

***ERIGERON FLORIBUNDUS* AND *E. SUMATRENSIS* (ASTERACEAE)
IN THE USA AND MEXICO**

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ABSTRACT

Erigeron sumatrensis Retz. is widely naturalized both in California and the southeastern USA (Texas, Louisiana, Mississippi, Alabama, Florida, Georgia, and South Carolina) as well as in southern Mexico. *Erigeron floribundus* (Kunth) Sch. Bip. is naturalized in California and Mexico. County-level maps (USA) are provided for the geographic range of both species, which are compared with the more widespread *E. bonariensis* by a key and illustrations. The three species also are mapped for Mexico. A formal nomenclatural summary provides typification and synonymy; a lectotype is designated for *Conyza bilbaoana* Remy (synonym of *E. floribundus*) and for *Erigeron linifolius* Willd. (synonym of *E. bonariensis*).

The South American native and worldwide weed *Erigeron bonariensis* L. (= *Conyza bonariensis* (L.) Cronq.) has become established in the USA from coast to coast. Two other conyzoid non-native species also have colonized California — *E. floribundus* (Kunth) Sch. Bip. and *E. sumatrensis* Retz. (Maps 1 and 2) — but their identifications have been inconsistent. The first inclusion of either species in a major California floristic treatment apparently was in Munz (1959), where it was identified as *Conyza floribunda*. Keil (1993) reported both species, identifying them as *C. floribunda* and *C. bilbaoana* Remy, but subsequent versions of the Jepson Manual (Keil & Nesom 2012, 2017) have identified only *Erigeron sumatrensis* Retz., with *E. floribundus* as a synonym, *C. bilbaoana* as misapplied). Strother (FNANM 2006) recorded only *E. floribundus* (as *Conyza*) for California (with *C. bilbaoana* as a synonym).

A naturalized population of *Erigeron sumatrensis* was documented for southeast Texas (Singhurst & Holmes 2013, as *Conyza floribunda*), but its occurrence in the southeastern USA has been mostly unnoticed. Early floras for the Southeast (e.g., Mohr 1901; Lowe 1921) included only *E. bonariensis* (as *Leptilon linifolium* (Willd.) Heller). Small's treatment (1933) of *Leptilon* included *L. linifolium* ("Waste-places, Coastal Plain, Fla. to Miss. and S.C.") and *L. bonariense* ("Waste-places, Fla."), which heretofore has seemed peculiar, but in the context of the present paper, it seems that Small probably used the name *Leptilon bonariense* to identify *E. sumatrensis* — perhaps referring to an early Curtis collection from Pensacola (see Collections examined). Duncan and Kartesz (1981) included *Conyza bonariensis* along with *C. floribunda* in a checklist of Georgia plants. Strother's inclusion of *Conyza floribunda* for Florida (2006, FNANM) referred to the Curtis collection from Pensacola (J. Strother, pers. comm.) identified and cited here as *E. sumatrensis*.

Erigeron sumatrensis clearly does occur in states east of Texas (Map 3) and study of existing collections probably will show it to be more widespread than documented here. Like *E. bonariensis*, it has become a world-wide weed. Good photos and other references are provided by Verloove (2018).

These three species also occur in Mexico (Maps 4, 5, and 6), although their distributions there are not continuous with those in the USA. Apparently in contrast to the USA, *Erigeron bonariensis* is the least common of the three — it is characteristic of urban habitats, particularly big cities.

Identification

Plants of *Erigeron floribundus* are immediately distinct in their glabrous to glabrate phyllaries, often chestnut brown in color and reduced vestiture of the stems and leaves. The capitulescence is broadly paniculate. In *E. canadensis* var. *pusillus* (Nutt.) Boivin, which also has glabrous phyllaries, the heads are smaller, phyllaries narrower, and the pistillate florets are distinctly ligulate.

Erigeron floribundus and *E. sumatrensis* both produce broadly columnar panicles, but those of *E. floribundus* usually are broader with fewer and more widely arranged heads and the leaves are less densely arranged.

1. Phyllaries glabrous to subglabrous, hyaline margins slightly wavy, sometimes shallowly lacerate; stems sparsely strigose, often with minute hairs, to nearly glabrous; leaf subglabrous to sparsely short-strigose **Erigeron floribundus**

1. Phyllaries loosely strigose, hyaline margins not wavy or lacerate; stems coarsely hirsute-strigose to hirsute-villous or villous; leaf surfaces densely and evenly hirsute **Erigeron sumatrensis**

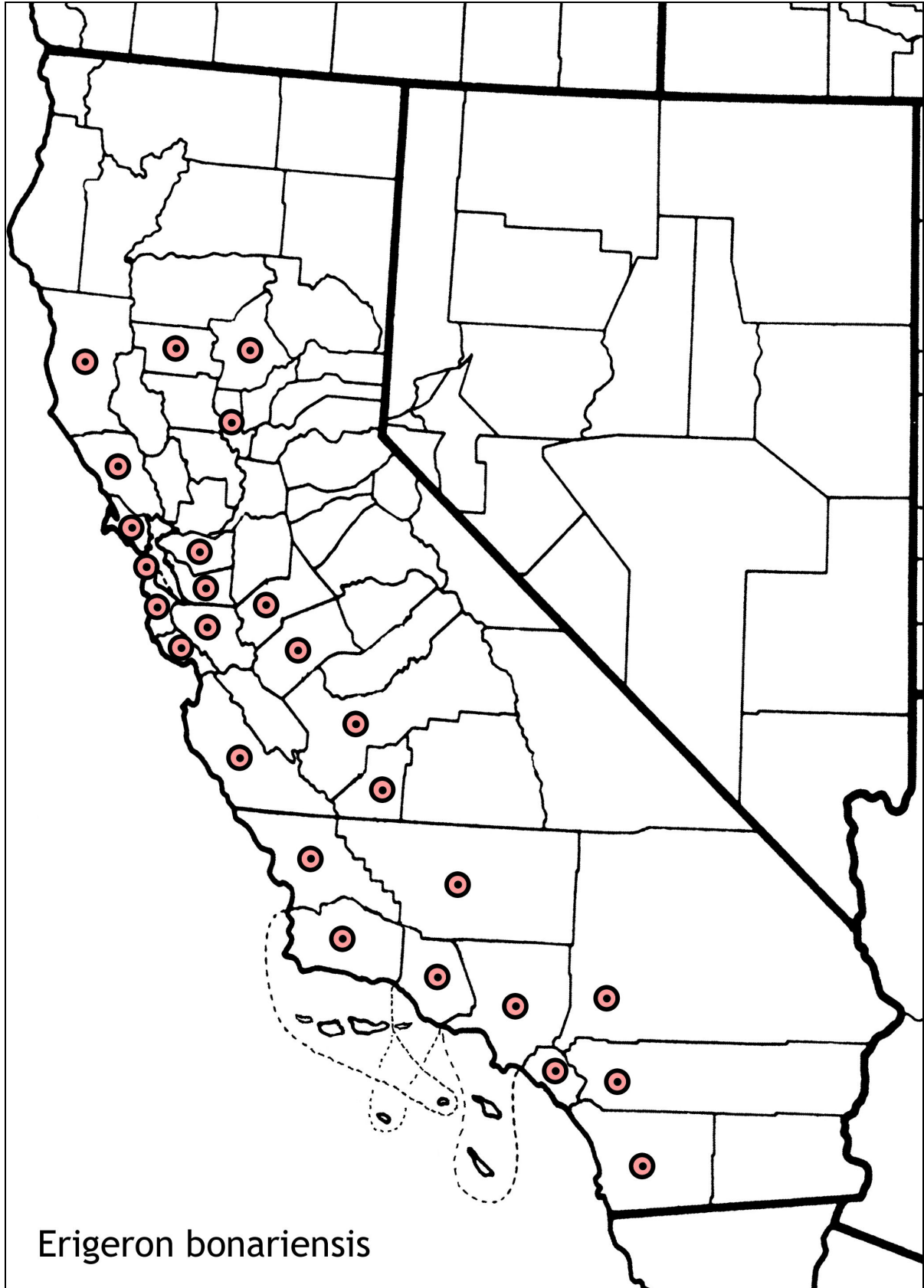
The difference between *Erigeron bonariensis* and *E. sumatrensis* is more problematic, especially since many collections of *E. sumatrensis* have been identified as *E. bonariensis*. Plants of *E. sumatrensis* often reach a meter tall and produce a broadly paniculate-thyrsoid capitulescence with more numerous heads. The heads are characteristically smaller (width of fruiting receptacles an indication) with pistillate florets fewer in number, phyllaries are flatter and thinner, strigose with thin-based hairs, and with a broad yellow-brown midportion, and the receptacles are shallowly alveolate (usually distinctly so but not always).

Plants of *Erigeron bonariensis* characteristically produce linear, closely ascending cauline leaves and the heads usually are mostly produced distally. With a greater number of florets and quickly accrescent pappus, the heads characteristically appear distinctly larger.

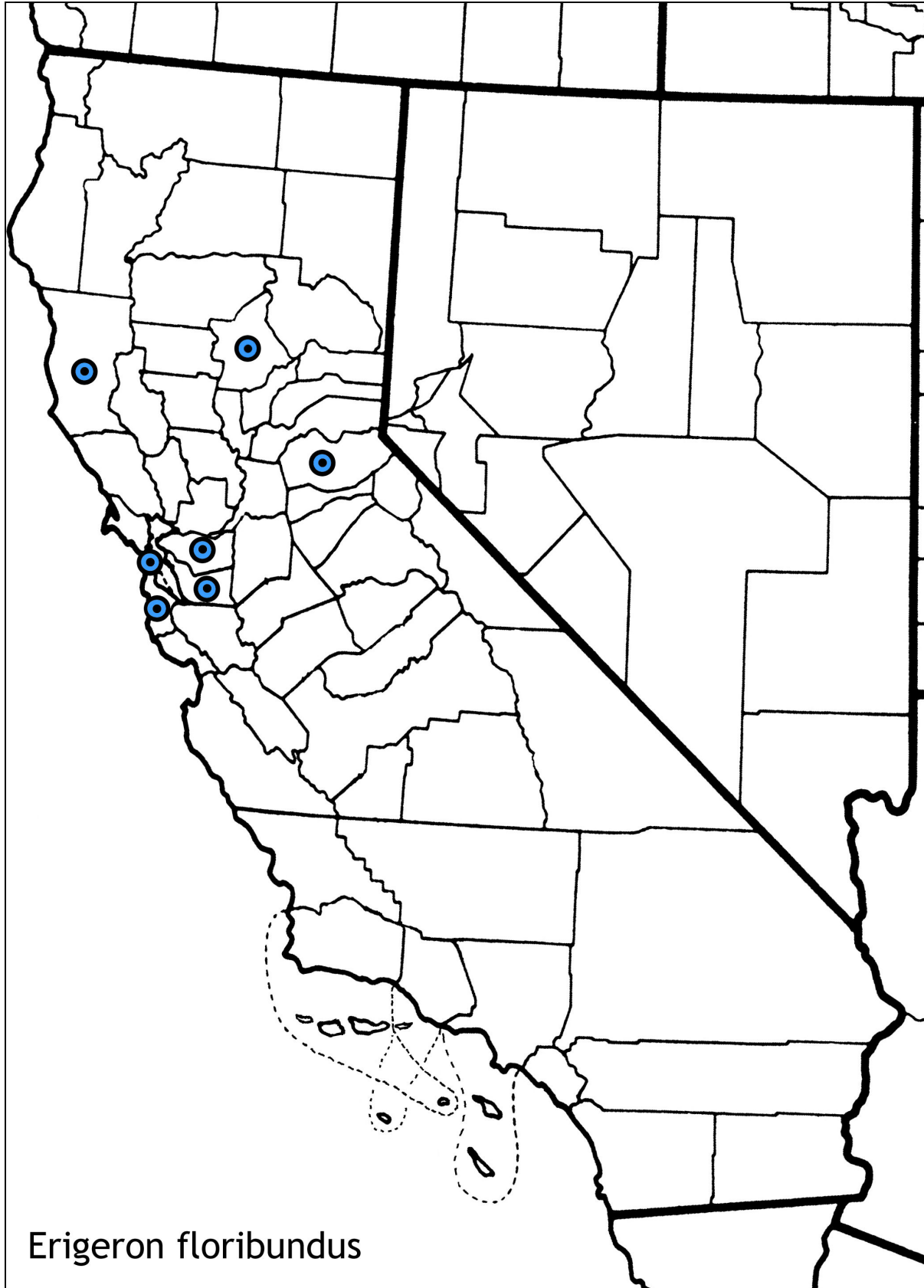
1. Cauline leaves characteristically linear to linear-ob lanceolate; capitulescence corymbiform to racemiform, less commonly thyrsoid-paniculate; fruiting receptacles (2-)2.5-4(-5) mm wide, not alveolate or sometimes the innermost 2-4 floret sockets barely so; phyllaries linear to linear-lanceolate, relatively thick and opaque, 0.3-0.5 mm wide, green to greenish brown with a narrow, orange-resinous midvein, hispid-hirsute to strigose-hirsute with thick-based hairs, inner often purple-tipped, inserted on a ring of fused tissue; pistillate florets ca. 40-150, in (2-)3-6 series **Erigeron bonariensis**

1. Cauline leaves characteristically narrowly lanceolate-elliptic to lanceolate or oblanceolate; capitulescence usually thyrsoid-paniculate; fruiting receptacles 1.5-2.5 mm wide, weakly but distinctly alveolate (lens), outer to inner florets; phyllaries triangular to narrowly ovate, relatively thin and translucent, 0.5-0.8 mm wide, central part yellow-brown with an inconspicuous midvein, loosely strigose with thin-based hairs, never purple-tipped, inserted at apex of peduncle; pistillate florets ca. 20-50, in 2-3 series **Erigeron sumatrensis**

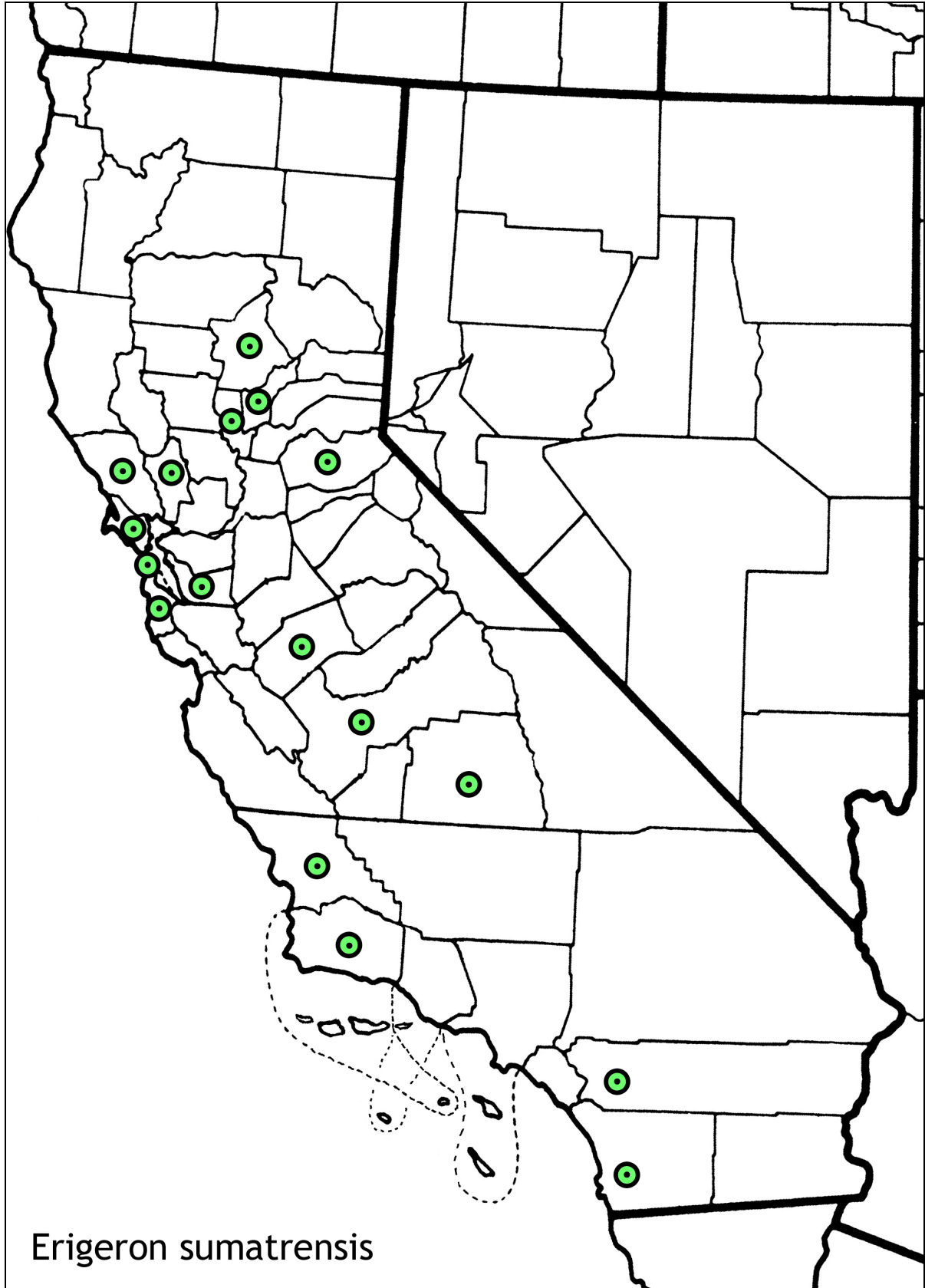
Representative habits, capitulescence forms, and involucre morphology for the three species are shown in Figures 1-4. A tentative guess at identification usually is possible with just a glance at the habit — with study of more technical features, identifications usually can be made with good confidence.



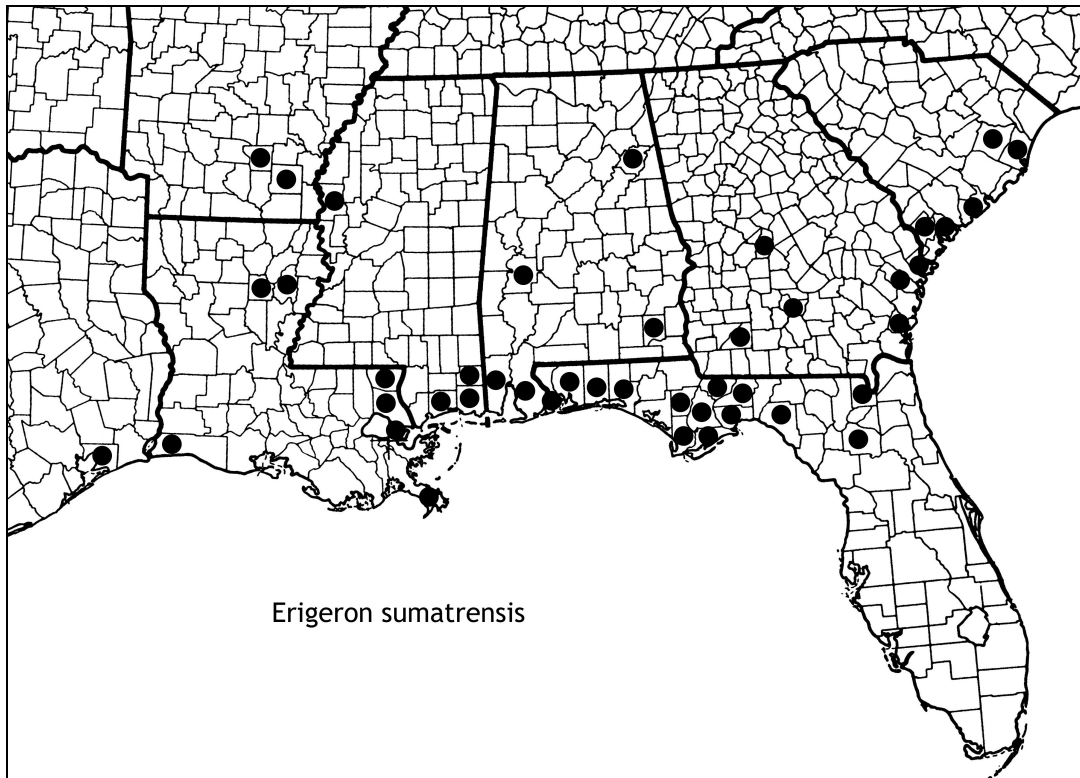
Map 1. Distribution of *Erigeron bonariensis* in California. Records from CAS-DS and UC-JEPS.



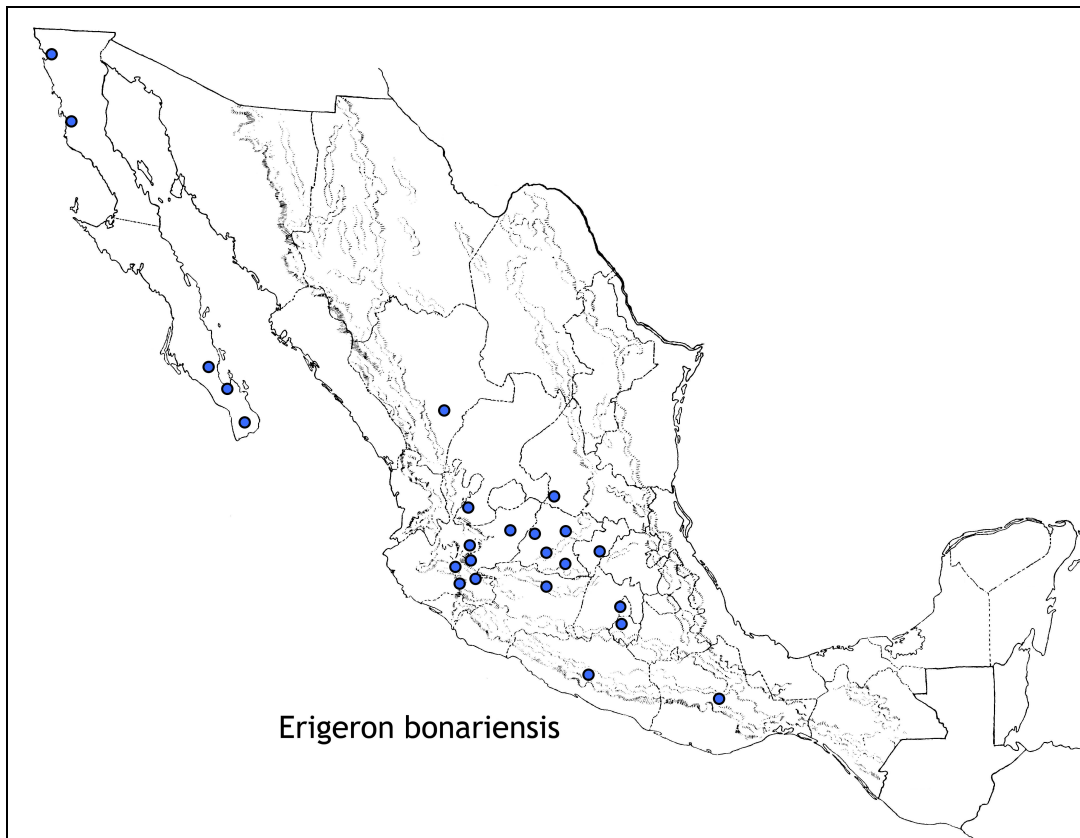
Map 2. Distribution of *Erigeron floribundus* in California. Records from CAS-DS and UC-JEPS.



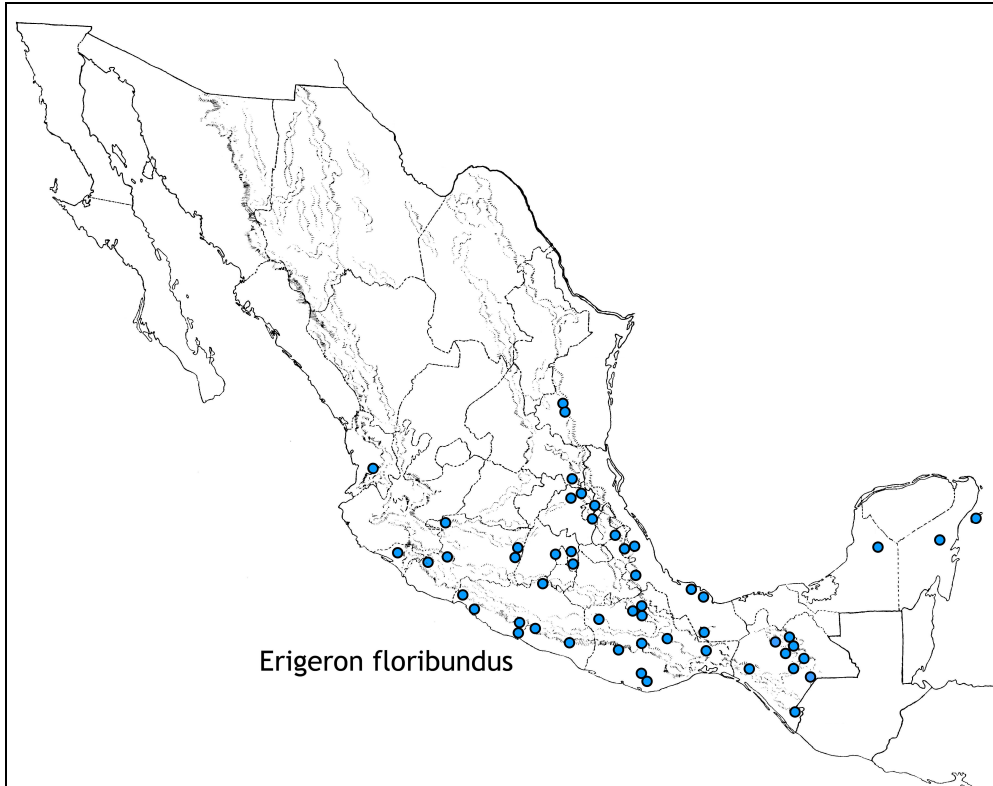
Map 3. Distribution of *Erigeron sumatrensis* in California. Records from CAS-DS and UC-JEPS.



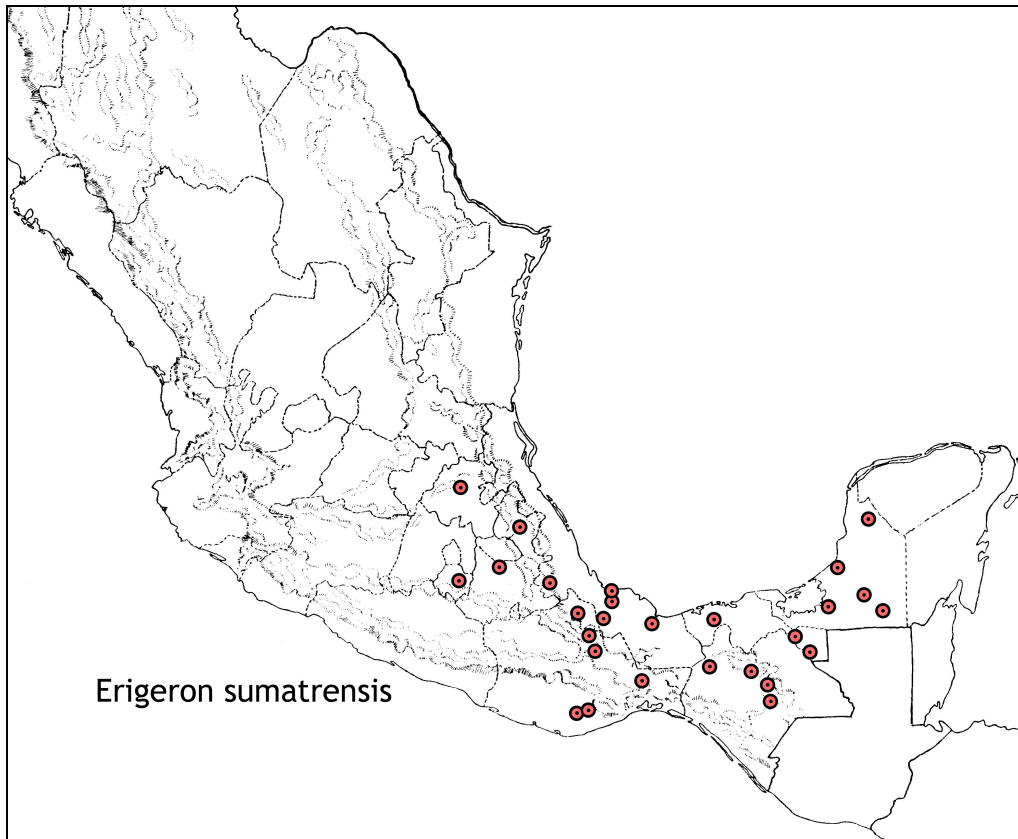
Map 4. Distribution of *Erigeron sumatrensis* in the southeastern USA. Vouchers cited in text.



Map 5. Distribution of *Erigeron bonariensis* in Mexico. Records from various herbaria.



Map. 6. Distribution of *Erigeron floribundus* in Mexico. Records from various herbaria.



Map. 7. Distribution of *Erigeron sumatrensis* in Mexico. Records from various herbaria.



Figure 1. Characteristic habit and capitulescence of *Erigeron bonariensis*.



Figure 2. Characteristic habit and capitulescence of *Erigeron floribundus*.



Figure 3. Characteristic habit and capitulescence of *Erigeron sumatrensis*.

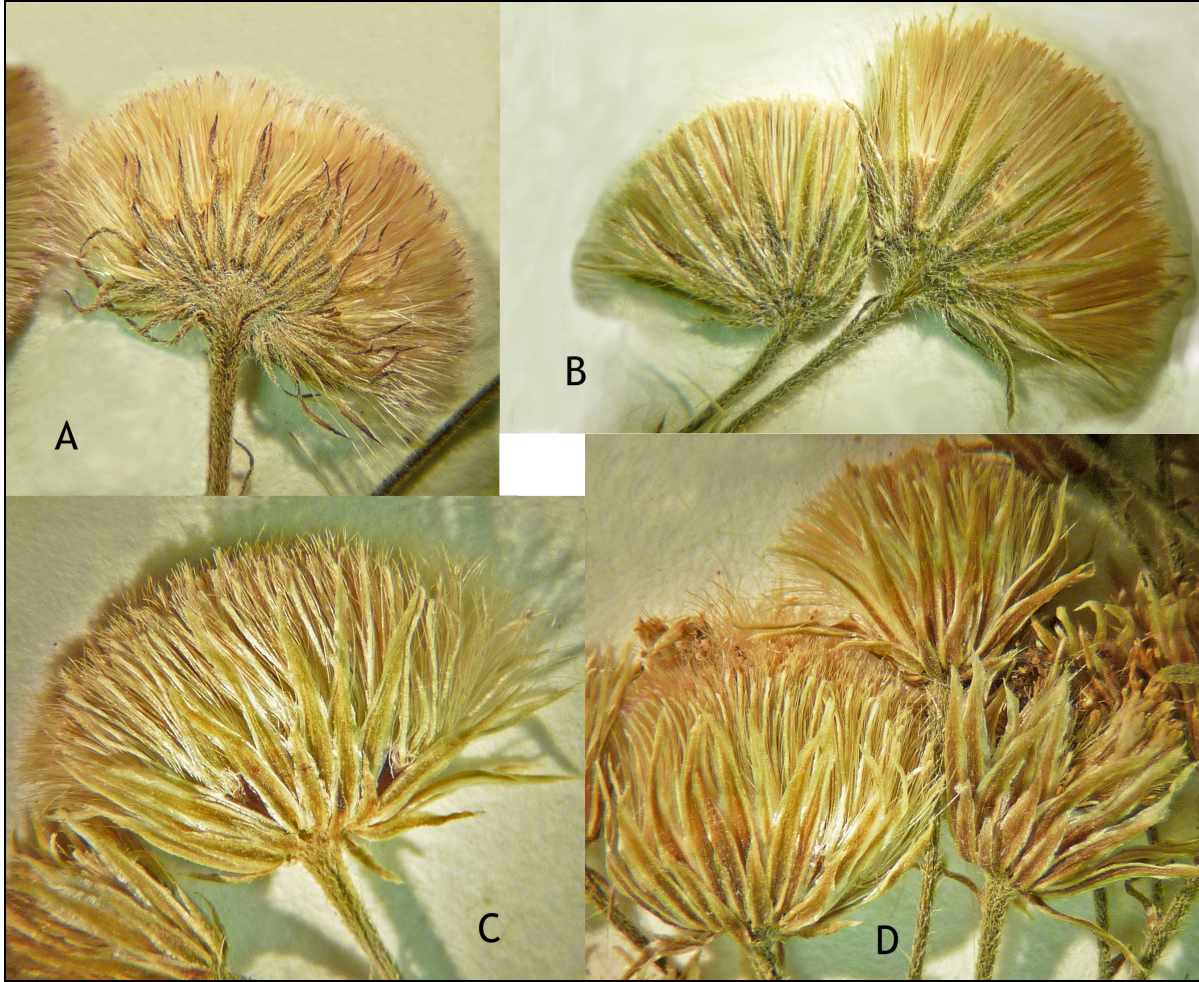


Figure 4. Characteristic involucre. A. *Erigeron bonariensis*. B. *Erigeron sumatrensis*. C, D. *Erigeron floribundus*.

1. **Erigeron bonariensis** L., Sp. Pl. 2: 863. 1753. *Leptilon bonariense* (L.) Small, Fl. S.E. U.S., 1340. 1903. *Conyza bonariensis* (L.) Cronq., Bull. Torrey Bot. Club. 70: 632. 1943. **LECTOTYPE** (D'Arcy 1975, p. 1021): "Habitat in America australi." (LINN 994.11 image!).

Erigeron undulatus Moench, Methodus (Moench) 598. 1794 [nom. illeg., *Erigeron bonariense* L. cited as synonym].

Erigeron crispus Pourret, Hist. & Mém. Acad. Roy. Sci. Toulouse 3: 318. 1788. *Conyza crista* (Pourr.) Rupr., Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg 14: 235. 1856. **TYPE: FRANCE.** "Frequens circa narbon et monspelim," 1779, P.A. Pourret s.n. (holotype: MPU image!). **Protologue:** "Dans les champs, aux environs de Narbonne & de Montpellier."

This sheet was annotated in 2013 by Danièle Domeyne as *Conyza bonariensis* (L.) Cronq.

Erigeron linifolius Willd., Sp. Pl. 3(3): 1955. 1803. *Conyzella linifolia* (Willd.) Greene, Fl. Francisc. 4: 386. 1897. *Leptilon linifolium* (Willd.) Small, Fl. S.E. U.S., 1340. 1903. *Conyza linifolia* (Willd.) Täckh., Stud. Fl. Egypt, 53. 1956 (nom. illeg., not *Conyza linifolia* L., 1753). **LECTOTYPE** (designated here): South America ("Habitat in America australi"), no data on the sheet (B-W 15685-03 image!; <http://herbarium.bgbm.org/object/BW15685030>).

There are 6 sheets of *Erigeron 'linifolium'* at B-W (Willdenow folder 15685, images!). The first 4 clearly are *Erigeron bonariensis* as identified here and are marked with Willdenow's "W." Sheets 5 and 6, "ex Mus. Paris," have relatively broad cauline leaves and are likely to be *Conyza apurensis* Kunth (*Erigeron laevigata* Rich. \equiv *Conyza laevigata* (Rich.) Pruski) or some other species.

Conyza rufescens Hoffmanns. & Link, Fl. Portug. [Hoffmannsegg] 2: 253. [1820-1834]. **TYPE:** **SPAIN.** Protologue: "Fréquent aux environs de Lisbonne le long des chemins et dans les champs incultes. Été" (not seen). *Erigeron bonariensis*, from the description.

Erigeron bonariensis var. *angustifolius* Cabr., Revista Mus. La Plata, Secc. Bot. 4: 88, fig. 24. 1941. *Conyza bonariensis* var. *angustifolia* (Cabr.) Cabr., Man. Fl. Alred. Buenos Aires, 481. 1953. **TYPE: ARGENTINA. Chaco.** Colonia Benítez, Feb 1932, A.G. Schulz 217 (holotype: presumably LP, not seen - cited as in Cabrera's herbarium). Figure 24 is diagnostic.

Erigeron bonariensis is widespread in the USA, including California, sympatric with *E. floribundus* and *E. sumatrensis*. It is mapped here for Mexico and California but not the rest of the USA. (Washington, Oregon, Idaho, Nevada, Utah, Arizona, New Mexico, Texas, Louisiana, Arkansas, Mississippi, Alabama, Georgia, Florida, South Carolina, North Carolina). Because of its confusion with *E. sumatrensis*, collections previously identified as *E. bonariensis* need to be reexamined for an accurate geographic assessment.

2. **Erigeron sumatrensis** Retz., Observ. Bot. 5: 28. 1789[1788]. *Conyza sumatrensis* (Retz.) E. Walker, J. Jap. Bot. 46: 72. 1971. **NEOTYPE** (McClintock & Marshall 1988, p. 172): **INDONESIA. Sumatra.** Berastagi, Feb 1921, H.N. Ridley s.n. (K image!). McClintock and Marshall (p. 172) noted that "there is no type or other specimen of Retzius' to check the application of the name ... [thus] ... we here designate a neotype."

Conyza ambigua DC., Fl. Franç. (ed. 3) 6: 468. 1815. *Erigeron ambiguus* (DC.) Sch. Bip., Hist. Nat. Îles Canaries 3(2): 208. 1836[1845] [non *Erigeron ambiguus* Nutt. 1818]. **TYPE:** **FRANCE.** "Cette plante a été trouvée aux environs de Nismes et de Montpellier, dans les prairies artificiels." The handwritten label says only "Montpellier," A.P. de Candolle s.n. (holotype: P image!).

Conyza ambigua has sometimes been considered a synonym of *E. bonariensis*, but the relatively reduced vestiture, elongate inflorescence (though immature), small heads, and characteristic phyllaries place it with *E. sumatrensis*.

Conyza erigeroides DC., Prodr. 5: 378. 1836. **TYPE: BRAZIL.** Bahia, Apr 1831, J. Lhotsky s.n. (holotype: G-DC 00452596 image!). Protologue: "In Brasilia circa Bahiam."

Conyza naudinii Bonnet, Bull. Soc. Bot. France 25: 208. 1878. *Erigeron crispus* subsp. *naudinii* (Bonnet) Bonnier, Fl. Illus. France 5: 72. 1922. *Erigeron naudinii* (Bonnet) Humbert, Fl. Madagasc. 189: 264. 1960. **TYPE: FRANCE.** Collioure, in Naudin's personal garden, Aug 1877, C.V. Naudin s.n. (possible holotype: MPU 024005 image!). Protologue: "Floret idibus augustis. Patria ignota. Planta, habitu *C. floribundae* H.B.K. sed longe diversa, in horto Caucolliberitano cl. Naudin, cui hanc eximiam speciem dicatam volui, sponte derepenteque enata et ibi per aliquot annos culta, nunc circa urbem, sua sponte, frequens recrescit."

Of 2 sheets at MPU, one (MPU 024005) has a handwritten label as "Conyza naudini Hort. M — H.M. aout 1877." Both collections were annotated in 2013 by Danièle Domeyne as *Erigeron sumatrensis* Retz. Naudin lived in Collioure, about 80 miles south of Montpellier, from 1865 to 1879 and maintained a garden there (Marza & Cerchez 1967).

Conyza gracilis Hoffmanns. & Link, Fl. Portug. [Hoffmannsegg] 2: 254. [1820-1834]. **TYPE:** **SPAIN**. Protologue: "Aux environs de Lisbonne avec la *Conyse roussatre* mais plus rare, Été. (not seen). *Erigeron sumatrensis*, from the description.

Conyza altissima Naudin ex Debeaux, Bull. Soc. Agr. Sci. Lit. Pyr.-Orien. 23: 151. 1878. **TYPE:** **FRANCE**. Collioure, in Naudin's personal garden, Aug 1877, *C.V. Naudin s.n.* (possible holotype: MPU 024005 image!). Apparently the same type as for *Conyza naudinii* Bonnet (see Guédès & Jovet 1975). Protologue: "Les vignes et les cultures de M. Naudin à Collioure, où cette plante se propage spontanément, ainsi que dans les vignes avoisinantes. ... Le *Conyza altissima* s'est montré tout-à-coup et en abondance dans les cultures de M. Naudin, il y a quelques années."

Conyza x flahaultiana Sennen, Bol. Soc. Aragonesa Ci. Nat. 4: 319. 1905. **TYPE:** **SPAIN**. Catalogne. Vilarnadal et Cabanas [Barcelone added in pencil], champs, Oct-Nov 1905-1906, *F. Sennen 164* (possible type material: DAO image!).

Described (in the protologue) as a hybrid, *Erigeron canadense* x *Conyza ambigua*, and so indicated on the specimen label.

Conyza x daveauana Sennen, Bol. Soc. Aragonesa Ci. Nat. 11: 194. 1912. *Erigeron daveauanus* (Sennen) Greuter, Willdenowia 37: 142. 2007. **TYPE MATERIAL:** Protologue: "Catalogne: Le Perthus; environs de Barcelone par les premières pentes du Tibidado." **ISOSYNTYPE** (fide annotation by Danièle Domeyne, 2013): **SPAIN**. Le Perthus (ferr. espagn.) lieux rag[ur], 1 Oct 1904, *Fre. Sennen s.n.* (MPU image!).

Described (in the protologue) as a hybrid, *Conyza naudinii* x *Conyza ambigua*, and so indicated on the specimen label. See comments by Verloove (2018).

Erigeron bonariensis var. *microcephalus* Cabr., Revista Mus. La Plata, Secc. Bot. 4: 88, fig. 23. 1941. *Conyza bonariensis* var. *microcephala* (Cabr.) Cabr., Man. Fl. Alred. Buenos Aires, 481. 1953. **TYPE MATERIAL:** **ARGENTINA**. Buenos Aires. Sierra de la Ventana, vertiente, 22 Apr 1939, *A.L. Cabrera 5160* (syntypes: LP, LPD, Cabrera's personal herbarium -- as cited by Cabrera; none seen). Figure 23 is diagnostic; identified as *Conyza sumatrensis* by Pruski and Sancho (2006).

Conyza bonariensis forma *subleiotheca* Cuatrec., Webbia 24: 227. 1969. *Conyza floribunda* var. *subleiotheca* (Cuatrec.) J.B. Marshall, Watsonia 9: 372. 1973. **TYPE:** **COLOMBIA**. Boyacá: Valle de Soatá, vert. árida, exp. E, 2130 m, 6 Sep 1938, *J. Cuatrecasas & H. García Barriga 1026* (holotype: US image!; isotypes: COL image!, F).

Conyza groegeri Badillo, Ernstia, ser. 2, 10: 5. 2000. **TYPE:** **VENEZUELA**. Amazonas. Atures, de Samariapo 100 km arriba El Orinoco, San Juan de Ucata, 1.5 km al NE, tobogán con una laja plana, 30 May 1993, *A. Gröger 956* (holotype: VEN image!).

Collections examined of *Conyza sumatrensis* from the southeastern USA (Map 3). **Alabama**. Baldwin Co.: E of Elberta, S of US Hwy 98, ca. 1 mi E of Prince of Peace Cemetery, roadside, 2 Aug 1987, *Burkhalter 10657* (UWF image); Battleship Park by causeway US 90-98, E of Mobile on the Bay, sandy area, 20 Aug 1968, *Kral 32756* (SMU); Magnolia Beach in Fairhope along Mobile Bay, jct of Laurel Ave and Mobile St. below American Legion, disturbed sandy beach, 10 Jun 2008, *Spaulding 12945* (TROY image, UWAL-2 sheets images). Calhoun Co.: Saks, corner of Saks Rd and Lenlock Rd, roadside, 12 Sep 2008, *Spaulding 13067b* (TROY image, UWAL image). Dale Co.: 1 mi S of intersection of Hwys 57 and 60, open grassy field, 20 Jul 2000, *Pennington 904* (TROY image). Marengo Co.: 3.6 air mi SSE of Magnolia, along W side of Ala Hwy 25 ca. 0.8 mi S of jct with Co. Road 32, clearcut near roadside, 28 Jun 2011, *England 2987* (UWAL); 1.8 air mi SE of Pin Hook, along N side of Ala Hwy 28 ca. 0.3 mi W of jct with Co. Road 19, roadside ditch, 16 Sep 2008, *England 1134* (UWAL). Mobile Co.: Dauphin Island, corner of Iberville Dr. and Bienville

Blvd, roadside, 2 Aug 1965, *Deramus D642* (MISSA image); Mobile, SE of Three Mile Creek Univ. of South Alabama property, sandy, longleaf pine woods, 29 Aug 1966, *Lelong 4038* (USAM image); upper part of Moore Creek between I-10 overpass and L&N RR bridge, weedy, marshy area, 15 Aug 1980, *Lelong 11302* (USAM image). **Arkansas.** Cleveland Co.: W of New Edinburg at Calhoun Co. line, Ark Hwy 8 at Moro Creek, along elevated roadbank, 10 Jul 1998, *Thomas 157,108* (NLU). Drew Co.: Monticello, wood margin, 2 Sep 2006, *Sundell 17448* (UARK image); Jerome, common along roadside of US Hwy 165, 1 Oct 1999, *Thomas 163,797* (BRIT). **Florida.** Alachua Co.: Kanapaha Botanical Gardens, roadside, W side of entrance road near parking lot, 28 Jul 2004, *Davis 1145A* (FLAS image); S of Gainesville, ca. 0.2 mi E of Hwy 121 (SW 34th street) & 1 mi SW of Hwy 441, mixed hardwood forest next to Williston Rd (Hwy 331), 27 Jun 1999, *Slaughter 11112* (FSU image). Baker Co.: Sand Bluffs S of St. Marys River and end of St. Marys Cove Rd, 4.3 mi E of State Rd 121, 14 Aug 2007, *Slaughter 15838* (FSU image, USF image). Calhoun Co.: Blountstown, Myers Dairy Rd, 0.6 mi N of Abe Springs Rd, weedy grassy field, 17 Aug 2006, *MacClendon 521* (FSU image, USF image). Escambia Co.: near Pensacola, W of University Mall shopping plaza, near drainage ditch, sandy, 11 Aug 1976, *Burkhalter 4463* (UWF image); near Pensacola, campus of Univ. of W Florida, corner of sewage treatment pond, 29 Jul 1990, *Burkhalter 12184* (UWF image); W end of Santa Rosa Island, Gulf Islands Natl Seashore, Ft. Pickens area, W of camping loop E, 25 May 2009, *Burkhalter 22289* (UWF image); Pensacola, 29 Jul 1899, *Curtiss 6499* (DS, UC); Pensacola, open, disturbed upland area, 6 Sep 1975, *Godfrey 74409* (FSU image); Gulf Islands Natl Seashore, Fort Pickens Unit, campground area including Loops B-E just N of Campground Store, 18 Oct 2005, *Gunn and Ferguson FP-192* (LSU image); Pensacola, 1/4 mi W of Pace Avenue bridge across Bayou Chico, sandy vacant lot, 11 Aug 1976, *Hansen 3905* (FSU image). Franklin Co.: just S of the Marshall House on bayside of island, coastal hammock beside West Gulf Road, 6 Sep 1985, *Anderson 8781* (FSU image); N side of town of Apalachicola, N side of Mill Pond of Scipio Creek, loamy sand of spoil site, 29 Aug 1986, *Anderson 9878* (FSU image); St. George Island, Dr. Julian Bruce State Park, sand and shell mixture of parking spaces in campground area just W of Sugar Hill, 26 Jun 1987, *Anderson 10713* (FSU image). Gadsden Co.: E side of road between Chattahoochee and Resrouce Manager's Office (Lake Seminole), clay soil, 6 Sep 1975, *Gholson 429* (FLAS image); W side of road between US 90 (at Chattahoochee) and the Lake Seminole Project Area, shoulder of paved road, 13 Aug 1976, *Gholson 3633* (FLAS image); E side of paved road on W side of Apalachee Game Mgt Area on Lake Seminole, near Salem Church, previously a cultivated field, 13 Aug 1976, *Gholson 3635* (FLAS image); on State Rd 279, ca. 1/4 mi W from jct of State Rds 270 and 269, fallow field with sandy loam, 13 Aug 1977, *Gholson 6533* (FLAS image); ca. 7 mi S of Chattahoochee, along Fla Hwy 270, just W of jct with Fla Hwy 269, dry sandy loam of fallow field, 13 Aug 1977, *Ward 9172* (FLAS image). Gulf Co.: 1 mi N of Wewahitchka, sandy, fallow field, 15 Aug 1970, *Godfrey 69894* (FSU image); vicinity of Wewahitchka, sandy fallow field, 4 Aug 1976, *Godfrey 75323* (FSU image). Leon Co.: ca. 2.5 air mi SW of Tallahassee Municipal Airport, by parking area on E shoreline of Dog Lake in Apalachicola Natl Forest, loamy sand of clearing, 15 Aug 2013, *Anderson 27323* (FSU image); Tallahassee, Timberlane Ravine Park, between interstate and fenceline (just S of I-10, W of Timberlane School Rd), disturbed site near trailhead, 30 Jun 2015, *Anderson 29001* (FSU image); Tall Timbers Research Station, frequent in fallow fields intermixed with an abundance of *C. canadensis* var. *canadensis* and *C. canadensis* var. *pusilla*, 9 Aug 1979, *Godfrey 77115* (FSU image, TTRS image). Liberty Co.: Torreya State Park, eroding bank of Apalachicola River, 24 Aug 1988, *Godfrey 82822* (FSU image). Okaloosa Co.: near Ft. Walton Beach, N of US Hwy 98, across from Beaseley State Park, roadside, 23 Jan 1988, *Burkhalter 10850* (UWF image); just S of Crestview town, intersection of US Hwy 89 and I-10, weedy lots, 26 Aug 1997, *Miller et al. 9199* (TEX). Santa Rosa Co.: Navarre, E of jct of US Hwy 98 and Pullam St, along drainage ditch, 4 Aug 1991, *Burkhalter 12791* (UWF image); between I-10 and Milton, weed on spoil banks bordering highway, 24 Jul 1974, *Godfrey 73767* (FSU image); off I-10 W of the Escambia River, borrow pit just next to the parking lot at the Stuckey's pit stop, 26 Jul 1989, *Godfrey 83391* (FSU image, TTRS image). Taylor Co.: St. Marks National Wildlife Refuge, by old cabin site

E of Mandalay Rd bordering Aucilla River bayou, loamy sand along edge of thicket, 10 Aug 2007, *Anderson 23415* (FSU image). Wakulla Co.: St. Marks National Wildlife Refuge (St. Marks Unit), between Picnic Pond and lighthouse road, 19 Dec 2014, *Anderson 28630* (FSU image); banks of marshes at St. Marks, 9 Aug 1965, *Godfrey 65905* (FSU image). Walton Co.: 10 mi E of De Funiak Springs, grassy roadsides, 6 Sep 1975, *Godfrey 74428* (FSU image). **Georgia.** Chatham Co.: Atlantic Coast Line Dock, 1.5 mi E of Savannah City Hall, open, well drained sandy soil, 9 Jun 1958, *Duncan 20868* (GA image); near Garden City Terminal, ditch in green space near Grange Road, 28 Aug 2015, *Lucardi et al. GPA CB9-14* (STAR image); Savannah-Ogeechee Canal Nature Center/Ogeechee River Nature Preserve, N side of Tow Path Trail at intersection with River Walk trail, on bricks of historic lock, 27 Jul 2012, *Zomlefer 2775* (GA image). Glynn Co.: Fort Frederica Natl. Monument, unmown border at marsh edge, 24 Jul 2003, *Schmidt s.n.* (GA image). Houston Co.: Oaky Woods WMA, roadside, loam over limestone, 456 ft, 20 Aug 2009, *Lynch 669* (ARIZ image, GA-2 images). Irwin Co.: Hwy 90, J. Robert's "Pigweed field," 12 Aug 2002, *Rausch 214* (GA image, VSC image). Liberty Co.: Ft. Stewart Military Reservation, Training Area A-17, 0.6 mi SW of jct Ga Hwy 144 and FS 48, roadside along Ga 144, sandy, 12 Aug 1992, *Carter 10344* (GA image); Ft. Stewart Military Reservation, sand pit S of Mill Creek, recently excavated and scraped with little vegetation, 13 Aug 1992, *Carter 10364* (GA-2 images, VDB); Ft. Stewart Military Reservation, Training Area D4, common along embankment of bridge over Taylor's Creek on Ga Hwy 119, between Ga Hwy 144 East and Ga 144 West, 4 Aug 1992, *Moore 1629* (GA image). Mitchell Co.: 3 mi S of jct of Ga Hwys 112 and 97, S of Camilla, sandy peat of drying edge of clay-base pond in cypress-pine flats, 17 Aug 2000, *Kral 90164* (VDB). **Louisiana.** Caldwell Par.: Riverton beside US Hwy 165 and RR tracks, 16 Oct 1983, *Thomas 86301* (NLU). Cameron Par.: W of Hackberry, ca. 2 mi N of Sabine Island, mixed woods beside the Sabine River, 6 Sep 1984, *Thomas 90808* (NLU-2 sheets). Franklin Par.: Winnsboro, along RR tracks beside La Hwy 15, unsprayed area, 11 Oct 1983, *Thomas 86183* (NLU). Orleans Par.: E of New Orleans, N of I-10 beside first exit E of La Hwy 47, 28 Jul 1974, *Thomas 40732* (NLU). Plaquemines Par.: Venice, common near Venice Inn along Hwy 23, 6 Nov 1979, *Montz 4918* (LSU image). St. Tammany Par.: Big Branch Marsh NWR, at intersection of Bayou Paquet Rd and Transmitter Rd, disturbed soils S of roadside, 5 Aug 2000, *Rosen 1277* (LSU image); S of Slidell, 1.6 mi E of North Shore and US Hwy 11, along fence N of restaurant at end of unmarked road, 17 Sep 1983, *Taylor 5789* (NLU); just S of St. Joe, woods beside US Hwy 11 and railroad, 21 Sep 1977, *Thomas 55330* (NLU). Washington Par.: W of La Hwy 438 near Hays Creek N of Hackley, pasture and woods edge, 17 Aug 1983, *Thomas 85410* (NLU); 0.5 mi E of Folsom, at La Hwy 40 bridge over Bogue Falaya River, woods and roadbank, 18 Aug 1983, *Thomas 85607* (NLU). **Mississippi.** George Co.: Gulfport, moist valley areas, 15 Aug 1953, *Demaree 33890A* (BRIT, SMU). Harrison Co.: Gulfport, near the coast, 11 Apr 1953, *Demaree 33231* (SMU, VDB); Gulfport, vacant lots, 26 Jul 1952, *Demaree 32293* (SMU, VDB-2 sheets). Jackson Co.: Horn Island, Gulf Islands Natl Seashore, extensive marsh system dominated by *Spartina patens* and *Panicum repens* near mid-island along West Cross Trail, 23 Aug 2005, *Gunn & Ferguson HI-94* (LSU image); Moss Point, roadside, 30 Mar 1969, *Rogers 2075-A* (VDB); Red Creek Mitigation Bank Property, E of Hwy 57, S of Red Creek, and N of Old River Rd, pine plantation uplands, 1 Aug 2006, *Sullivan 06-1439c* (MMNS image); ca 2 mi E of Pascagoula River along US Hwy 90, 18 Jul 1970, *Temple 12434* (MMNS image). Washington Co.: Ca. 3.5 air mi NNE of Leland, near jct of Napanee and L&H Road along edge of soybean field, clay soil, 7 Sep 2010, *Bryson 23632* (MMNS image); 5 mi NE of Lake Lee on sides of levee, 23 Sep-1 Oct 1976, *Gunn 12106* (MMNS image). **South Carolina.** Beaufort Co.: Lady's Island, intersect. of Cougar Drive and Hwy 21, 18 Sep 2005, *Payne 3794* (CLEMS image). Charleston Co.: Awendaw, Flat Farm Rd, 1.0 mi from intersect. with Moores Landing Road, 2.2 mi E of int. with US Hwy 17, 19 Sep 2001, *McMillan 5885* (CLEMS image). Georgetown Co.: Huntington Beach State Park, E side of Hwy 17, ca. 12 mi N of Georgetown, along path in maritime forest remnant, immediately W of host's campsite, 22 Aug 2003, *Nelson 24208* (USCH image); Huntington Beach State Park, E side of US Hwy 17 just S of Murrells Inlet, sandy ground at parking lot edge, 6 Sep 2006, *Nelson 26184* (USCH image). Jasper Co.: Pocotaligo,

immediately E of I-95, N side of US Hwy 17, 30 Jul 2009, *Nelson 27799* (USCH image). Williamsburg Co.: 3.1 mi W of downtown Trio, Trio School, wet ground at edge of baseball field, 21 Aug 2016, *Nelson 36001* (USCH image). **Texas. Chambers Co.**: High Island, Boy Scout Woods (Louis B. Smith Bird Sanctuary Preserve), 0.2 mi E of jct Texas Hwy 124 and 5th Street, 2 Jan 2013, *Singhurst 19326* (BAYLU image).

The earliest collection of *Erigeron sumatrensis* in California was from San Diego in 1952; others from 1967 to 1983 were made in Butte, El Dorado, Sutter, Tulare, and Yuba counties. Those from coastal localities (except San Diego) have been more recently.

In contrast, *Erigeron bonariensis* was early collected in 1895 (San Diego Co.). Collections were made in Los Angeles Co. in 1905, 1906, and 1909 — a collection from Pasadena in 1906 noted that it was a "street weed recently introduced" (7 Aug 1906, *Grant 7157*, CAS, JEPS). From 1905 to 1920, collections also were made in Alameda, Marin, Riverside, San Bernadino, San Francisco, and Santa Cruz counties. It was included in the accounts of Hall (1907) and Jepson (1925) (in both as *Erigeron linifolius* Willd.) — by 1925 it had been documented as far north as Alameda Co. and by 1940 from other coastal and near-coastal localities (CCH 2018).

Erigeron floribunda is the most recently arrived in California and least widespread adventive among the conyzas. Early collections are from San Francisco (1956) and El Dorado Co. (1976). Others are from 1983 to 2003.

In the southeastern USA, early establishment of *Erigeron sumatrensis* along the Gulf Coast is documented by collections from Pensacola (1899) and areas around Gulfport (1952), St. Marks (1965), Mobile (1968), and New Orleans (1974). At least by 1983, it had reached inland localities in Louisiana (Caldwell and Franklin parishes) and a cluster of counties in Arkansas (Drew and Cleveland cos.) and adjacent Mississippi (Washington Co.); more recent inland collections are from Alabama (Calhoun and Marengo cos.) and Georgia (Houston and Irwin cos.). On the Atlantic coast, an early collection was from near Savannah (1958).

3. *Erigeron floribundus* (Kunth) Sch. Bip., Bull. Soc. Bot. France 12: 81. 1865. *Conyza floribunda* Kunth, Nov. Gen. Sp. (folio ed.) 4: 57. 1820 [1818]. *Erigeron bonariensis* var. *floribundus* (Kunth) Cuatrec., Trab. Mus. Nac. Ci. Nat., Ser. Bot. 33: 132. 1936. *Conyza sumatrensis* var. *floribunda* (Kunth) J.B. Marshall, *Watsonia* 10: 167. 1974. **LECTOTYPE** (Green 1994, p. 49): **ECUADOR**. Pichincha: juxta urbem Quito, Jul 1802, *Humboldt & Bonpland 3100* (P-HBK image! [ICD microfiche 6209. 95.III.7]). Protologue: "Crescit frequentissime locis frigidis et temperatis juxta urbem Quiti et pagum Guancabambae Peruvianorum, alt. 1330-1500 hex. Floret Julio-Augusto."

Conyza albida Willd. ex Spreng., Syst. Veg., ed. 16, 3: 514. 1826. *Erigeron albidus* (Willd. ex Spreng.) A. Gray, Proc. Amer. Acad. Arts 5: 319. 1862. **TYPE: BRAZIL**. Without specific locality, *Hoffmannsegg s.n.* (B-Willd. 15658 image!).

This sheet was annotated by G. Wagenitz in 1962 as the type of *Conyza albida* and identified by him as *C. bonariensis* var. *microcephala* (Cabr.) Cabr.; its identity is unambiguously *C. floribunda*.

Conyza bilbaoana Remy, Fl. Chil. 4: 75. 1849. *Erigeron bilbaoanus* (Remy) Cabr., Revista Mus. La Plata, Secc. Bot. 2: 254. 1939. **LECTOTYPE** (designated here): **CHILE**. Prov. Valdivia, *Mr. Cl. Gay 342* (P 00691985 image!; possible isolectotypes: NY-3 sheets images!).

Three sheets at P collected by Gay are labeled "TYPE." Two probably are duplicates — both have stems with immature heads (but phyllaries diagnostic) and each has a printed "Herb. Mus. Paris" label with handwritten "*Conyza bilbaoana*" — one has the apparently original handwritten label by Gay, identified as "Erigeron." The third sheet has mature heads and a label with handwritten "342" but there is a small "317" seemingly out of place at the top of the label — this suggests that the sheet

perhaps is a duplicate of three sheets at NY with mature stems and with "Herb. Mus. Paris labels" as *Gay 317*. The "317's" on the P and NY sheets are in a distinctive script and almost surely were written by the same hand. No specimens were cited in the original description, but Gay noted that "Se cria en la vecindad de Valdivia y la dedicamos al joven Bilbao, Chileno de grande provecho y mucho talento."

Erigeron bonariensis var. *leiothecus* Blake, Contr. Gray Herb. 52: 28. 1917. *Marsea bonariensis* var. *leiotheca* (Blake) Badillo, Bol. Soc. Venez. Ci. Nat. 10: 256. 1946. *Conyza bonariensis* var. *leiotheca* (Blake) Cuatrec., Phytologia 9: 5. 1963. *Conyza sumatrensis* var. *leiotheca* (Blake) Pruski & Sancho, Novon 16: 98. 2006. **TYPE: GUATEMALA.** [probably Dept. Guatemala]: San Rafael, 2135 m, 8 Jan 1915, *E.W.D. Holway 39* (holotype: GH image!).

Biological notes

Erigeron sumatrensis and *E. floribundus* have been treated as conspecific varieties (as *Conyza*, e.g., Sancho & Ariza Espinar 2003; Pruski & Sancho 2006), In South America, both species occur at least in Bolivia, Brazil, Colombia, Ecuador, Peru, and Venezuela; their sympatry extends northward through Central America into southern Mexico. Their sympatry in California apparently reflects independent introductions into that region.

Erigeron sumatrensis and *E. floribundus* may occur in close proximity but they are consistent in morphology, apparently with few obvious intermediates or intergrades. Occasional apparent intergrades between them have been encountered in this study among Mexican collections. *Kral 90164* from Mitchell Co., Georgia (see citations), perhaps is a hybrid between *E. sumatrensis* and *E. bonariensis* — all cauline leaves are linear like those of *E. bonariensis* but it has small heads in broadly paniculate capitulescence and *sumatrensis*-like phyllaries.

Thebaud and Abbott (1995) found that naturalized *Erigeron floribundus* and *E. sumatrensis* are consistently distinct from each other in France (in nature and in a common garden in Montpellier) as well as from naturalized *E. bonariensis*. Spontaneous hybrids between *E. sumatrensis* and *E. blakei* Cabr. were formed in the common garden but were mostly sterile; no other morphological intermediates appeared in the garden where all four of these taxa were cultivated, suggesting to the authors that crossing barriers may exist.

Based on similarities in morphology and electrophoretic data, two pairs were evident in the analysis by Thebaud and Abbott: *E. sumatrensis/bonariensis* and *E. floribundus/blakei*. Each of these four is hexaploid and observations of fixed heterozygosity at isozyme loci suggested that each is allopolyploid in origin. They hypothesized that the taxa are derived from "various combinations of different parental species."

Erigeron bonariensis and *E. sumatrensis* occur worldwide, from tropical to temperate zones. Pruski and Sancho (2006) noted that *E. floribundus* in the strict sense is restricted to the Neotropics, but its distribution needs to be reevaluated based on narrower species definitions — Thebaud and Abbott (1995, and citing Rivière 1987) noted that it is spreading in western France and northeastern Spain, and it is documented here from California. *Erigeron blakei* apparently is naturalized only in England, France, Spain, and Italy (Jovet & de Vilmorin 1975; Guedes & Jovet 1975; Clement & Foster 1994; GCW 2018).

Conyza vs. *Erigeron*

Species identified as *Conyza* have arisen evolutionarily from within *Erigeron* at least twice independently (e.g., Noyes 2000; Brouillet et al. 2009). *Erigeron bonariensis*, *E. floribundus*, and *E. sumatrensis* are included in a clade with the type species of *Conyza* (*C. chilensis* Spreng.); *Erigeron canadensis* L. arose within a separate clade (*Conyzella* Fabr. 1759, *Leptilon* Raf. 1818). North American/Mesoamerican species have formal names within *Erigeron* (completed in Nesom 2018) but

in South America, where the greatest number of species occurs, the taxonomy and nomenclature are in need of revision.

Cronquist (1943) sought to clarify the distinction of *Conyza* from *Erigeron*, based on the presence or absence of ligules on the pistillate florets and, in part, the ratio of pistillate to staminate flowers, with the assumption that two genera indeed existed. *Conyza* as recognized since then includes species varying in habit, capitulescence form, head size, and biology (including chromosome number). Current evidence and current trends in nomenclature favor the identification of remaining American 'conyzoid' species within *Erigeron*.

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