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Reinstatement of the Genus *Piofontia*: A Phylogenomic-based Study Reveals the Biphyletic Nature of *Diplostephium* (Asteraceae: Astereae)

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Abstract—A recent phylogenomic study has shown that *Diplostephium* in its broad sense is biphyletic. While one of the clades comprises 60 species distributed mainly in the Northern Andes, the clade that contains the generic type, *Diplostephium ericoides*, contains 48 species, and primarily inhabits the Central Andes. Here, I propose to reinstate the generic name *Piofontia* and transfer to it the species of *Diplostephium* in the Northern Andean clade. *Piofontia* consists, then, of 60 species of woody subshrubs, shrubs, and small trees inhabiting high Andean forests and páramos of Costa Rica, Colombia, Venezuela, and Ecuador. A morphological description is provided for the genus *Piofontia* along with a species list with 60 new combinations. *Dysaster cajamarcensis* is shown to be a synonym of *Diplostephium serratifolium*. Finally, a brief discussion about the morphological evolution of South American Astereae is provided.

Keywords—Andes, South America, páramo.

Kunth (1820) proposed *Diplostephium* Kunth with a single species, *D. lavandulifolium* Kunth (= *D. ericoides* (Lam.) Cabrera), and defined the genus with the following diagnostic characteristics: branched shrubs with dense foliage, alternate linear leaves, solitary capitula, hemispherical involucres with numerous imbricate phyllaries, epaleate foveolate receptacles, radiate heterogamous capitula, tubular hermaphrodite disk florets, peripheral ray florets, and double pappus with a short exterior row of scale-like bristles and an inner row of longer barbellate bristles. Weddell (1855) reinterpreted *Diplostephium*, adding a geographic component to his concept by defining the genus as Andean shrubs of montane habitats with alternate and often tomentose leaves, terminal solitary capitula on branchlets or in a corymb, foveolate receptacles, and white or purple rays. Weddell's (1855) definition expanded the morphological boundaries of *Diplostephium* and demarcated its geographical distribution. Weddell (1855) also described 11 new taxa, transferred five species into the genus, and proposed a subgeneric division of two groups: plants with solitary capitula and plants with capitula borne in a corymb. Hieronymus (1894, 1896, 1900, 1905) added ten taxa to the genus, five of which are now considered synonyms of previously described species (Vargas 2011).

In the twentieth century, Blake described 28 new taxa for *Diplostephium* and published two major revisions. In his first revision, Blake (1922) proposed a subgeneric classification of five series based on foliar and floral characters, partially following the subgeneric division proposed by Weddell (1855). In the second revision, Blake (1928) recognized a total of 43 *Diplostephium* species but reduced the number of series to three. Subsequently, Cuatrecasas (1943b, 1969) added numerous names to *Diplostephium* and published two comprehensive studies of the genus. In his second work, Cuatrecasas (1969) dealt only with the Colombian species and proposed a generic subdivision of 12 series for *Diplostephium* consisting of Blake's (1922) original five plus seven new series. Cuatrecasas (1969) listed 53 species for Colombia and estimated a total of 90 species for the genus. Although some species have been added to *Diplostephium* since 1969, Cuatrecasas' (1969) study is the most comprehensive taxonomic work of the genus to date. In its recent circumscription (Vargas and Madriñán 2006; Vargas 2011), *Diplostephium* s. l. comprises 111 species distributed in the mountains of Central and South America in Costa Rica, Colombia, Venezuela, Ecuador, Peru, Bolivia, and northern Chile.

A recent phylogenomic study (Vargas et al. 2017) showed that *Diplostephium* sensu Cuatrecasas (1969) is biphyletic, based on a double-digest restriction site-associated DNA sequencing (ddRAD) tree obtained by the authors (Fig. 1). A monophyletic group of *Diplostephium* s. l. species, distributed mainly in the Northern Andes, is sister to a clade that comprises *Blakiella* Cuatrec., *Hinterhubera* Sch.Bip. ex Wedd., and *Laestadia* Kunth ex Less. A second group of mainly Central Andean species, *Diplostephium* s. s., forms a clade with *Parastrephia quadrangularis* (Meyen) Cabrera. The Central Andean clade is nested in a clade with *Archibaccharis* Heering, *Aztecaster* G.L.Nesom, *Baccharis* L., *Exostigma* Sancho, *Floscaldasia* Cuatrec., *Heterothalamus* Less., *Laennecia* Cass., *Lagenophora* Cass., and *Westoniella* Cuatrec. When the *Diplostephium* s. l. species not sampled by Vargas et al. (2017) are morphologically assigned to the two recovered clades (see below), the Northern Andean and the Central Andean clades contain 60 and 48 species, respectively.

Because the nomenclatural type of *Diplostephium*, *D. ericoides* (Lam.) Cabrera, is part of the Central Andean clade, the correct generic name for the species comprising the Northern Andean clade is *Piofontia* Cuatrec. Cuatrecasas (1943a) proposed *Piofontia* as a monotypic genus consisting of *P. colombiana* Cuatrec. but later (Cuatrecasas 1953) transferred *P. colombiana* into *Diplostephium* as *D. colombianum* (Cuatrec.) Cuatrec. The previous Cuatrecasas' series, erected primarily for the Colombian species, are not recognized here because, for the most part, they do not correspond to natural groups in either *Piofontia* and *Diplostephium*. In addition to the monotypic series, the only monophyletic series are *Diplostephium* ser. *Denticulata,* albeit with low support (clade 1, Fig. 1), and *Diplostephium* ser. *Schultziana* if *Piofontia apiculata* is included in the series (clade 2, Fig. 1).

Finally, I propose *Dysaster cajamarcensis* H.Rob. & V.A.Funk as a taxonomic synonym of *Diplostephium serratifolium* Cuatrec. based on morphology and the phylogeny of Vargas et al. (2017).

Taxonomic Treatment

Piofontia Cuatrec. Caldasia 2: 5. 1943. Type: *Piofontia colombiana* Cuatrec., Caldasia 2: 5. 1943.

Small trees, shrubs or subshrubs 0.1–10 m tall, woody, branching sympodial by substitution with branches

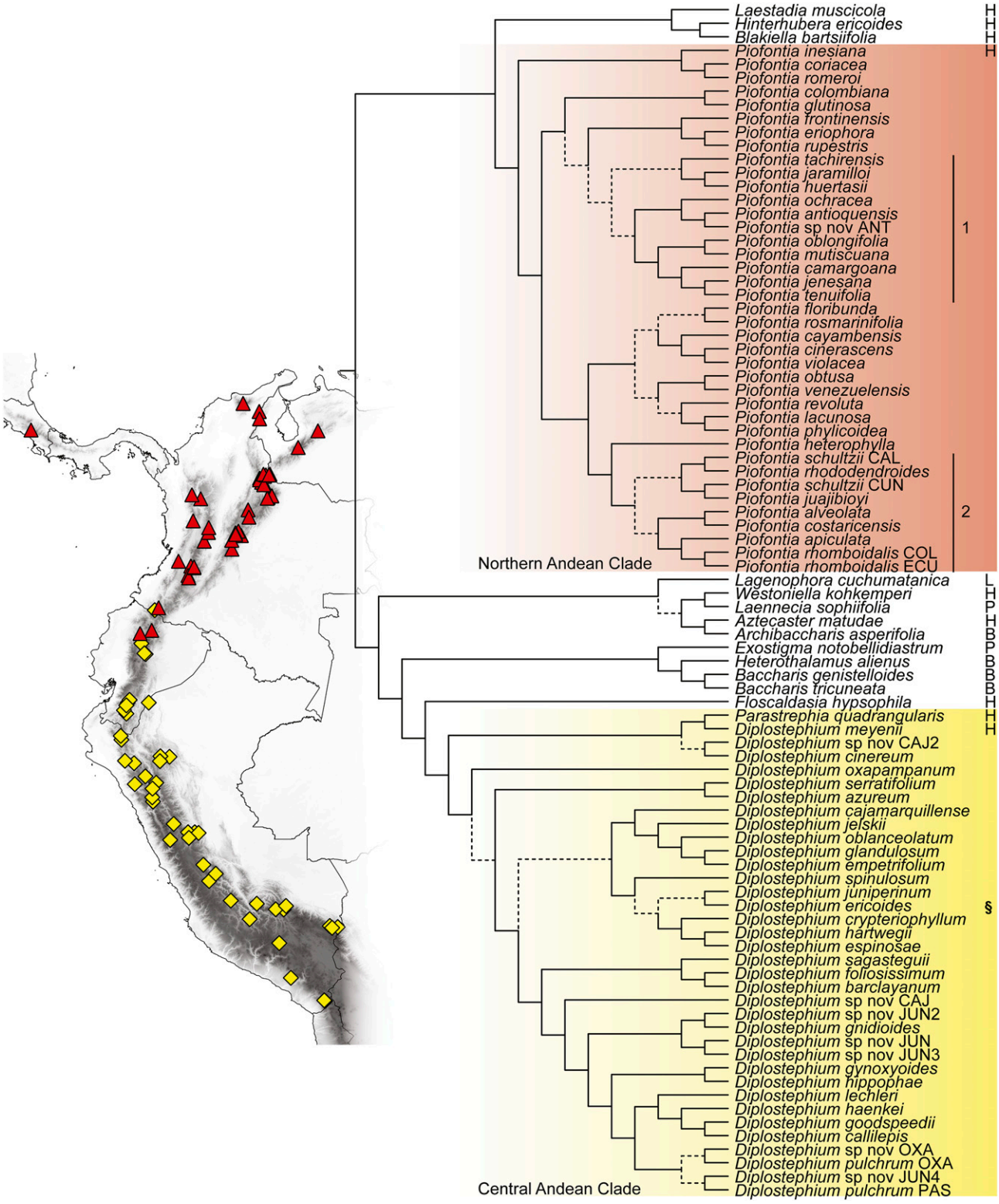

FIG. 1. Cladogram of *Diplostephium*, *Piofontia*, and their allies obtained with nuclear double-digest restriction site-associated DNA sequencing (ddRAD) by Vargas et al. (2017) using maximum likelihood. Edges with bootstrap support < 90 are dashed. Letters next to species indicate the subtribe to which the genus belongs: B = Baccharidinae, H = Hinterhuberinae, L = Lagenophorinae, and P = Podocominae. 1) Indicates the *Denticulata* clade, and 2) indicates the *Schultziana* clade (both defined in the main text). The section mark (§) indicates the type species of *Diplostephium*. The map shows the type localities for the species of *Diplostephium* (diamonds) and *Piofonta* (triangles). Figure modified from Vargas et al. (2017).

terminated by capitulescences. Branches cylindrical, minutely ribbed, tomentose or glabrous, glandular or eglandular, striate when old; terminal shoots often tomentose. Leaves alternate with phyllotaxis of five, petiolate, pseudopetiolate, or sessile, often mucronate; lamina 3–230 × 0.7–85.0 mm, linear, lanceolate, ellipsoid, oblong, ovate, or obovate; margins entire, denticulate, or serrate, membranous to coriaceous, usually revolute, sometimes flat, often with adaxial and abaxial

surfaces of a different color; adaxial surface often lanate when young and glabrous when old, glandular or eglandular, with central vein impressed and canaliculate, secondary venation usually conspicuous in leaves wider than 12 mm and tertiary venation usually conspicuous in leaves wider than 15 mm; abaxial surface often densely lanate, whitish, yellowish, or ocherous, central vein prominent, with secondary and tertiary venation impressed or inconspicuous.

Capitulescence of terminal solitary or multiple heads arranged in corymbs, racemes, or umbels. Capitula heterogamous, radiate, rarely disciform; involucre 4–15 mm long, 3–15 mm diam, tubular, cupulate, campanulate, or subconical, 3–7 seriate; phyllaries numerous, imbricate, unequal, 0.5–12.0 × 0.4–2.8 mm, ovate to linear, semicoriaceous or coriaceous, often dorsally lanate and colored towards the apex. Ray florets 5–140, with corolla 2.5–15.0 mm long, white to purple; tube 1–6 mm long, usually papillose-pilose, rarely with one or two lobes opposite to the limb; limb 0.5–12.0 × 0.4–2.0 mm, linear, oblong-elliptic, oblong-ovate, oblong-obovate, with 3–4 veins; lobes (2–)3(–4), 0.1–0.8 mm long, triangular and unequal; stigmatic branches 0.2–2.0 mm long, linear or subulate with papillose margins; ovary 0.6–5.0 mm long, glabrous or pilose, oblong, ovate, obovate, or oblong-ellipsoid, ribbed, glandular or eglandular, always ovulate and fertile; pappus biseriate, straw-colored, reddish, or purplish, outer bristles 0.1–5.0 mm long, filiform and barbellate, interior bristles 2.0–8.0 mm long, barbellate, often with flattened and widened apex. Disk florets 3–114, staminate, corollas actinomorphic, 3.0–9.0 mm long, tubular, tubular-campanulate, or tubular-infundibuliform, whitish, green, yellow, or purple, usually papillose-pilose, 5-lobed; tube 2.0–6.0 mm long; throat 1.0–4.0 mm long, usually papillose-pilose; lobes triangular 0.4–2.6 mm long, usually with papillose apex; anthers 1.0–2.5 mm long, oblong, briefly auriculate at the base, apical appendix membranous, triangular, and obtuse; stigmatic branches 0.3–1.2 mm long, linear or lanceolate, exteriorly papillose; ovary 0.8–7.0 mm long, linear or oblong, ribbed, glabrous to pilose, glandular or eglandular; pappus biseriate, straw-colored, reddish, or purplish, outer bristles always filiform, usually barbellate, 0.1–4.5 mm long, interior bristles 3–8 mm long, usually barbellate, often with flattened and widened apex. Receptacle 1–5 mm in diam, alveolate, often muricate.

Piofontia currently consists of 60 species and is a major component of the flora of the Northern Andes, the Sierra Nevada of Santa Marta, and the Talamanca Cordillera. The southern boundary of *Piofontia* is central Ecuador, near the Huancabamba depression, which defines the southern boundary of the Northern Andes (Weigend 2004; Luebert and Pliscoff 2006; Luebert and Weigend 2014). Most of the species inhabit the páramo ecosystem, but a clade of approximately 16 species, which contains the species of *Diplostephium* ser. *Denticulata* sensu Cuatrecasas (1969), occurs in the cloud forest (clade 1, Fig. 1).

I propose the following new combinations, taking into account the evidence discussed above. Morphological evidence (Cuatrecasas 1969; Vargas and Madriñán 2006) was employed to place the species not sampled by Vargas et al. (2017) in *Piofontia* or *Diplostephium*. Finally, I describe two clade names within *Piofontia* to facilitate communication in future studies in the genus.

1. ***Piofontia alveolata*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium alveolatum* Cuatrec., Caldasia 2: 224. 1943. Type: Colombia. Boyacá: páramo del Alto del Escobal, entre Soatá y Cocuy, 3800–3900 m, arbolito 2–4 m, Sep 15 1938, *Cuatrecasas & García-Barriga 1758* (holotype: COL!, isotypes: BC, F!, P, US!).

2. ***Piofontia anactinota*** (Wedd.) O.M.Vargas, comb. nov. *Diplostephium anactinotum* Wedd., Chlor. And. 1: 201. 1856. Type: Colombia. Magdalena: Sierra Nevada de Santa Marta, frútex, flores albi, 1843, *Funck 390* (lectotype: P, isotypes: G, P).

3. ***Piofontia antioquensis*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium antioquense* Cuatrec., Proc. Biol. Soc. Wash. 74: 12. 1961. Type: Colombia. Antioquia: Medellín, monte El Boquerón, Alto de los Baldíos, páramo 3150 m, bosque andino fragmentario marginal, árbol 4–5 m, hoja crasiúscula, verde amarillenta oscura haz, blanquecina envés, inflorescencia blanquecina, borde de las brácteas involucrales algo pardusco, lígulas blancas, Apr 9 1958, *Cuatrecasas, Llano & Gutierrez 24226* (holotype: US!, isotypes: B, F!, G, MEDEL, NY, P, US!).

4. ***Piofontia apiculata*** (S.F.Blake) O.M.Vargas, comb. nov. *Diplostephium apiculatum* S.F.Blake, Proc. Biol. Soc. Wash. 49: 79. 1936. Type: Colombia. Norte de Santander: Páramo de Santurbán, entre Tona y Mutiscuá, 3900 m, matita leñosa, lígulas blancas, flósculas verdes, Jan 19 1927, *Killip & Smith 19571* (holotype: US!, isotypes: A, COL!, GH, NY).

5. ***Piofontia bicolor*** (S.F.Blake) O.M.Vargas, comb. nov. *Diplostephium bicolor* S.F.Blake, Contr. U. S. Natl. Herb. 24: 85. 1922. Type: Colombia. Cauca: Central Cordillera head waters of RíoPalo, Tierra Adentro, 2500–3000 m, small tree 2–4 m, Jan 1906, *Pittier 1084* (holotype: US!, isotypes: GH, F!).

Diplostephium tabanense Cuatrec., Caldasia 2: 216. 1943. Type: Colombia. Nariño: Páramo del Tábano, alto de la cordillera entre Pasto y El Encano, vert occid., 3200 m, arbolito, Jan 11 1941, *Cuatrecasas 11932* (holotype: COL!, isotypes: BC, F!, US!).

6. ***Piofontia camargoana*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium camargoanum* Cuatrec., Phytologia 23: 351. 1972. Type: Colombia. Boyacá: Arcabuco, alrededores de la población 2739–2850 m, Oct 20 1965, *Huertas & Camargo 6309* (holotype: US!, isotype: COL!).

7. ***Piofontia cayambensis*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium cayambense* Cuatrec., Brittonia 8: 183. 1956. Type: Ecuador. Napo-Pastaza: páramo NE Volcán Cayambe, 12,500 ft, woody Compositae on moist páramo and ravines leading to alpine lake, Feb 10 1953, *Prescott 329* (holotype: NY).

8. ***Piofontia chrysotricha*** (S.Díaz & B.L.Restrepo) O.M.Vargas, comb. nov. *Diplostephium chrysotrichum* S.Díaz & B.L. Restrepo., Revista Acad. Colomb. Ci. Exact. 19: 243. 1994. Type: Colombia. Tolima: Cajamarca, corregimiento de Anaime, Páramo de los Valles, La Cascada, Hacia Santa Helena, 3710 m, Arbolito 2.5 m alt, 3 cm diám., lígulas blancas, flores vino tinto, en turbera, hojas con olor a mentol, pegajosas al tacto, Jun 1994, *Restrepo 371* (holotype: COL!, isotype: US!).

9. ***Piofontia cinerascens*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium cinerascens* Cuatrec., Caldasia 3: 422. 1945.

TYPE: COLOMBIA. Valle del Cauca: Cordillera Occidental, Los Farallones de Cali, filo de la cordillera, matorrales de páramo en el cerro de La Torre, 4000 m, arbolito, hoja verde claro, mate haz, blanquecina envés, nervio medial verdoso blanquecino, involucro violáceo sucio, lígulas blancas, corolas centrales blanco verdosas, Oct 10 1944, *Cuatrecasas 17851* (holotype: VALLE, isotypes: COL!, F!, P, US!).

9.1. ***Piofontia cinerascens*** subsp. ***puracensis*** (Cuatrec.) O.M. Vargas, comb. nov. *Diplostephium violaceum* var. *puracense* Cuatrec., Caldasia 3: 424. 1945. *Diplostephium cinerascens* subsp. *puracense* (Cuatrec.) Cuatrec., Webbia 24: 138. 1969. TYPE: COLOMBIA. Cauca: Cordillera Central, al sur del Volcán Puracé, filo de la cordillera en San Francisco, 3400–3450 m, arbolito muy ramoso de hoja muy compacta y redondeada, hoja verde vivo en la haz, blanco tomentoso en el envés, involucro verdoso en la base, violáceo en el extremo superior, lígulas blancas, flósculos blanco-verdosos, anteras violáceas, Aug 23 1943, *Cuatrecasas 14602* (holotype: VALLE, isotypes: COL!, F!, P, US!).

Diplostephium cinerascens var. *centrale* Cuatrec., Caldasia 3: 423. 1945. TYPE: COLOMBIA. Cauca: Cordillera Central, cabeceras del Río Palo, quebrada del Río López, Alto del Duende, matorrales y bosquecillo de páramo, 3300–3350 m, arbolito, hoja verde grisácea clara haz, blanquecina envés, brácteas involucrales violáceas, lígulas blancas, "guasgüín", Dic 1 1944, *Cuatrecasas 18796* (lectotype: US!, isotypes: A, COL!, F).

10. PIOFONTIA COLOMBIANA Cuatrec., Feddes Repert. Nov. Regni Veg. 55: 153. 1953. *Diplostephium colombianum* (Cuatrec.) Cuatrec., Caldasia 2: 5. 1943. TYPE: COLOMBIA. Boyacá: Sierra Nevada del Cocuy, alto valle de Las Lagunillas, pendientes rocosas mas abajo de los arenales, 4300–4400 m, frútex achaparrado, lígulas blancas que al secarse se vuelven rosado-amarillosas, Sep 12 1938, *Cuatrecasas & García-Barriga 1492* (holotype: COL!, isotypes: F!, US!).

11. ***Piofontia coriacea*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium coriaceum* Cuatrec., Webbia 24: 123. 1969. TYPE: COLOMBIA. Magdalena: Sierra Nevada de Santa Marta, flanco occidental, páramo 3100 m, arbusto 3 m, tomento amarillo-ferrugíneo-pálido, lígulas crema, flósculos rojizos, Jan 30 1959, *Romero-Castañeda 7162* (holotype: COL!, isotype: US!).

12. ***Piofontia costaricensis*** (S.F.Blake) O.M.Vargas, comb. nov. *Diplostephium costaricense* S.F.Blake, Contr. U. S. Natl. Herb. 24: 82. 1922. TYPE: COSTA RICA. San José: Cerro de la Muerte, 3100 m, Jan 1987, *Pittier 10459* (holotype: US!, isotype: G).

13. ***Piofontia crassifolia*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium crassifolium* Cuatrec, Bull. Torrey Bot. Club 80: 401. 1953. TYPE: COLOMBIA. Cesar: Sierra del Perijá, 10 km, 12 km al noreste de Manaure, 48 km al este de Valledupar, 1 km de la frontera con Venezuela, páramo 3000 m, capítulos blancos, Feb 5 1945, *Grant 10865* (holotype: US!, isotypes: NY, VEN).

14. ***Piofontia cyparissias*** (Wedd.) O.M.Vargas, comb. nov. *Diplostephium cyparissias* Wedd., Chlor. And. 1: 203. 1856. TYPE: COLOMBIA. Magdalena: Sierra Nevada de Santa Marta, vertiente N, flores albi, [without date], *Funck 387* (holotype: P, isotypes: G, F! [fragment], US! [fragment]).

15. ***Piofontia elliptica*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium ellipticum* Cuatrec., Caldasia 2: 212. 1943. TYPE: COLOMBIA. Norte de Santander: Páramo de Fontibón, 2600–2750 m, entre Pamplona y Chitagá, arbolito, Oct 16 1941, *Cuatrecasas, Schultes, & Smith 12336* (holotype: COL!, isotype: F!, US!).

16. ***Piofontia eriophora*** (Wedd.) O.M.Vargas, comb. nov. *Diplostephium eriophorum* Wedd., Chlor. And. 1: 206. 1856. TYPE: COLOMBIA. Tolima: Monte Tolima, en el límite inferior de la nieve, 1844, *Goudot s.n.* (holotype: P, isotypes: F! [fragment], FI, G, GH, P).

17. ***Piofontia farallonensis*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium floribundum* subsp. *farallonense* Cuatrec., Caldasia 3: 423. 1945. *Diplostephium farallonense* (Cuatrec.) Cuatrec., Webbia 24: 135. 1969. TYPE: COLOMBIA. Valle del Cauca: Cordillera Occidental, Los Farallones de Cali, filo de la cordillera, matorrales de páramo en el cerro de La Torre, 4000 m, arbolito, hoja coriácea, rígida, verde claro haz, blanquecina envés, involucro verdoso-amarillento, lígulas blancas, flósculos violáceos, Oct 10 1944, *Cuatrecasas 17855* (holotype: VALLE, isotype: COL!, F).

18. ***Piofontia floribunda*** (Benth.) O.M.Vargas, comb. nov. *Linochilus floribundus* Benth., Pl. Hartw. 203. 1845. *Diplostephium floribundum* (Benth.) Wedd., Chlor. And. 1: 205. 1856. TYPE: COLOMBIA. Cauca: Popayán, Páramo de Guanacas, [without date], *Hartweg 1126* (holotype: NY, isotypes: F!, K, LD, P).

Linochilus ochraceus Sch.Bip., as a synonym in Weddell Chl. And. 1: 205. 1857. Nom. nud.

Diplostephium ochroleucum Klatt, Engl. Bot Jahrb. 8: 37. 1886. Type: Colombia. Cauca: [illegible] von Paletará, 3000 m, Feb 5 1884, *Lehmann 3579* (holotype: K, isotype: US!).

Aster ochroleucus (Klatt) Kuntze Rev. Gen. Pl. 3: 131. 1898.

19. ***Piofontia fosbergii*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium fosbergii* Cuatrec., Bull. Torrey Bot. Club 80: 403. 1953. TYPE: COLOMBIA. Meta: Cordillera Oriental, Río Arroz arriba de la confluencia con la Quebrada del Pedregal, márgenes con matorrales, 3445 m, arbusto 3 m, capítulos pardo verdosos, Aug 29 1943, *Fosberg 20912* (holotype: F!, isotype: US!).

20. ***Piofontia frontinensis*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium frontinense* Cuatrec., Revista Acad. Colomb. Ci. Exact. 18: 123. 1991. TYPE: COLOMBIA. Antioquia: Mpio. Urrao, Páramo de Frontino, Llano Grande and hill to north, small areas of dense mossy forest intermixed with open Espeletia páramo, 3320–3450 m, shrub 1.5 m, rays white disk dull gray, foliage sticky-glandular, Mar 2 1989, *McDougal, Roldán, & Betancur 4424* (holotype: US!).

21. ***Piofontia glutinosa*** (S.F.Blake) O.M.Vargas, comb. nov. *Diplostephium glutinosum* S.F.Blake, Proc. Biol. Soc. Wash. 49: 78. 1936. TYPE: COLOMBIA. Santander: Páramo de los Colorados, arriba de La Baja, 3900–4100 m, frutex 30 cm, brácteas con manchas purpúreas, lígulas blancas, flósculos con tubo amarillo verdoso y lóbulos rosados,

estilos rosados, Jan 27 1927, *Killip & Smith 18440* (holotype: US!, isotypes: A, COL! GH, K, NY).

22. ***Piofontia grantii*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium grantii* Cuatrec., Bull. Torrey Bot. Club 80: 403. 1953. TYPE: COLOMBIA. Cesar: Sierra del Perijá, 10 km este-noreste de Manaure, 46 km al este de Valledupar, 3 km de la frontera con Venezuela, 2550 m, arbusto 2.6 m, hojas pardo amarillentas envés, lígulas blancas, Feb 4 1947, *Grant 10791* (holotype: F!, isotype: NY, US!).

23. ***Piofontia heterophylla*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium heterophyllum* Cuatrec., Caldasia 2: 230. 1943. TYPE: COLOMBIA. Cundinamarca: Macizo de Bogotá, Páramo de Cruz Verde, 3400–3500 m, árbolito achaparrado, 1–1.5 m, lígulas blancas, Sep 15 1940, *Cuatrecasas 10457* (holotype: COL!, isotypes: BC, F!, G, P, US!).

24. ***Piofontia huertasii*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium huertasii* Cuatrec., Webbia 24: 126. 1969. TYPE: COLOMBIA. Cundinamarca: municipio de Fómeque, páramo de Chingaza, finca la Laja, 3000 m, orillas del camino, arbusto 2 m, hojas verdes opacas haz, estilos de los flósculos del disco morados, Jan 10–18–20 1965, *Huertas & Camargo 5951* (holotype: US!, isotype: COL!).

25. ***Piofontia inesiana*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium inesianum* Cuatrec., Webbia 24: 192. 1969. TYPE: COLOMBIA. Magdalena: Sierra Nevada de Santa Marta, flanco occidental, 3140 m, arbusto 4 m, Jan 29 1959, *Romero-Castañeda 7127* (holotype: COL!, isotype: US!).

26. ***Piofontia jaramilloi*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium jaramilloi* Cuatrec., Phytologia 31: 317. 1975. TYPE: COLOMBIA. Boyacá: Cerro Berlín, between Arcabuco and la Palma (borderline between Boyacá and Santander), in degraded Andean Forest, 2900 m, frutex 1.5–3 m tall, leaves coriaceus, thick, yellowish green dull above, ochraceous below, inflorescences and involucres ochraceous, ligules white, disc corollas brownish, Mar 28 1973, Cuatrecasas, *García-Barriga & Jaramillo 28667* (holotype: US!, isotype: COL!).

27. ***Piofontia jenesana*** (S.Díaz & M.E.Morales) O.M.Vargas, comb. nov. *Diplostephium jenesanum* S.Díaz & M.E. Morales, Revista Acad. Colomb. Ci. Exact. 26: 7. 2002. TYPE: COLOMBIA. Boyacá: municipio de Jenesano, 2500 m, arbusto, hojas verde intenso, flores blancas, [without date], *Molano 14* (holotype: UPTC, isotype: COL!).

28. ***Piofontia juajibioyi*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium juajibioyi* Cuatrec., Webbia 24: 140. 1969. TYPE: COLOMBIA. Norte de Santander: entre Chitagá y El Cerrito, Páramo del Almorzadero, un poco abajo (al sur) del punto más álto del páramo, 3900 m, frútex 1 m, hojas verde haz, casi blancas envés, involucro verde velloso, lígulas blancas, estrechas, vilano violeta-rojizo, flores de disco verdes con ápices purpúreos, Dic 31 1959 –Jan 1 1960, *Barclay & Juajibioy 10388* (holotype: US!, isotypes: COL!, F!, MO, U).

29. ***Piofontia juliani*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium juliani* Cuatrec., Webbia 24: 127. 1969. TYPE: VENEZUELA. Táchira, debajo del Páramo de Tamá, cerca de la frontera con Colombia, faldas con bosque enano y subpáramo, 2750–2950 m, shrubby vining, leaves coriaceous, dark green above, buff brown below with reticulate nerves, bracts brownish green, Jun 20–23 1967, *Steyermark & Dunsterville 98616* (holotype: US!, isotype: NY).

30. ***Piofontia lacunosa*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium lacunosum* Cuatrec., Bull. Torrey Bot. Club 80: 406. 1953. TYPE: COLOMBIA. Boyacá: Sierra Nevada del Cocuy, alto valle de Las Lagunillas, 4000–4300 m, arbusto 2–3 m, Sep 12 1938, Cuatrecasas 1443 (holotype: F!, isotypes: COL!, US!).

31. ***Piofontia leioclada*** (S.F.Blake) O.M.Vargas, comb. nov. *Diplostephium leiocladum* S.F.Blake, Amer. J. Bot. 15: 62. 1928. TYPE: COLOMBIA. Caldas: Cordillera Occidental, Cerro Tatamá zona de matorral al borde del páramo, 3300–3500 m, arbusto, lígulas blancas, Oct 8–10 1922, *Pennell 10531* (holotype: US!, isotypes: GH, PH).

32. ***Piofontia micradenia*** (S.F.Blake) O.M.Vargas, comb. nov. *Diplostephium micradenium* S.F.Blake, Amer. J. Bot. 15: 49. 1928. TYPE: COLOMBIA. Caldas: Cordillera Occidental, Cerro Tatamá, 3300–3500 m, matorrales en subpáramo, lígulas blancas, flores de disco pardo-amarillas, Oct 8 1922, *Pennell 10533* (holotype: US!, isotype: GH).

33. ***Piofontia mutiscuana*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium mutiscuanum* Cuatrec., Webbia 24: 117. 1969. TYPE: COLOMBIA. Norte de Santander: entre Mutiscua y Pamplona, 3400 m, shrub 10–12 ft, rays white, anthers deep purple, pappus light brown, Feb 23 1927, *Killip & Smith 19708* (holotype: US!, isotypes: A, GH).

34. ***Piofontia nevadensis*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium nevadense* Cuatrec., Brittonia 8: 182. 1956. TYPE: COLOMBIA. Magdalena: Sierra Nevada de Santa Marta, hasta 15,500 pies de altitud (4724 m), entre peñas, hasta el nivel de las nieves perpetuas, flor amarilla, Jan 13 1924, *Wollaston 6* (holotype: K).

35. ***Piofontia oblongifolia*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium oblongifolium* Cuatrec., Caldasia 2: 220. 1943. TYPE: COLOMBIA. Norte de Santander: cerro al noreste de Pamplona, vertiente oriental, páramo entre matorrales de bosque andino, 2770 m, arbolito, lígulas blancas, Sep 26 1940, *Cuatrecasas & García-Barriga 10238* (holotype: COL!, isotypes: BC, F!, US!).

36. ***Piofontia obtusa*** (S.F.Blake) O.M.Vargas, comb. nov. *Diplostephium obtusum* S.F.Blake, Contr. U. S. Natl. Herb. 24: 84. 1922. TYPE: VENEZUELA. Trujillo: Páramo del Jabón, 3000–3200 m, Oct 2 1910, *Jahn 24a* (holotype: US!).

37. ***Piofontia ocanensis*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium ocanense* Cuatrec., Brittonia 8: 182. 1956. TYPE: COLOMBIA. Norte de Santander: entre Ocaña y Pamplona, 1878–1879, *Kalbreyer 1199* (holotype: K).

38. ***Piofontia ochracea*** (Kunth) O.M.Vargas, comb. nov. *Aster ochraceus* Kunth, Nov. Gen. Sp. Pl. 4: 94. 1820. *Diplostephium ochraceum* (Kunth) Nees, Gen. Sp. Aster. 201. 1832. *Tetramolopium ochraceum* (Kunth.) DC., Prodr. 5: 262. 1836. TYPE: COLOMBIA. [erroneously cited as Ecuador. Quito: monts de Quito, likely collected near Bogotá, Colombia], [without date], *Humboldt & Bonpland s.n.* (holotype: P, F! [fragment]).

Diplostephium denticulatum S.F.Blake, Contr. Gray Herb. 53: 25. 1918. TYPE: COLOMBIA. Cundinamarca: Macizo de Bogotá: Cerro de Guadalupe, 3000 m, Jul 1911, *Apollinaire & Arthur 11* (holotype: GH, isotype: US!).

39. ***Piofontia parvifolia*** (S.F.Blake) O.M.Vargas, comb. nov. *Diplostephium microphyllum* Wedd., Chl. And. 1: 201. 1857. *Diplostephium parvifolium* S.F.Blake, Contr. U. S. Natl. Herb. 24: 74. 1922. TYPE: COLOMBIA [erroneously cited as Venezuela]. Magdalena: Sierra Nevada de Santa Marta, 3000 m, arbustito, flores violáceas, [without date], *Funck 388* (holotype: P, isotypes: GH [fragment], P [fragment]).

Linochilus microphyllus Sch.Bip., as a synonym in Wedd. Chl. And. 1: 201. 1857. Nom. nud. Not *Diplostephium microphyllum* (Vent.) Nees. Nom. illeg.

40. ***Piofontia perijaensis*** (S.Díaz & G.P.Méndez) O.M.Vargas, comb. nov. *Diplostephium perijaense* S.Díaz & G.P.Méndez, Revista Acad. Colomb. Ci. Exact. 21: 406. 1997. TYPE: COLOMBIA. Cesar, Manaure, Serranía del Perijá, camino entre casa de vidrio y Cerro del Avión, 2900 m, 72°53′W 10°N, arbolito de 5 m, hojas seríceo-ferrugíneas por el envés, verde nítido por la haz, brácteas verdes variegadas con morado, lígulas blancas, flósculos pajizos, Nov 6 1993, *Rangel, Franco, Rudas, Olmos, Pardo y Clavijo 11212* (holotype: COL!, isotype: COL!).

41. ***Piofontia phylicoidea*** (Kunth) O.M.Vargas, comb. nov. *Aster phylicoides* Kunth, Nov. Gen. Sp. Pl. 4: 93. 1820. *Tetramolopium phylicoides* (Kunth) DC., Prodr. 5: 262. 1836. *Diplostephium phylicoides* (Kunth) Wedd., Chlor. And. 1: 205. 1856. TYPE: COLOMBIA. [errouneously cited as Mexico, see note below], [without date], *Humboldt & Bonpland s.n.* (holotype: P "Herb. Bonpland", isotype: P "Herb. Bonpland", F! [fragment]).

Linochilus phylicoides Sch.Bip., as a synonym in Wedd. Chl. And. 1: 205. 1857. Nom. nud.

Aster crassifolius Klatt, Abhandl. Natur. Gesell. Halle 15: 326. 1882. TYPE: COLOMBIA. [without specific locality and date], Linden 1 (lectotype: MA, isotypes: BM, F! [fragment], LIL).

Diplostephium umbelliferum S.F.Blake, Contr. U.S. Nat. Herb. 24: 80. pl. 26. 1922. TYPE: COLOMBIA. Cundinamarca: Cerro de Guadalupe, 1917, *Ariste-Joseph s.n.* (holotype: US!).

42. ***Piofontia pittieri*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium pittieri* Cuatrec., Caldasia 2: 221. 1943. TYPE: COLOMBIA. Valle del Cauca: Cordillera Central en el macizo del Huila, Páramo de Buena Vista, 3000–3600 m, Jan 1906, *Pittier 1174* (holotype: US!, isotype: F!).

43. ***Piofontia rangelii*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium rangelii* Cuatrec., Phytologia 49: 74. 1981. TYPE: COLOMBIA. Magdalena: Sierra Nevada de Santa Marta, transecto de Buritaca, Filo la Cumbre, 3850 m, arbustillo 1 m, lígulas blancas con tintes violáceos. Hojas blancas por el envés, Aug 19 1977, *Rangel & Cleef 994* (holotype: COL!, isotypes: COL!, U, US!).

44. ***Piofontia revoluta*** (S.F.Blake) O.M.Vargas, comb. nov. *Diplostephium revolutum* S.F.Blake, Contr. U. S. Natl. Herb. 24: 78. 1922. TYPE: COLOMBIA. Cundinamarca: Bogotá, 1917, *Ariste-Joseph A233* (holotype: US!).

Diplostephium revolutum var. *longifolium* Cuatrec., Trab. Mus. Nac. Ci. Nat., Ser. Bot. 33: 134. 1936. TYPE: COLOMBIA. Tolima: Vertiente sur del Nevado del Tolima, Las Mesetas, 3800 m, "romero", Jun 13 1932, *Cuatrecasas 2892* (holotype: MA).

Diplostephium revolutum var. *rubrum* Cuatrec., Caldasia 2: 236. 1943. TYPE: COLOMBIA. Boyacá: Páramo de la Rusia, vertiente SE, Boca de Monte, 3300–3400 m, arbusto, hojas pegajosas, copa densa verde clara, Aug 4 1940, *Cuatrecasas 10416* (holotype: COL!, isotypes: BC, F!, U, US!).

Diplostephium revolutum f. *macrocephalum* Cuatrec., Caldasia 2: 236. 1943. TYPE: COLOMBIA. Santander: Páramo del Almorzadero vertiente norte, 3600–3800 m, arbolito, lígulas blancas, Nov 28 1941, *Cuatrecasas 13513* (holotype: COL!, isotypes: BC, F!, US!).

45. ***Piofontia rhododendroides*** (Hieron.) O.M.Vargas, comb. nov. *Diplostephium rhododendroides* Hieron., Bot. Jahrb. Syst. 21: 340. 1896. TYPE: COLOMBIA. Nariño: Azufral de Túquerres, Laguna Verde, Jan 1840, *Stubel 429* (holotype: US! [fragment from destroyed specimen in B], F! [photo]). Ibid: Volcán Azufral, 3400–3500 m, escamas rojo carmín brillante, Feb 10 1972, *Mora 1878A* (topotype: US!).

Diplostephium cochense Hieron., Bot. Jahrb. Syst. 21: 341. 1896. Type: Colombia. Nariño: llanura del Río Cocha con el frailejón, Aug 1869, *Stubel 353* (holotype: US! [fragment from destroyed specimen in B]).

46. ***Piofontia rhomboidalis*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium rhomboidale* Cuatrec., Webbia 24: 151. 1969. TYPE: COLOMBIA. Boyacá, Sierra Nevada del Cocuy, alto valle de Las Lagunillas, 4000–4300 m, arbusto 2–3 m, lígulas azafrandas, vilanos rojizos, Sep 12 1938, *Cuatrecasas & García-Barriga 1450* (holotype: US!, isotypes: COL!, F!, P).

47. ***Piofontia ritterbushii*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium ritterbushii* Cuatrec., Phytologia 23: 350. 1972. TYPE: COLOMBIA. Huila: west slope below Pico Norte of Nevado del Huila, 4200 m (range is 4150–4250 m), very abundant, Jan 11 1970, *Ritterbush s.n.* (holotype: US!).

48. ***Piofontia romeroi*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium romeroi* Cuatrec., Webbia 24: 173. 1969. TYPE: COLOMBIA. Magdalena: Sierra Nevada de Santa Marta, flanco occidental, 3180 m, arbolito 5 m, flores rojas, Jan 29 1959, *Romero-Castañeda 7115* (holotype: COL!, isotypes: MO, US!, VEN).

49. ***Piofontia rosmarinifolia*** (Benth.) O.M.Vargas, comb. nov. *Linochilus rosmarinifolius* Benth., Pl. Hartw. 197. 1845. *Diplostephium rosmarinifolium* (Benth.) Wedd., Chlor. And. 1: 202. 1856. TYPE: COLOMBIA. Cundinamarca: Bogotá, alrederores, [without date], *Hartweg 1092* (holotype: K, isotypes: F!, G, LD, NY, P, US!, W).

Diplostephium baccharideum Blake, Contr. U. S. Natl. Herb. 24: 77. 1922. TYPE: COLOMBIA. Cundinamarca: Bogotá, Monserrate, 1917, *Aristhe-Joseph B34* (holotype: US!).

Diplostephium rosmarinifolium var. *baccharideum* (Blake) Cuatrec., Trab. Mus. Nac. Ci. Nat., Ser. Bot. 33: 135. 1936.

50. ***Piofontia rupestris*** (Kunth) O.M.Vargas, comb. nov. *Aster rupestris* Kunth, Nov. Gen. Sp. Pl. 4: 94. Table 334. 1820.

Tetramolopium rupestre (Kunth) Ness, Gen. Sp. Ast. 203. 1832. *Diplostephium rupestre* (Kunth) Wedd., Chlor. And. 1: 206. 1856. TYPE: ECUADOR. Rucu Pichincha, [without date], *Humboldt & Bonpland 3047* (holotype: P "Herb. Bonpl", isotype: P "Herb. Bonpl").

Aster pichinchensis Willd. ex Nees, Gen. Sp. Ast. 203. 1832. Nom. nud.

Diplostephium mutisii Cuatrec., Trab. Mus. Nac. Ci. Nat., Ser. Bot. 29: 25. 1935. TYPE: COLOMBIA. Tolima: páramo del Nevado del Tolima, vert. S y SE, 4000–4300 m, Jun 15 1932, *Cuatrecasas 2882* (holotype: MA).

51. ***Piofontia santamartae*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium santamartae* Cuatrec., Phytologia 52: 174. 1982. TYPE: COLOMBIA. Magdalena: Sierra Nevada de Santa Marta, "Transecto del Río Buritaca", 3000 m alt, arbolito 3 m, brácteas e involucro de color vino tinto, hojas haz verdosas envés amarillo pálido, Aug 1977, *Rangel & Cleef 928* (holotype: COL!, isotypes: COL!, US! [fragment]).

52. ***Piofontia saxatilis*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium saxatile* Cuatrec., Proc. Biol. Soc. Wash. 74: 14. 1961. TYPE: COLOMBIA. Magdalena: Sierra Nevada de Santa Marta, flanco suroriental, hoya del Río Donachí entre la Laguna Esacuriba y unos enormes cantos y peñascos, 7870 m, árbolito 2–6 m, hoja blanda haz verde clara, envés ceniciento, involucro violáceo, corolas tubulosas amarillentas, Oct 6 1959, *Cuatrecasas & Romero-Castañeda 24620* (holotype: US!, isotypes: COL!, F!, G, NY, P).

53. ***Piofontia schultzii*** (Wedd.) O.M.Vargas, comb. nov. *Diplostephium schultzii* Wedd., Chlor. And. 1: 204. 1856. TYPE: COLOMBIA. Tolima: Volcán Tolima, 9200 toeses, 21 fl. Pourpres, Jan 1843, *Linden 901* (holotype: P, isotypes: BM, F!, G, K, P, W, US! [fragment]).

Linochilus jodopappus Sch.Bip. ex Wedd., Chl. And. 1: 204. 1857. Nom. nud.

54. ***Piofontia tachirensis*** (V.M.Badillo) O.M.Vargas, comb. nov. *Diplostephium tachirense* V.M.Badillo, Bol. Soc. Venez. Ci. Nat. 10: 305. 1946. TYPE: VENEZUELA. Táchira, Páramo de Tamá, Jul 15 1944, *Steyermark 57360* (holotype: VEN, isotypes: F!, NY, US!).

55. ***Piofontia tamana*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium tamanum* Cuatrec., Caldasia 2: 214. 1943. TYPE: COLOMBIA. Norte de Santander: Páramo de Tamá, alrededores de La Cueva, residuos del bosque andino límite, 3000–3200 m, lígulas blancas, flósculos verdosos, Oct 28 1941, *Cuatrecasas, Schultes, & Smith 12710* (holotype: COL!, isotypes: F!, P, S, U).

56. ***Piofontia tenuifolia*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium tenuifolium* Cuatrec., Caldasia 2: 211. 1943. TYPE: COLOMBIA. Boyacá, Valle de la Uvita, El Hatico (entre Soata y Cocuy), bosque andino y matorrales, 3350 m, árbol grande, Sep 15 1938, *Cuatrecasas & García-Barriga 1793* (holotype: COL!, isotypes: F!, P, US!).

57. ***Piofontia tergocana*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium tergocanum* Cuatrec., Webbia 24: 175. 1969. TYPE: COLOMBIA. Magdalena: Sierra Nevada de Santa Marta, en las cabeceras del Río Sevilla, entre grandes piedras en la base la subida al segundo pico al este de la cabecera de la hoya, flanco occidental del pico, 3770 m, "station 19", arbusto de 3 m, olor de Espeletia, tallos inferiores desnudos, hojas verdes haz, blanco lanosas envés, brácteas involucrales purpúreas, vilanos de blanco a rosado, muy resinoso, pegajoso, Jan 28 1959, *Barclay & Juajibioy 6762* (holotype: US!).

58. ***Piofontia venezuelensis*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium venezuelense* Cuatrec., Caldasia 2: 233. 1943. TYPE: VENEZUELA. Mérida, Tabay, 2500–3000 m, arbusto de 2–5 m de altura, hojas aromáticas, cabezuelas amarillo ocre, Nov 18 1930, *Gehriger 473* (holotype: VEN, isotypes: G, MO, NY, F!, US!).

59. ***Piofontia violacea*** (Cuatrec.) O.M.Vargas, comb. nov. *Diplostephium violaceum* Cuatrec., Caldasia 2: 232. 1943. TYPE: COLOMBIA. Caldas: Cordillera Central, vertiente occidental, vert. SW del Nevado del Ruiz, Termales, 3400 m, arbusto de 2 m, o árbol hasta 8 m, flores centrales violáceas, lígulas blancas, "romerillo," Jun 4 1940, *Cuatrecasas 9229* (holotype: COL!, isotypes: P, F!, US!).

60. ***Piofontia weddellii*** (S.F.Blake) O.M.Vargas, comb. nov. *Diplostephium weddellii* S.F.Blake, Contr. U. S. Natl. Herb. 24: 79. 1922. TYPE: COLOMBIA. Guajira: Sierra Nevada de Santa Marta, prov. del Riohacha, 4000–4400 m, arbusto, flores amarillas, Mar 1 1852, *Schlim 806* (holotype: P, isotypes: BM, F!, G, K).

Diplostephium sessiliflorum Wedd., Chlor. And. 1: 204. Nom. illeg. 1856. Not D. sessiliflorum Spreng. 1826.

Denticulata new clade name. Node based definition: the clade originating with the most common ancestor of *Piofontia antioquensis, P. camargoana, P. huertasii, P. jaramilloi, P. jenesana, P. mutiscuana, P. oblongifolia, P. ochracea, P. tachirensis, and P. tenuifolia* (clade 1, in Fig, 1). Name originally proposed by Blake (1922) and later redefined by Cuatrecasas (1969).

Schultziana new clade name. Node based definition: the clade originating with the most common ancestor of *Piofontia alveolata, P. apiculata, P. costaricensis, P. juajibioyi, P. rhomboidalis, and P. schultzii* (clade 2, Fig. 1). Name originally proposed by Cuatrecasas (1969).

Additional Taxa—The following taxa described by earlier studies as species of *Diplostephium* also belong in *Piofontia,* but combinations have not been made here because they will become taxonomic synonyms of recognized species of *Piofontia* in the systematic treatment of the genus for Colombia (Vargas in prep.)

1. *Diplostephium dentatum* Cuatrec.
2. *Diplostephium fernandez-alonsoi* S.Díaz.
3. *Diplostephium floribundum* subsp. *aequatoriense* Cuatrec.
4. *Diplostephium floribundum* subsp. *llanganatense* Cuatrec.
5. *Diplostephium floribundum* subsp. *putumayense* Cuatrec.
6. *Diplostephium floribundum* subsp. *cundinamarcense* Cuatrec.
7. *Diplostephium tolimense* Cuatrec.

A New Synonym for Diplostephium serratifolium—In 2014, Robinson and Funk (2014) erected the genus *Dysaster* H.Rob. & V.A.Funk for a plant specimen with affinities to *Diplostephium* (Robinson and Funk 2014: 35) but which they thought differed

significantly from any species previously described in that genus. Apparently, unknown to Funk and Robinson, a conspecific from the same location (near Contumazá, Peru), *Diplostephium serratifolium* Cuatrec., had been described by Cuatrecasas (1982). Robinson and Funk (2014) focused their diagnosis on the morphological features that, in their opinion, supported the description of a new species and a genus: 1) compressed achenes with only two ribs; 2) fully bisexual disk florets with stigmatic lines; 3) involucral bracts narrowly lanceolate, striped and pointy; 4) outer row of pappus differentiated in short squamae; and 5) exserted inflorescence with few heads borne by long peduncles. While all the aforementioned characteristics match the description of *D. serratifolium* made by Cuatrecasas (1982), these features are not unique to *Diplostephium serratifolium* (=*Dysaster cajamarcensis*) and therefore do not support the segregation of a new genus: 1) the compression of the achenes is commonly not reported in the description of new species and is mostly unknown in other species of *Diplostephium* s. s., therefore it is premature to assign this characteristic as diagnostic; 2) fertile ovaries in disk flowers and stigmatic lines are also present in at least in *D. haenkei* (DC.) Wedd. (Cuatrecasas 1982), and the state for this character for numerous species is unknown; 3) striped narrow involucre bracts are not uncommon in *Diplostephium* s. s. (e.g. *D. cajamarquillensis* Cabr., *D. callaensis* Cuatrec.); 4) squamate-like outer pappus is at least also present in *D. ericoides* and *D. azureum* Cuatrec. and probably in other species too; and 5) long peduncles are also present in *D. wurdackii* Cuatrec. Because of the evidence explained above and the position of *Diplostephium serratifolium* falling within the phylogenetic circumscription of *Diplostephium* s. s. (Fig. 1), *Dysaster cajamarcensis* should be considered a synonym of *Diplostephium serratifolium*.

Diplostephium serratifolium Cuatrec. Phytologia 52: 176. 1982. Type: Peru. Cajamarca: Contumazá, circa Contumazá, 2700 m, Jun 1960, *Alza s.n.* (holotype: LP, isotype: USM!, US! [fragment, photo]).

Dysaster cajamarcensis H.Rob. & V.A.Funk. Type: Peru. Cajamarca: Prov. Contumazá. 14 km S of Contumazá on gravel road, rocky slopes, western cordillera, evergreen forest, 2620 m, Jul 1992, *Stuessy, Crawford & Sagastegui 12686* (holotype: US).

Artificial Key for the Identification of *Diplostephium* and *Piofontia*

1. Ray corollas comparatively short, rarely long, 5–9(15) mm long. Subshrubs, shrubs, and small trees, 0.1–10.0 m tall, always with determinate branches leading to a candelabrum-like branching pattern in which every branch is terminated by a capitulescence. Leaves 0.3–23 cm long. Adaxial leaf surface usually eglandular or sparse-glandulose. Capitulescences of solitary capitula or with up to 100 heads. Distribution: Costa Rica, Colombia, Venezuela, northern and central Ecuador (Azuay, Bolivar, Carchi, Chimborazo, Cotopaxi, Imbabura, Napo, Pastaza, Pichincha, Tungurahua, Sucumbios) . . . . . *Piofontia*

1. Ray corollas long, 8–22 mm long. Subshrubs and shrubs 0.2–3.0 m tall, with long indeterminate branches that bear short branchlets topped with solitary capitula or a candelabrum-like branching pattern in which every branch is terminated by a capitulescence. Leaves 0.2–8.0 cm long. Adaxial leaf surface usually eglandular or sometimes densely-glandulose. Capitulescences comprised of solitary capitula or with up to 20 heads. Distribution: southern Colombia (Cauca, Huila, Nariño, Putumayo), Ecuador, Peru, Bolivia, northern Chile (Arica y Parinacota, Tarapacá, Antofagasta) . . . . . *Diplostephium*

Discussion

Despite the overlapping morphological characteristics among species of *Piofontia* and *Diplostephium* (microphyllous leaves, heterogamous capitula, ray florets with a 2–3-lobed limb, rays white to purple, and double pappus) a combination of morphological characters can separate these clades (Table 1). *Piofontia* species are characterized by being subshrubs (0.10–0.49 m tall) or shrubs (0.5–3.9 m tall) with leaves 0.3–4.0 cm long, to small trees (4–10 m tall) with leaves 4–23 cm long (Fig. 2). Subshrubs and small shrubs in *Piofontia* have solitary or few (< 20) capitula per capitulescence (Fig. 2E–G), while taller shrubs and small trees always bear 20–100 heads per capitulescence (Fig. 2D). The branching pattern of *Piofontia* is very consistent, with flowers occurring on terminal branches determining their growth (Fig. 2E); typically, three or four branches develop from the axillary buds close to the capitulescence, continuing the vertical growth of the plant. This architecture gives *Piofontia* species a characteristic candelabrum branching pattern (Fig. 2A–B). Ray corollas in *Piofontia* are short or medium in length (Fig. 2D–G), 5–9 mm long,

Table 1. Comparative aspects between *Diplostephium* and *Piofontia*.

	Piofontia	*Diplostephium*
Habit	Subshrubs, shrubs, or small trees up to 10 m tall.	Subshrubs, shrubs up to 3 m tall.
Branching pattern	Candelabrum-like, every branch is terminated by a capitulescence.	Candelabrum-like, or long indeterminate branches bearing short branches topped by solitary capitula.
Capitulescence	Subshrubs bearing mostly solitary capitula. Shrubs and trees with multiple heads per capitulescence. Number of capitula increases with plant size and leaf width, up to 100 heads per capitulescence.	Subshrubs bearing mostly solitary capitula. Shrubs bearing up to 20 heads per capitulescence.
Ray corollas length	5–9(15) mm	8–22 mm
Distribution	Northern Andes, Sierra Nevada de Santa Marta, and Talamanca Cordillera; Costa Rica, Colombia, Venezuela, northern and central Ecuador (Azuay, Bolivar, Carchi, Chimborazo, Cotopaxi, Imbabura, Napo, Pastaza, Pichincha, Tungurahua, Sucumbios).	Central Andes and southern Northern Andes; southern Colombia (Cauca, Huila, Nariño, Putumayo), Ecuador, Peru, Bolivia, northern Chile (Arica y Parinacota, Tarapacá, Antofagasta).
Habitat	Páramo and high Andean forest.	Dry puna, humid puna, páramo, and upper boundary of the high Andean forest.
Number of species	60	48

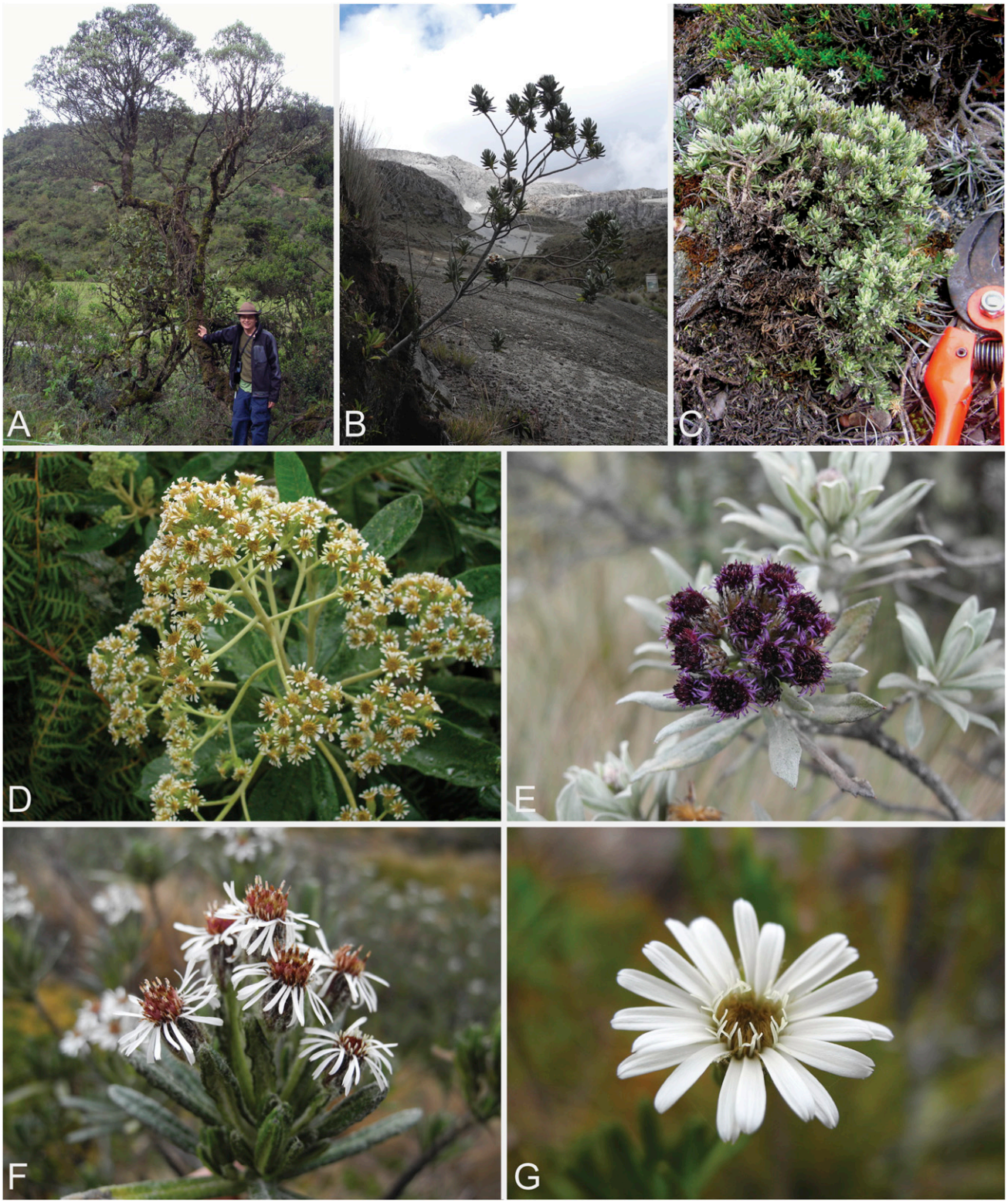

FIG. 2. A. *Piofontia oblongifolia*. B. *P. eriophora*. C. *P. apiculata*. D. *P. camargoana*. E. *P. schultzii*. F. *P. rupestris*. G. *P. frontinensis*. Notice the candelabrum-like branching pattern in B and the short and medium length ray corollas in D–G.

relative to *Diplostephium* with only some species reaching lengths of 9–15 mm.

Diplostephium species are subshrubs or shrubs up to 3 m tall (Fig. 3); subshrubs and medium-sized shrubs have leaves 0.2–3.0 cm long; scandent and large-sized shrubs have leaves 4–8 cm long. Most species have solitary capitula (Fig. 3A, C–D), but scandent and large-sized shrubs exhibit up to 20 heads per capitulescence (Fig. 3B, E, F). A distinctive feature of most *Diplostephium* species with solitary capitula is an architectural pattern in which long, indeterminate branches bear short branchlets topped with solitary capitula (Fig. 3C–D). Ray corollas in *Diplostephium* are always long, 8–22 mm in length

FIG. 3. A. *Diplostephium meyenii*. B. *D. haenkei*. C. *D. hartwegii*. D. *D. gnioides*. E. *D. barclayanum*. F. *D. lechleri*. G. *D. oxapampanum*. Notice the short branches topped with solitary capitula in C–D and the long ray corollas in D–G.

(Fig. 3D–G). *Diplostephium* now comprises 48 species that inhabit the puna and the humid puna (high yunga) in Peru, Bolivia, and northern Chile, and the páramo in Ecuador and southern Colombia (where its distribution overlaps with *Piofontia*). *Diplostephium* taxonomy remains largely unstudied since the last revision of the genus that included Peruvian species (Blake 1928); a morphological study is necessary to properly define the morphological boundaries of the genus.

The ddRAD phylogeny of Vargas et al. (2017) places *Parastrephia quadrangularis* as sister to *Diplostephium meyenii*

Wedd. nested within *Diplostephium.* Even though this position suggests that *Parastrephia* Nutt. species should be transferred to *Diplostephium*, the phylogenetic position of *Parastrephia* in the Vargas et al. (2017) phylogeny may be biased by the high indices of hybridization and introgression found among *P. quadrangularis* and *D. cinereum*, *D. meyenii*, and *D. sp. nov.* CAJ2 (Vargas et al. 2017). Simulations have shown that gene flow can affect phylogenetic topologies, producing support for erroneous inferences of species trees (Leaché et al. 2014). Therefore, it is possible that *Parastrephia* is an independent lineage from *Diplostephium* as suggested by the nuclear ribosomal phylogeny of Vargas et al. (2017). *Parastrephia* comprises three species of densely branched cupressiform shrubs distinguished by having sessile microphyllous leaves, disciform heads, yellow corollas, pistillate flowers in one series with tubular or limbate corollas, disc flowers functionally staminate and tubular, and receptacles epaleate (Nesom 1993; Nesom and Robinson 2007). Extended sampling that includes a broader *Parastrephia* sampling is needed to resolve its position relative to *Diplostephium*.

Incompatibility between the traditional classification of Astereae (Nesom and Robinson 2007) and molecular phylogenies (Noyes and Rieseberg 1999; Sancho and Karaman-Castro 2008; Brouillet et al. 2009; Karaman-Castro and Urbatsch 2009; Sancho et al. 2010; Vargas and Madriñán 2012; Vargas et al. 2017) demonstrates morphological lability in the tribe and calls for a revaluation of its subdivision. These results suggest that it is possible that similar morphologies among genera in the tribe are the product of parallel evolution, confounding morphological classification relative to the true phylogeny of the tribe. In the specific case of *Diplostephium* and *Piofontia,* the morphological tendency to present a reduced vegetative morphology with increasing altitude (shrubs/subshrubs, microphyllous leaves), is likely the result of convergent adaptation to the physiological stress produced by lower temperatures and daily climate oscillations in the high Andes (Meinzer et al. 1994). Alternatively, these overlapping characters may be of plesiomorphic nature. Future phylogenetic studies in Astereae should focus on sequencing numerous nuclear loci to obtain a robust phylogeny of the tribe as chloroplast and mitochondrial phylogenies are often misleading in cases of recent and ancient hybridization (Vargas et al. 2017). Recent studies (Lagomarsino et al. 2014; Uribe-Convers and Tank 2016; Vargas et al. 2017) demonstrate the utility of employing multiple loci and phylogenomic approaches in systematics studies to elucidate novel taxa in biodiversity hotspots.

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