surprisingly, Erodium macrophyllum Hook. & Arn. has no staminodes, but has a quite distinctive staminal structure: the filaments have a widely dilated basal portion with two lateral wing-like expansions apically rounded or almost auriculate (fig. 1c, d). The normal narrow apical part being aparently insert in the upper third of this basal structure (fig. 1d). This peculiar staminal filament has a certain resemblance to each of the five groups of stamens of M. brevirostrata (Aldasoro & al., 2001).

Characters from leaves and fruits are much more variable within the Geraniaceae and usually not used to recognize different genera, but they serve to distinguish infrageneric taxa. Some of them also support the segregation of E. macrophyllum from Erodium. On the surface of Erodium mericarps there are stout bristles which may serve to facilitate burying, adherence and dispersal (fig. 1e; figs. 2A-D). At the base, Erodium species have a nearly semicircular rim surrounding each bristle, which is formed by fusion of papillae (fig. 2D). It serves to prevent the bristle from returning and avoid unburying (El-Oqlah, 1989; Aldasoro & al., 2001). The only Erodium without these rims is E. macrophyllum (fig. 2C). In the Geraniaceae, similar rims are only found in some species of Monsonia (Aldasoro & al., 2001). The mericarp apex of many species of Erodium has two pits which are frequently filled by glands. These pits are in most Erodium obliquely situated with respect to the awn (fig. 2B), whereas they are almost perpendicularly disposed in E. macrophyllum (fig. 1e; fig. 2A). Monsonia has also these two types of pits (oblique and perpendicularly placed) depending on the species (Aldasoro & al., 2001).

Finally, E. macrophyllum leaves are also distinctive. They are rounded, with a cordate base and subpalmate veins (fig. 1a, b), while all other species of Erodium have subpinnate or pinnate veins. Monsonia has both subpalmate (or palmate) and pinnate veins, depending on the species.

As discussed above, E. macrophyllum features resemble in some cases Erodium, in
Fig. 1.—California macrophylla: a, habit; b, basal leaf; c, open flower showing androecium and gynoecium; d, stamen; e, fruit and mericarp; f, mericarp (based on Heller 7831 P). [a, b by L.I. Sáez; c-f by J. Castillo].
Fig. 2.–SEM micrographs of mericarps of *California* and *Erodium*: A, *C. macrophylla* mericarp apex (b. bristles; p. pit) (based on Heller 7831 P); B, *E. laciniatum* mericarp apex (based on Rigual s.n., MA 371870); C, *C. macrophylla* bristle base; D, *E. atlanticum* bristles base (based on Ball s.n., COI).
others Monsonia. This, together with a unique androecium type (figs. 1c, d), leads us to segregate it in a different genus, especially taking into account the androecium, the most reliable diagnostic character in Geraniaceae taxonomy (Knuth, 1912; Yeo, 1990).

Moreover, a preliminary phylogeny of Geraniaceae using trnL-F sequences from representatives of the five genera plus E. macrophyllum allow us to hypothesize a relatively distant relationship between this species and Erodium. The two most-parsimonious trees resolve E. macrophyllum as sister to Erodium, even with low bootstrap support (< 50 %), and indicate an ancient divergence between them.

**Key to Geraniaceae Genera**

(see below for exceptions)

1. Androecium of 15 stamens ....................... 2
   - Androecium of 2-10 stamens ....................... 3
2. Plants succulent; stems covered with waxy cuticle; longest petioles persisting as spines ........................................................... Sarcocaulon
   - Plants usually not succulent; stems not covered with waxy cuticle; longest petioles not persisting as spines ........................................................... Monsonia
3. Flowers with only a nectary which is deeply embedded into the receptacle (rarely without nectary), generally zygomorphous; 2-7 monadelphous stamens ...................................... Pelargonium
   - Flowers with five nectaries not deeply embedded into the receptacle, actinomorphic or slightly zygomorphous; 5 or 10 free stamens ...................... 4
4. Flowers with 10 fertile stamens .......... Geranium
   - Flowers with 5 fertile stamens ..................... 5
5. Flowers with a whorl of 5 staminodes placed between the stamens; mericarps with a semicircular rim surrounding each bristle base ......................................................... Erodium
   - Flowers without staminodes; mericarps without a semicircular rim surrounding each bristle base ............................................................... California

Some exceptions for Geranium (G. pusillum), Monsonia (M. brevirostrata), Pelargonium (P. incarnatum) have not been included in the above key. Preliminary phylogenies suggest that G. pusillum androecium (5 stamens) is a derivative state from 10 stamens in Geranium sect. Batrachioidea W.D.J. Koch (Aedo & al., 1998); the androecium of M. brevirostrata (5 stamens) is a result of reduction of stamen number (Aldasoro & al., 2001). As far as we know, there is no information on the phylogenetic position of Pelargonium incarnatum.

**California** Aldas., C. Navarro, P. Vargas, Ll. Sáez & Aedo, gen. nov.

Typus: California macrophylla (Hook. & Arn.) Aldas. & al. [Erodium macrophyllum Hook. & Arn.]

Differt ab affini gen. Erodium staminodiis nullis, uninucuusque foveola versus aristam perpendiculariter disposita et mericarpiorum pilis bursicula basali carentibus.

Novum genus, ut patet, nomen trahit e terris ubi habitat.

This genus is similar to Erodium, from which can be distinguished by the androecium, lack of staminodes, mericarp pit perpendicularly disposed with respect to the awn, bristle rims absent and leaves subpalmately veined.

We choose this generic epithet to honour a Floristic Province of America named California, where this genus occurs.

**California macrophylla** (Hook. & Arn.) Aldas., C. Navarro, P. Vargas, Ll. Sáez & Aedo, comb. nov.


Ind. loc.: “California, Mr. Douglas”

Typus: USA. California, 1834, Douglas s.n. (lectotype, here designated, BM!; isolecotype, GH)

Erodium californicum Greene, Fl. Francisc.: 99 (1891); Erodium macrophyllum var. californicum (Greene) Jeps., Fl. W. Calif.: 247 (1901)

Ind. loc.: “Berkeley Hills and eastward in the Mt. Diablo Range”

Typus: USA. California, Berkeley Hills, 3 Apr. 1887, Greene s.n. (lectotype, here designated, NDG 28051; seeing colour slide!)
Annual or biennial plant, shortly caulescent or nearly acaule. Roots short, slightly ramified. Stems 10-40 cm long, ascending, hairy, with eglandular hairs 0.3-0.5 mm long and glandular hairs 0.4-0.6 mm long, all nearly patent or retrorse, the glandular producing a reddish secretion. Leaves long petiolate, rounded or cordate, crenate-dentate, shallowly lobed (rarely deeply lobed), with eglandular hairs 0.3-0.5 mm long and glandular hairs 0.5-0.6 mm long; sub-palmately nerved, with 1-2 pairs of secondary nerves; basal leaves 11-43 × 10-44 mm (ratio leaf width/leaf length : 0.9-1.1); cauline leaves 10-33 × 8-32 mm; stipules 3-4.1 mm long, oval-lanceolate, not membranous, hairy, with glandular hairs 0.4-0.6 mm long along the margin and on the abaxial side. Inflorescence 1-5 flowered, with peduncles arising from the rootstock; bracts 2-5, 3.2-5 × 1.3-1.6 mm, free, acuminate, with a narrow scarious margin, with eglandular hairs 0.2-0.3 mm long on the abaxial side, glabrous adaxially; pedicels hairy, with eglandular hairs c. 0.2 mm long and glandular hairs 0.3-0.6 mm long. Flowers actinomorphic, hermaphrodite. Sepals 5-7.1 × 2.3-3.2 mm, awned, adnate (11-14 × 4.3-5.6 mm in fruit), awn 0.8-1.5 mm long (0.9-1.3 long in fruit); abaxial side with crowded eglandular hairs 0.2-0.3 mm long and glandular hairs 0.5-0.6 mm long. Petals 6.2-8 × 2-3.2 mm, all similar, pink or white. Stamen 5; filament 2.5-3.5 mm long, with a glabrous, slender, free part (1.6-1.8 × 0.4-0.7 mm) inserted on the upper third of a dilatate basal portion with two lateral appendage-like wings; the basal portion 2.3-2.6 × 1.3-1.4 mm, with the two lateral wings apically auriculate, sparsely ciliate; anthers 0.8-0.9 mm long; pollen 35-50 m in diam., reticulate, lumen of cells 3-5 m in diam.; without supractetal processes, tricolpate, yellow; staminodes absent. Nectaries 5, 0.4-0.5 × 0.5-0.6 mm, oval to rounded in transversal and longitudinal sections, adnate to the base of staminal filament, color unknown. Gynoecium 4.8-5.6 mm long, densely hairy, with long glandular hairs; stigmas 0.8-1 mm long. Fruit a schizocarp 44-54 mm in length; columella stout; awns not plumose (with short hairs in the upper part); mericarp length 9-12 mm (20-25 % of fruit length); mericarp surface without papillae, with crowded bristles of variable size, without basal rims; apical pit present, perpendicularly situated respect the awn, without ridges or furrows beside, with small glands inside, which are also in the start of awn. Seed 1 per mericarp, 5-5.5 × 1.2-1.4 mm, with elliptic longitudinal section; hilum length 2.2-4.4 mm (40-46 % of the seed length). Cotyledon leaves ovate in outline, with a cordate base.

**Chromosome number.** Unknown.

**Illustrations.** TRELEASE (1888, pl. 10 fig. 12); fig. 1.

**Phenology.** Collected in flower from March to the beginning of June.

**Vernacular names.** Large-leaved Filaree (THOMAS, 1961)

**Distribution.** South Oregon and California (USA), and Baja California (Mexico); also reported from Arizona and S Utah (TAYLOR, 1993: 672); fig. 3.

**Habitat.** Open habitat on friable clay soils; 50-1200 m.

**Representative specimens examined**

Fig. 3.—Distribution of *California macrophylla* based on examined specimens.


MEXICO. BAJA CALIFORNIA: 20 m SW of Tia Juana, near Rancho Cuevas, 32°5'N, 116°50'W, 3-IV-1931, Wiggins 5123, CAS. Arroyo de la Escopeta, 30°42'N, 115°49'W, 3-VI-1975, Moran 22375, CAS.

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