BOTANY



Taxonomic novelties in Orthaea (Ericaceae: Vaccinieae)

Novedades taxonómicas en Orthaea (Ericaceae: Vaccinieae)

Nelson R. Salinas

• Received: 5/jun/2019

- Accepted: 13/feb/2020
- Published online: 13/mar/2020

Citation: Salinas NR. 2020. Taxonomic novelties in *Orthaea* (Ericaceae: Vaccinieae). Caldasia 42(2):241–249. doi: https://dx.doi.org/10.15446/caldasia.v42n2.79922.

ABSTRACT

Several taxonomical novelties of the genus *Orthaea* (Ericaceae: Vaccinieae) are presented. Two new species, *O. eteocles* and *O. fissiflora*, are described and illustrated, the limits of *O. glandulifera* are redefined to include *O. oedipus* as a synonym, and the status of a poorly known species, *O. ignea*, is also discussed.

Keywords. Andean flora, biodiversity, neotropical plants

RESUMEN

Se presentan varias novedades taxonómicas del género *Orthaea* (Ericaceae: Vaccinieae). Se describen e ilustran dos especies nuevas, *O. eteocles* y *O. fissiflora*, los límites taxonómicos de *O. glandulifera* son re-circunscritos, incluyendo *O. oedipus* como sinónimo, y el estatus taxonómico de una especie pobremente conocida, *O. ignea*, es también discutido.

Palabras clave. Biodiversidad, flora de los Andes, plantas neotropicales

INTRODUCTION

The plant family Ericaceae, with more than 4100 species, is an important floristic element of tropical montane ecosystems (Stevens *et al.* 2004). In the northern Andes, this family is represented by more than 600 species, most of them restricted to mid-elevation rain forests (Luteyn 2002). *Orthaea* Klotzsch, which includes 37 currently accepted species (Salinas 2015), is one of the least studied genera of neotropical Ericaceae. Traditionally, this genus has been delimited by the presence of conspicuously dimorphic stamens with filaments of alternating lengths and equal-sized anthers (Luteyn 1987). Although most species of *Orthaea* are found in Andean forests from Colombia to Bolivia, some are found in the Guiana Shield (Venezuela and Guyana) and Central America (S Mexico–Panama).

Phylogenetic affinities of Orthaea have remained largely elusive. Phylogenetic analyses have established that the genusas traditionally circumscribed-is paraphyletic (Kron et al. 2002, Pedraza-Peñalosa et al. 2015, Salinas 2015). Species from the Guiana Shield–along with O. stipitata (Luteyn) Luteyn (Mexico)-belong to a clade of extra-neotropical origin that includes some Vaccinieae from Southeast Asia, such as Paphia Seem. and Dimorphanthera J.J. Sm. Although all Andean species belong to the Neotropical clade (sensu Kron et al. 2002), there are multiples lineages within. With the exception of Orthaea madidiensis Pedraza & Luteyn, that has been recovered within a clade of Bolivian species of Thibaudia J. St.-Hil. and Satyria Klotzsch, the remaining species of the genus belong to a clade of heterandrous (highly anisomorphic stamens) taxa that contains most of the diversity of Cavendishia Lindl., Satyria, and Andean Orthaea. Although most of the species of Orthaea belong to the latter clade, relations within such lineage are poorly supported (Pedraza-Peñalosa et al. 2015, Salinas 2015). Therefore, such studies do not recommend a re-circumscription of Orthaea until more robust and copiously sampled phylogenies were procured.

As a result of a recent detailed taxonomic and phylogenetic study on *Orthaea* (Salinas 2015), several taxonomic novelties were discovered, including two new species, the re-circumscription of a poorly known species, and a new synonym, all of which are here presented.

MATERIALS AND METHODS

Specimens from the herbaria AAU, BM, CAS, COL, CUVC, E, F, G, GB, HUA, JAUM, K, L, MO, NY, LOJA, LPB, P,

QCA, QCNE, U, UC, US, and W where examined. Additional collections were procured through fieldwork in Colombia and Ecuador. Description of leaf venation characters follows the recommendations of Pedraza-Peñalosa *et al.* (2013). Specimen and morphological data was manipulated through a MySQL database, and accessed through custom Perl-DBI scripts.

RESULTS AND DISCUSSION

Orthaea eteocles N. R. Salinas, sp. nov. TYPE. ECUADOR. Esmeraldas: Near Lita, 0°55' N, 78°34' W, 600 m, 19 May 1987 (fl), *H. H. van der Werff 9497* (holotype QCNE!; isotypes AAU!, MO!, NY!). (Fig. 1).

Orthaea eteocles differs from *O. glandulifera* Luteyn by having longer inflorescence axis (77–116 mm vs. 1.7–5 mm in *O. glandulifera*), fewer flowers per inflorescence (6–13 vs. 15–24), longer stamens (14–15.5 vs. 8–10.2), longer anthers (4.3–6.6 mm vs. 2.9–3.4 mm), glabrous young branchlets (vs. pubescent), and v-shaped calyx sinuses (vs. u-shaped).

Epiphytic shrubs, scandent. Young branchlets terete or complanate, 1.5-2.0 mm diam., smooth, glabrous; mature branchlets glabrous, bark not exfoliating. Axillary buds globose, stipitate, stalk 0.5-1.0 mm long; prophylls 2, valvate, ovate or deltoid, 0.5-1.1 mm long, carinate or ecarinate, margin entire, eciliate, apex obtuse, abaxial side glabrous. Leaves alternate, internodes 1.0-2.9 cm long; petiole canaliculate, 3.0-5.0 mm long, rugose in dried material, glabrous; lamina chartaceous, elliptic, 6.1-11.5 \times 2.0–4.8 cm, base rounded or obtuse, margin entire, revolute in dried material, eciliate, apex rostrate or caudate, glabrous on both sides; laminar glands absent; venation acrodromous, basal, perfect or imperfect, midvein raised on abaxial side, impressed on adaxial side, secondary venation camptodromous, prominent lateral veins 1-2, raised on abaxial side, impressed or raised on adaxial side. Inflorescence axillary or terminal, a 15-24-flowered raceme or panicle; axis 77-116 mm long, hirsute, hairs glandular and multicellular, peduncle 15-60 mm long, rachis 17-100 mm long; floral bracts early caducous, not seen; pedicel fleshy, 21-48 mm long, markedly swollen at apex, 0.5-1.0 mm diam. at base, 5-6 mm diam. at apex, glabrous, articulate with calyx; bracteoles early caducous, not seen. Flower 5-merous, diplostemonous. Calyx aestivation valvate, pink, tubular, 7-8 mm long, sessile or stipitate, terete, apophysate at base, apophysis perpendicular,



Figure 1. Orthaea eteocles. a. branchlet and inflorescence; b. flower; c. stamens; d. calyx and style.

entire, glabrous or apically hirsute, the hairs glandular and multicellular; tube cylindric, $3-6 \text{ mm} \log$, $4.0-6.5 \text{ mm} \dim$; limb straight, chartaceous or membranose, $3-5 \text{ mm} \log$, lobes deltoid or ovate, $0.8-2.0 \times 2.4-3.5 \text{ mm}$, margin eciliate, marginal gland present, apex round and apiculate, sinuses v-shaped. Corolla aestivation valvate, white at base, white at apex, membranose, bistratose, tubular, terete, $34-37 \text{ mm} \log$, $4-6 \text{ mm} \dim$, $3-4 \text{ mm} \dim$ at throat, abaxial side hirsute, the hairs glandular and multicellular, adaxial side glabrous; lobes deltoid, $0.5-0.7 \times 0.7-0.9 \text{ mm}$. Stamens 10, distinct, not adherent to corolla, included, filaments alternately unequal.

Long stamens 15.0-15.5 mm long; filaments straight, $10.5-11.0 \times 1.1-1.2$ mm, apically puberulous, the hairs eglandular and unicellular; anthers 4.3-4.7 mm long; thecae non-prognathous, 2.4-2.9 mm long, 0.6-0.8 mm wide, glabrous, not appendiculate; tubules parallel, 2.8-3.0 mm long, 0.7 mm diam., dehiscing by latrorse pores, pores 0.5-1.2 mm long, margin entire. Short stamens like those of the longer cycle except for 14-15 mm long, filaments $7.0-7.5 \times 1.0-1.4$ mm, anthers 5.8-6.6 mm long, thecae 2.9-3.0 mm long, 0.8 mm wide, tubules 3.0-3.4 mm long, 0.6-0.7 mm diam., dehiscing by introrse pores. Ovary 5-locular, placentation axile. Nectary disk flat,

glabrous; style 38 mm long, included, stigma truncate. Berry not seen.

Distribution and ecology. *Orthaea eteocles* is endemic to Esmeraldas province, Ecuador, in tropical rain forests at 600–900 m. Flowering specimens have been collected in May and June, fruiting only in May.

Specimens examined. ECUADOR. Esmeraldas: vicinity of Alto Tambo, Lita–San Lorenzo rd., 10–20 km NW of Lita, 0°54'–55' N, 78°32'–34' W, 800–822 m, 20 Jul 2000 (fl), *T. B. Croat 84239* (QCNE); 12 May 1991 (fl, fr), *A. H. Gentry 70107* (MO, NY); Alto Tambo, finca El Paraíso, carretera Lita–S. Lorenzo km 9, 0°55' N, 78°34' W, 700–900 m, 5 Jun 2003 (fl), *G. Villa 2021* (NY).

Etymology. Named after Eteocles, a mythological Greek character. Eteocles was the son of Oedipus and succeeded him as king of Thebes. Several classic tragedies are based on the story of his fight against his brother Polynices, such as "Thebaid" (Statius 2008), "Oedipus at Colonus" (Sophocles 2007), and "Seven against Thebes" (Aeschylus 1956). The epithet is an analogy to the fact that *Orthaea eteocles* is a segregate of *O. oedipus* Luteyn, which is now considered a synonym of *O. glandulifera*—see below.

Orthaea eteocles is morphologically similar to some species of *Orthaea* from western Colombia, such as *O. glandulifera* Luteyn, *O. medusula* Pedraza, and *O. peregrina* A. C. Sm. All these species bear glandular and multiseriate hairs on the calyx and corolla (sometimes extending into pedicels and inflorescence axis), and usually have pedicels notoriously swollen at the apex. Their differences are summarized in Table 1. All specimens of *O. eteocles* were previously annotated as *O. oedipus* Luteyn, a taxon synonymized under *O. glandulifera* herein.

Orthaea fissiflora N. R. Salinas & Pedraza, sp. nov. TYPE. BOLIVIA. La Paz: Murillo, Yungas, valle del río Zongo, 24.2 km al N de la cumbre, 16°7' S, 68°7' W, 2900 m, 11 Apr 1987 (fl, fr), *J. C. Solomon 16538* (holotype LPB!; isotypes G!, MO!, NY!). (Fig. 2).

Orthaea fissiflora differs from *O. pinnatinervia* Mansf. because of its basally green corolla that usually splits longitudinally after anthesis (vs. red and without tears in *O. pinnatinervia*), connate staminal filaments (vs. distinct), and longer stamens (long cycle 7.4–8.4 mm vs. 6.5–7.0 mm; short cycle 6.3–7.0 mm vs. 4.8–5.5 mm).

Terrestrial or epiphytic shrubs 1-2 m tall, scandent. Young branchlets ridged or terete, 1-4 mm diam., smooth or striate, glabrous; mature branchlets glabrous, bark not exfoliating. Axillary buds complanate, stipitate, stalk 0.2-0.8 mm long; prophylls 2, imbricate, ovate or lanceolate, 1.0-2.6 mm long, ecarinate, margin entire, ciliate, the hairs glandular and multicellular, apex acuminate, abaxial side glabrous. Leaves alternate, subopposite or opposite, internodes 0.1-1.4 cm long; petiole semiterete, 1-3 mm long, rugose in dried material, glabrous; lamina chartaceous or coriaceous, elliptic, ovate or lanceolate, 2.6-6.6 \times 0.5–2.0 cm, base rounded, obtuse or cuneate, margin entire, revolute, flat or revolue in dried material, eciliate, apex acuminate, adaxial side glabrous, abaxial side glabrous or strigose, the hairs glandular and multicellular; laminar glands absent; venation acrodromous, suprabasal, imperfect, midvein raised on abaxial side, impressed on adaxial side, secondary venation camptodromous or brochidodromous, prominent lateral veins 1-2, raised or flat on abaxial side, impressed on adaxial side. Inflorescence axillary or terminal, a 6-15-flowered raceme; axis

Table 1. Morphological differences among	Orthaea eteocles and other similar species.
--	---

Character	O. eteocles	O. glandulifera	O. medusula	O. peregrina
Inflorescence	raceme	raceme	panicle	raceme
Calyx lobe margin	eciliate	ciliate or eciliate	eciliate	eciliate
Calyx lobe marginal gland	present	absent	present	present
Corolla shape	tubular	tubular	urceolate	tubular
Corolla color	white	white	red	white or pink
Corolla size (mm)	34-37	25-33	7.5-8.3	16-20
Staminal filaments	distinct	distinct	connate	distinct
Long stamens (mm)	15-15.5	7.5-10.3	5-6.5	7.5-9.8
Short stamens (mm)	14-15	6.5-8.2	3.9-4.2	5.5-8.4



Figure 2. Orthaea fissiflora. a. branchlet and inflorescence; b. stamens, anterior view; c. stamens, lateral view; d. flower; e. pedicel, calyx, and style.

10–20 mm long, glabrous, peduncle 0.5–3.0 mm long, rachis 7.0–19.5 mm long; bracts of the inflorescence early caducous, chartaceous, ovate or deltoid, $1.0-1.5 \times 1.0-1.4$ mm, smooth, margin entire, ciliate or eciliate, the hairs glandular and multicellular, apex acute, obtuse or obtuse-mucronate, glabrous on both sides; floral bracts early caducous, chartaceous, shape and size homogeneous along the rachis, ovate, $2.5-4.5 \times 1.4-2.0$ mm, smooth, margin erose or entire, eciliate or ciliate, the hairs glandular and multicellular, apex acute or obtuse-mucronate, glabrous on both sides; pedicel stout, 7–13 mm long, not markedly swollen at apex, 0.5–1.0 mm diam. at base, 1.0-1.5 mm diam. at apex, glabrous, articulate with calyx; bracteoles early caducous, basal or medial, subopposite, ovate or lanceolate, $1.0-2.0 \times 0.6-1.0$ mm, margin entire, eciliate, apex acuminate or acute, glabrous on both sides. Flower 5-merous, diplostemonous. Calyx aestivation valvate, green, campanulate (tubular *in vivo*), 3–5 mm long (5.2– 6.5 mm *in vivo*), sessile, terete, apophysate or truncate at base, apophysis perpendicular, entire, glabrous; tube cylindric, 1.5-2.8 mm long (3.0–4.0 mm *in vivo*), 2.0–3.0 mm diam. (4.0–5.5 mm *in vivo*); limb flaring (straight *in vivo*), chartaceous, 2–3 mm long, lobes deltoid, 0.3–0.5 × 0.3–1.0 mm, margin eciliate, marginal gland absent, apex acute, sinuses u-shaped. Corolla aestivation valvate, green at base, green or white at apex, membranose, tubular, terete, 14–18 mm long (17–21 mm *in vivo*), 3.0–7.0 mm diam. (6.3–6.5 mm *in vivo*), 2.5–4.5 mm diam. at throat

(5.2 mm in vivo), glabrous on both sides; lobes deltoid, 1×1 mm. Stamens 10, distinct, not adherent to corolla, included, filaments alternately unequal. Long stamens 7.4–8.4 mm long; filaments straight, $3.9-4.4 \times 0.6-0.8$ mm, apically puberulous, the hairs eglandular and unicellular; anthers 4.5–4.8 mm long; thecae non-prognathous, 2.7-3.1 mm long, 0.5-0.7 mm wide, glabrous, not appendiculate; tubules divergent, 1.5-2.0 mm long, 0.5-0.7 mm diam., dehiscing by latrorse pores, pores 0.9-1.2 mm long, margin entire. Short stamens like those of the longer cycle except for 6.3-7.1 mm long, filaments $2.5-3.0 \times 0.8-1.0$ mm, anthers 4.5–4.9 mm long, thecae 2.0–2.5 mm long, 0.6-0.7 mm wide, tubules parallel, 1.8-2.5 mm long, 0.6-0.8 mm diam., dehiscing by introrse pores. Ovary 5-locular, placentation axile. Nectary disk flat, glabrous; style 18-21 mm long, included, stigma truncate. Berry subconic or spherical, 6-9 mm long, 8 mm diam., lobes reflexed, glabrous; seeds ellipsoidal or isodiametric, $0.8-1.4 \times$ 0.4–0.9 mm.

Distribution and ecology. *Orthaea fissiflora* is restricted to La Paz department, Bolivia, in humid montane forests at 2100–3400 m. Flowering in March–May. Fruiting in January, March, April, May, July, September, and November.

Specimens examined. BOLIVIA. La Paz: Murillo, Valle del Río Zongo, 18-24 km N La Cumbre, 16º7'-16º10' S, 68°4'-68°10' W, 2150-2950 m, 10 May 1990 (fl, fr), J. L. Luteyn 13618 (LP, MO, NY); 2 Mar 2000 (fl), J. L. Luteyn 15439 (NY); 14 Apr 2005 (fl), J. L. Luteyn 15634 (NY); 18 Mar 1987 (fl, fr), J. C. Solomon 16371 (G, MO, NY); Yungas, 24.5 km N of the pass at the head of the Zongo Valley, 16°19' S, 68°7' W, 3100 m, 16 Sep 1984 (fr), J. C. Solomon 12311 (MO, NY, U); Sur Yungas, old town of Unduavi, 16°19' S, 67°54' W, 3139 m, 19 May 1990 (fr), J. L. Luteyn 13758 (NY); Inquisivi, Cuchiwasi, bajando Pabellonani, 7 km NE de Choquetanga, 16º48' S, 67º16' W, 3300 m, 19 Jan 1994 (fr), N. Salinas 2144 (NY); comunidad Choquetanga, serranías de Lulini, a 13.5 Km de Choquetanga, 16°43' S, 67°19' W, 3310 m, 3 Mar 1994 (fl, fr), N. Salinas 2542 (NY); desvío Unduavi-Sud Yungas, 16º16' S, 67º50' W, 3100 m, 20 Jul 2001 (fr), C. Antezana 1548 (NY); La Paz-Coroico road, Unduavi, at junction with road to Chulumani, 16º16'-16º18' S, 67º51'-67º54' W, 3170-3292 m, 4 Mar 2000 (fl), J. L. Luteyn 15445 (NY); 4 Mar 2000 (fr), J. L. Luteyn 15449 (NY); 15 Apr 2005 (fl), J. L. Luteyn 15603 (NY); 15 Apr 2005 (fl, fr), 15610 (NY); 15 Apr 2005 (fl), J. L. Luteyn 15611 (NY); La Paz-Coroico road, 0.5 km NW of Chuspipata, 16º16' S, 67°46' W, 3050 m, 16 Mar 2000 (fl), J. L. Luteyn 15468 (NY); Nor Yungas, 3.5 Km W de Chuspipata, 1.5 km E de Cotapata, camino a Unduavi, 16º18' S, 67º50' W, 3300 m, 5 Apr 1984 (fl), J. C. Solomon 12268 (LPB, MO, NY); entre Cotapata y Chuspipata, 16º16' S, 67º49' W, 3200 m, 11 Apr 1989 (fl), S. G. Beck 14927 (NY); La Paz-Coroico road, camino prehispanico Sillutinkara, ca. 5 km below Unduavi, Parque Nacional Cotopata, 16º18' S, 67º54' W, 3100-3300 m, 26 Apr 2007 (fl, fr), J. L. Luteyn 15734 (NY); La Paz-Coroico road, 16º17' S, 67º52' W, 3300 m, 27 Apr 1999 (fl), E. Hennipman 8003 (LPB); near Unduavi, 16°19' S, 67°53' W, 3000 m, 15 Apr 1939 (fl), T. H. Goodspeed 25400 (K); Chuspipata 5 km vía Unduavi, 16º16' S, 67º49' W, 3150 m, 2 Apr 1982 (fl), S. G. Beck 7603 (L, NY); Yungas, Cotapata, 8.8 km E Unduavi por el camino a Coroico, 16º16' S, 67°49'-67°50' W, 3200-3290 m, 30 Mar 1977 (fl), J. D. Boeke 1395 (NY, US); 11 Apr 1988 (fl, fr), J. C. Solomon 18223 (NY); Unduavi, 16º19' S, 67º54' W, 3300 m, Nov 1900 (fr), O. Buchtien 2902 (NY); Sud Yungas, Unduavi-Chaco road, towards Florida, 16º18' S, 67º52' W, 3250 m, 14 May 2001 (fl), J. Schönenberger 494 (LPB).

J. L. Luteyn 15609 (NY); 15 Apr 2005 (fl), J. L. Luteyn

Etymology. The specific epithet makes reference to the senescence of the corolla after anthesis, tearing along a longitudinal slit.

Orthaea fissiflora is characterized by its small leaves (up to 6.6×2 cm), short inflorescence axis (up to 20 mm long), and small green corollas (14–18 mm long) that very often tear apart longitudinally after anthesis, exposing the style and stamens. Morphologically, the closest species is *O. pinnatinervia*, from which it differs by the characters mentioned in the diagnosis.

Most of the specimens of *Orthaea fissiflora* were previously annotated as *O. ignea* Sleumer. However, Sleumer (1934) described *O. ignea* exclusively on a single specimen (*Herrera 3656*, holotype), which was destroyed during World War II (Hiepko 1987). Despite that no collections are remaining, it is clear from the information provided in the protologue that *O. ignea* cannot be conspecific with *O. fissiflora* because of its bigger leaves (8.5–11.5 × 2–2.8 vs. 2.6–6.6 × 0.5–2 cm), connate stamens (vs. distinct), and shorter staminal filaments (long cycle 2.2 mm long vs. 3.9–4.4 mm, short cycle 1.5 mm long vs. 2.5–3 mm). Therefore, all known specimens at G, LPB, MO, NY, U and US previously annotated as *O. ignea* were incorrectly identified. Unfortunately, in the absence of a type specimen or any paratypes, the taxonomic status of *O. ignea* remains unresolved.

Orthaea glandulifera Luteyn, Nordic J. Bot. 7(1): 34-36, fig. 1 D-E. 1987. TYPE. COLOMBIA. Antioquia: Yarumal, 9-18 km N of Yarumal, 7°1' N, 75°30' W, 1975–2015 m, 25 May 1984 (fl), *J. L. Luteyn 10727* (holotype JAUM!; isotypes AAU!, CAS!, COL!, E!, F!, L!, MO!, MEXU, NY!, STE, U!, US!, W!).

Orthaea oedipus Luteyn, Nordic J. Bot. 7(1): 36, fig. 1 F-G. 1987, *syn. nov.* TYPE. COLOMBIA. Chocó: Bolívar–Quibdó road, 37–40 km W of El Cármen, 5°50' N, 76°14' W, 671–1360 m, 21 May 1984 (fl), *J. L. Luteyn 10652* (holotype JAUM!; isotypes AAU!, CAS!, COL!, NY!, US!).

Terrestrial or epiphytic shrubs 3-8 m tall, scandent. Young branchlets terete, 1-3 mm diam., smooth, pubescent or glabrous, the hairs glandular and multicellular; mature branchlets glabrescent, the hairs glandular and multicellular, bark not exfoliating. Axillary buds complanate or globose, stipitate, stalk 0.4-1.0 mm long; prophylls 2, valvate, ovate, 0.8-1.5 mm long, ecarinate, margin entire, ciliate, the hairs glandular and multicellular, apex rounded or obtuse, abaxial side glabrous. Leaves alternate, internodes 0.6-3.8 cm long; petiole canaliculate or semiterete, 2-4 mm long, rugose or smooth in dried material, glabrous; lamina chartaceous, ovate or elliptic, 4.0-10.8 × 1.2-4.5 cm, base rounded, obtuse or cuneate, margin entire, slightly revolute in dried material, eciliate, apex acuminate, adaxial side glabrous; laminar glands absent; venation acrodromous, basal, perfect, midvein raised on abaxial side, impressed on adaxial side, secondary venation brochidodromous, prominent lateral veins 1-2, raised on abaxial side, impressed on adaxial side. Inflorescence terminal or axillary, a 6-15-flowered raceme or solitary flower; axis 17-50 mm long, red or pink, puberulous or glabrous, hairs glandular and multicellular, peduncle 1-6 mm long, rachis 11-49 mm long; bracts of the inflorescence persistent or early caducous, membranose, oblong or ovate, $1-15 \times 2-7$ mm, striate, margin entire, eciliate, apex obtuse, glabrous on both sides; floral bracts early caducous, membranose, shape and size heterogeneous along the rachis, elliptic, $2.5-5.0 \times 1.5-2.0$ mm, smooth, margin entire, ciliate, the hairs glandular and multicellular, apex acute, glabrous on both sides; pedicel pink or red, stout or slender, 10-42 mm long, markedly swollen at apex, 0.5-1.0 mm diam. at base, 2.5-6.0 mm diam. at apex, scarcely puberulent or glabrous, the hairs glandular and multicellular, articulate with calyx; bracteoles early caducous, basal, subopposite, lanceolate or elliptic, $2-3 \times$ 1 mm, margin entire, ciliate, the hairs glandular and multicellular, apex acute, adaxial side puberulent, the hairs glandular and multicellular, abaxial side glabrous. Flower 5-merous, diplostemonous. Calyx aestivation valvate, pink or red, tubular, 4–6 mm long (6–7 mm in vivo), sessile, terete, apophysate at base, apophysis perpendicular, entire, scarcely puberulent or glabrous, the hairs glandular and multicellular; tube cylindric, 2-4 mm long (3.5-4.8 mm in vivo), 2.5-4.0 mm diam. (4.5-5.3 mm in vivo); limb straight or flaring (straight in vivo), membranose, 2.2-4.0 mm long, lobes deltoid, 0.4-1.0 × 1.2-2.5 mm, margin eciliate or ciliate, the hairs glandular and multicellular, marginal gland absent, apex acute or obtuse, sinuses u-shaped or v-shaped. Corolla aestivation valvate, white at base, white at apex, membranose, tubular, terete, 25-33 mm long (26-35 mm in vivo), 5.5-9.0 mm diam. at base, 3.0-4.8 mm diam. at throat, abaxial side pubescent or glabrous, the hairs glandular and multicellular, adaxial side glabrous; lobes deltoid, 0.8-1.0 × 1.0-1.5 mm. Stamens 10, distinct, adherent to corolla in the basal 2.0-4.5 mm or not adherent, included, filaments alternately unequal. Long stamens 7.5-10.3 mm long; filaments straight, 5.8- 8.0×1.2 mm, apically puberulous or glabrous, the hairs eglandular and unicellular; anthers 2.3-3.2 mm long; thecae non-prognathous, 1.5-1.8 mm long, 0.8 mm wide, glabrous, not appendiculate; tubules parallel, 0.7-1.3 mm long, 0.6 mm diam., dehiscing by acroscopic pores, pores 0.1-0.3 mm long, margin entire. Short stamens like those of the longer cycle except for 6.5-8.2 mm long, filaments 4.1-6.0 × 1.9 mm, anthers 2.4-3.4 mm long, thecae 1.5-2.0 mm long, tubules 1.0-1.5 mm long. Ovary 5-locular, placentation axile. Nectary disk flat, glabrous; style 27-33 mm long, exerted, stigma truncate. Berry spherical, 6-9 mm long, 6-10 mm diam., lobes ascending, glabrous, the hairs purple; seeds ellipsoidal, $1.0-1.5 \times 0.7-0.9$ mm.

Distribution and ecology. Northwestern Colombia, along the western slope of the western Cordillera and the northern limit of the Central Cordillera, at 800–3200 m. Usually found in rain forests, but occasionally collected in vegetation remnants of perturbed areas. Flowering and fruiting throughout the year.

Specimens examined. COLOMBIA. Antioquia: Yarumal-Valdivia road km 124, ca. 12 km N of Yarumal, 7°4' N, 75°27' W, 2050 m, 23 Mar 1979 (fl, fr), J. L. Luteyn 7073 (COL, GH, NY); Parque Nacional Natural Las Orquídeas, sector Calles, río Calles, 4º34'-6º32' N, 76º13'-76º19' W, 1200-1500 m, 3 Apr 1992 (fr), D. Cárdenas López 3289 (MO); 30 May 1988 (fl), A. Cogollo 3100 (COL, JAUM, MO); 2 May 1995 (fl), R. Fonnegra G. 5435 (COL, NY); 3 May 1995 (fr), 5517 (COL, MO); 25 Jan 2011 (fl, fr), P. Pedraza-Peñalosa 1932 (NY); 28 Jan 2011 (fl, fr), 2071 (NY); 6 Dec 1992 (fr), J. J. Pipoly 16633 (MO); 26 Mar 1991 (fr), J. G. Ramírez 4026 (JAUM, MO); Frontino, corregimiento Nutibara, Sitio Murrí, vía Nutibara-La Blanquita, Alto de Cuevas, 6º40'-6º45' N, 76º19'-76º27' W, 1330-2080 m, 19 Oct 1987 (fl), A. E. Brant 1406 (CAS×2, COL×2, MO, NY, US); 13 Feb 1991 (fl), R. Callejas Posada 9864 (NY, QCA); 4 Mar 1992 (fl), A. H. Gentry 76172 (MO, NY); 19 Apr 1988 (fl), J. L. Luteyn 12072 (NY, QCA, US); 19 Apr 1988 (fl), J. L. Luteyn 12083 (NY); 21 Apr 1988 (fl), J. L. Luteyn 12179 (MO, NY); 20 Oct 1987 (fl), D. Sánchez 1720 (COL); ca. 0.5 km W of road to La Magdalena, 9 km SW of Urrao-Betulia road, 6°9' N, 76°3' W, 2060 m, 1 Nov 1987 (fl, fr), A. E. Brant 1606 (COL, MO, NY); vereda La Magdalena; camino La Magdalena-río Ocaidó, pasando por el Alto del Caballo, cuencas de los ríos Orougo, Orouguito y Ocaidó, 6º15' N, 76º14' W, 1730-2150 m, 13 Dec 2007 (fr), P. Pedraza-Peñalosa 1753 (CUVC, NY); Yarumal, Yarumal–Ventanas road, ca. 12 km N of Yarumal, 7º1' N, 75º30' W, 2050 m, 31 Oct 1996 (fl, fr), J. L. Luteyn 14997 (NY). Chocó: Medellín–Quibdó road, km 125-138, río Atrato Valley, 5°40'-5°50' N, 76°14'-76°19' W, 950-1463 m, 11 Mar 1984 (fr), A. Juncosa 2431 (MO, NY); 3 Apr 1979 (fr), J. L. Luteyn 7210 (COL×2, NY); 28 Jan 1986 (fl), B. A. Stein 3310 (COL, JAUM, MO, NY); Carmen del Atrato-Quibdó road, 7-11 km W of El Siete, 5°45' N, 76°25' W, 950-1500 m, 26 May 1988 (fl), J. *L. Luteyn 12438* (NY, US); Ansermanuevo–San José del Palmar road, from Chocó–Valle border W 10 km towards San José del Palmar, 4°57' N, 76°8' W, 1524–2050 m, 15 May 1984 (fl), *J. L. Luteyn 10540* (NY, US). Risaralda: Apía, vereda Tatamá, reserva Karagabí, Grupo GER, camino a la Quebrada Tatamá, 5°9' N, 76°1' W, 1900–3200 m, 13 Jul 2004 (fl), *P. Pedraza-Peñalosa 1084* (COL, NY); 14 Jul 2004 (fr), *P. Pedraza-Peñalosa 1092* (COL, NY); Mistrató, corregimiento Jeguadas, entre Puerto de Oro y Jeguadas, 5°25' N, 75°54' W, 900–1400 m, 19 Sep 1991 (fr), *J. C. Betancur 2815* (COL, NY).

Luteyn (1987) distinguished Orthaea glandulifera from O. oedipus because of the pedicel apex (slightly swollen vs. greatly swollen in O. oedipus), the leaf base (rounded and cordate vs. obtuse to rounded), the glandular indumentum in the inflorescence axis (absent vs. present), and the calyx lobes (elongated and ciliate vs. reduced and eciliate). Four collections were then cited by Luteyn (1987), two from eastern Chocó, along Quidbó-Medellín road (O. oedipus), and two from Yarumal, northern Antioquia (O. glandulifera). Certainly, those collections agree with the diagnostic characters noted by Luteyn (1987). However, many new collections are now available from other regions in northwestern Colombia, such as western Antioquia (Frontino and Urrao), southern Chocó (San José del Palmar), and Risaralda. From their study it is now evident that the diagnostic characters fail to set the two taxa apart; therefore, they are here synonymized. Furthermore, the Ecuadorian specimens previously considered O. oedipus by Luteyn (1996) represent an undescribed species and morphologically the closest taxon to O. glandulifera (see discussion under O. eteocles). The description is updated on the basis of the taxonomical changes here proposed, and the increased morphological variation recorded in poorly sampled populations.

CONFLICT OF INTEREST

The author declares that he has no conflict of interest.

ACKNOWLEDGMENTS

The New York Botanical Garden, the City University of New York, and the National Science Foundation (DBI-1203278, PI: Lisa Campbell) provided financial support. Fieldwork and herbarium visits were supported by the Garden Club

of America Award in Tropical Botany, the Graduate Student Award from the Society of Systematic Biologists, and the Graduate Research Award from the American Society of Plant Taxonomists. McCoy Tyner and several alumni of the NYBG graduate studies program gave pertinent counsel and motivation. Paola Pedraza-Peñalosa and two anonymous reviewers contributed helpful comments. Marcela Morales drew the excellent plant illustrations.

LITERATURE CITED

- Aeschylus. 1956. Seven against Thebes. Chicago: The University of Chicago Press.
- Hiepko P. 1987. The collections of the Botanical Museum Berlin-Dahlem (B) and their history. Englera. 7:219–252.
- Kron KA, Powell EA, Luteyn JL. 2002. Phylogenetic relationships within the blueberry tribe (Vaccinieae, Ericaceae) based on sequence data from matK and nuclear ribosomal ITS regions, with comments on the placement of *Satyria*. Am. J. Bot. 89:327–336. doi: http://dx.doi.org/10.3732/ajb.89.2.327
- Luteyn JL. 1987. Orthaea (Ericaceae-Vaccinieae): New species and redefinition of the genus. Nord. J. Bot. 7:31–37.
- Luteyn JL. 1996. Ericaceae. In: Harling G, Andersson LA, editors. Flora of Ecuador, Vol. 54. Göteborg – Stockholm - Quito: University of Götenborg, Riksmuseum, Pontificia Universidad Católica del Ecuador. p. 1–404.
- Luteyn JL. 2002. Diversity, adaptation, and endemism in neotropical Ericaceae: biogeographical patterns in the Vaccinieae. Bot. Rev. 68(1):55–87. doi: https://doi.org/10.1663/0006-810 1(2002)068[0055:DAAEIN]2.0.CO;2
- Pedraza-Peñalosa P, Salinas NR, Wheeler WC. 2013. Venation patterns of neotropical blueberries (Vaccinieae: Ericaceae) and their phylogenetic utility. Phytotaxa. 96:1–53. doi: https://doi. org/10.11646/phytotaxa.96.1.1

- Pedraza-Peñalosa P, Salinas NR, Virnig AS, Wheeler WC. 2015. Preliminary phylogenetic analysis of the Andean clade and the placement of new Colombian blueberries (Ericaceae, Vaccinieae). PhytoKeys. 49:13–31. doi: https://doi.org/10.3897/phytokeys.49.8622
- Salinas NR. 2015. Systematics and Biogeography of *Orthaea* Klotzsch (Ericaceae: Vaccinieae) [PhD dissertation] [New York City]: City University of New York.
- Sleumer HO. 1934. Ericaceae americanae novae vel minus cognitae, I. Notizbl. Bot. Gart. Berlin-Dahlem. 12(112):119–140. doi: https://doi.org/10.2307/3995031
- Sophocles. 2007. The Theban plays of Sophocles. New Haven: Yale University Press.
- Statius PP. 2008. Thebaid: a Song of Thebes, translated, with introductions, commentary, and a glossary by Jane Wilson Joyce. Ithaca: Cornell University Press.
- Stevens PF, Luteyn JL, Oliver EGH, Bell TL, Brown EA, Crowden RK, George AS, Jordan GJ, Ladd P, Lemson K, McLean CB, Menadue Y, Pate JS, Stace HM, Weiller CM. 2004. Ericaceae. In: Kubitzki K, editor. The Families and Genera of Vascular Plants, volume VI. Flowering Plants Dicotyledons: Celastrales, Oxalidales, Rosales, Cornales, Ericales. Berlin: Springer-Verlag. p. 145–194. doi: https://doi.org/10.1007/978-3-662-07257-8_19