

Three New Species of *Disterigma* (Ericaceae: Vaccinieae) from western Colombia, with comments on morphological terminology

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Pedraza-Peñalosa, P. (The New York Botanical Garden, Institute of Systematic Botany, Bronx, NY 10458, U.S.A.; e-mail: ppedraza@nybg.org). Three New Species of *Disterigma* (Ericaceae: Vaccinieae) from western Colombia, with comments on morphological terminology. *Brittonia* 00: 000–000. 200X. Three new endemic species are described and illustrated from the floristically diverse western mountain ranges of Colombia. ***Disterigma appendiculatum***, ***D. hiatum***, and ***D. verruculatum*** have interesting floral characters that are unique in the genus and in the Vaccinieae. These new morphological characters and the terminology adopted for bracteoles and staminal appendages are briefly discussed.

Key words: cloud forest, Colombia, *Disterigma*, Ericaceae, stamen appendages, bracteoles, Vaccinieae.

The Ericaceae are among the most conspicuous flowering plant families of the cloud forest of northern South America, predominantly between 1000 to 3000 m altitude. Colombia alone has the largest number of genera (22) and species (268) of Ericaceae in the Neotropics, and speciation has been thought to be accelerated by the variety of climatic, topographic, and ecological components found across and along the three cordilleras of the country (Luteyn, 1989, 2002). Studies have shown that the tribe Vaccinieae, which groups the inferior-ovary genera, possesses the highest number of endemics in the western ranges of Colombia, with 107 endemic species out of the 244 species known from that tribe in the country (Luteyn, 2002). Biotic exploration and inventory of Colombia is far from complete, and novelties are expected as more areas become available to researchers. Such is the case of the cloud forests of the western cordillera, where the three new species described herein occur.

The genus *Disterigma* (Klotzsch) Nied. (Vaccinieae) has 35-40 species, distributed from southern Mexico to central Bolivia. It is abundant in the high elevation cloud forest, although it also occurs at lower frequencies and densities in the páramos and low-elevation cloud forests. Five out of the 16 species of *Disterigma* occurring in Colombia are endemic, and although the three new species herein described grow in the same general area, Serranía de los Paraguas (Valle del Cauca-Chocó border), they are morphologically distinct and very different from each other. More interestingly, each bears one or more morphological characters that are rare or new in the genus as well as in the tribe, namely pustulate ornamentation on flowers, a micropapillose style, stamens with connate filaments, anthers basally appendaged or with spurs, thecae dehiscing by a cleft that extends from the tip of the tubule almost the base the theca, and seeds that are viviparous or covered by a mucilaginous coat. The significance of these features and the

relationships of these three new taxa with the rest of *Disterigma* are being addressed in a monograph of the genus, which is under preparation. Given the importance of these characters in *Disterigma*, a brief discussion is offered on the terminology here adopted for staminal appendages and bracts/bracteoles.

Morphological terminology

Ericaceae is a diverse family characterized by the presence of staminal appendages, but the various forms and positions in which the appendages occur have made it difficult for ericologists to reach a consensus on the terminology that best describes them. Palser (1961) and Herman and Palser (2000) distinguished two principal types of appendages in Ericaceae, awns and spurs, based on either developmental or morphological studies from representatives of a variety of lineages (*Rhododendron* L., *Kalmia* L., *Elliottia* Muhl. ex Elliott, *Erica* L., *Calluna* Salisb., *Enkianthus* Lour., *Pieris* D. Don., *Gaultheria* L., *Vaccinium* L., and *Gaylussacia* Kunth). However, the authors noted that more compelling developmental studies are necessary to address the underlying homologies of the staminal appendages, both because of their great diversity (for example, spurs may arise in slightly different places and take various shapes), and because their studies were more concentrated on temperate taxa.

Taxonomists have widely adopted Palser and Herman's definitions of awns and spurs and applied them, in a rather consistent manner, in modern and compelling taxonomic revisions of Ericaceae (Smith, 1932, 1933; Stevens, 1970, 1971; Luteyn, 1976, 1983, 1995, 1996; Middleton & Wilcock, 1990; Oliver, 2000; Stevens et al., 2004; Powell, 2005; for comparative illustrations of stamen types see Luteyn and Wilbur 2005). Yet, Vander Kloet et al. (2003) offered a different nomenclature for the staminal appendages (named horns, awns, spurs, and bristles), based on a

bibliographic revision of the different ways in which the appendages of *Vaccinium* have been described since 1737. Given that the terms introduced by Vander Kloet et al. (2003) contradict the actual meaning and usage of awns and spurs in the Ericaceae, and because the authors did not offer biological evidence to refute previous anatomical studies, their terminology is not followed here. Nevertheless, Vander Kloet et al. (2003) called attention to a poorly-known third kind of appendage, located at the very base of the anther, but they incorrectly referred to it as a “spur.” The definition of the basal appendages, as well as that for awns and spurs is briefly discussed below.

Awns and spurs are well documented in both temperate and tropical members of Ericaceae. The elongations at the apex of each mature anther half are developmentally and morphologically similar structures. They are called awns when they are bristle-like and sit above the dehiscence aperture, and are called tubules when they are hollow extensions of the thecae that bear the aperture distally, through which pollen is shed. Awns can be single or bifurcate, whereas tubules are one per theca but can fuse laterally to become one per anther with its cavity double, lobed, or single (Palser, 1961; Hermann & Palser, 2000). On the other hand, spurs arise on the abaxial (dorsal) side of the stamen either from the apex of the filament, the connective, and/or from the adjacent area of the thecae. Spurs are usually two per anther and are more variable than awns in size and shape (shaped as horns, fish tails, flaps, etc.). The less conspicuous basal appendage, as suggested by its name, is a sterile extension of either the thecae or the connective located at the base of the anther. At least in *Disterigma* and *Sphyrospermum* Poepp. & Endl., the basal appendage is not considered taxonomically useful or phylogenetically important because its size and occurrence can vary within species or sometimes within the same flower; basal appendages have also been scantily mentioned or illustrated in species of *Arbutus* L., *Anthopterus* Hook.,

Enkianthus, *Vaccinium*, and *Thibaudia* Ruiz & Pav. ex J. St.-Hil. (Smith, 1943; Palser, 1961; Luteyn, 1996; Herman & Palser, 2000; Luteyn & Wilbur, 2005). It is important to note that the basal appendage is not equivalent to prognathous anthers, as defined by Herman and Palser (2000). Prognathous anthers are those in which the entire basal portion of the anther projects inwards in an extension of the pollen chambers, giving the anthers a pronounced J shape in side view, whether they have a basal appendage or not [see illustration of *Disterigma balslevii* (Luteyn, 1996)]. To summarize, the hollow extensions at the apex of the mature anthers of all species of *Disterigma* are tubules, and the abaxial flap-like appendages at the apex of the filaments in *D. appendiculatum* are spurs (Fig. 1). Regarding the basal appendages of the anthers of *Disterigma*, the great majority seem to originate in the connective instead of the thecae base, usually poking out through the basal cavity formed between the four sacs.

Terminology that applies to inflorescences, bracts, and bracteoles has also been used inconsistently. *Disterigma* is characterized by subsessile and multibracteate flowers. The bracts at the base of the pedicels are usually inconspicuous and undifferentiated, gradually growing in length and width centripetally. Therefore, all the bracts at the base of the pedicel are here treated together without singling out a so-called floral bract. However, it is important to differentiate the bracts at the base of the pedicel from bracteoles, which come later in the development of the inflorescence and are born on the pedicel (Font Quer, 1953; Weberling, 1989; Harris & Harris, 1999). Bracteoles are not uncommon in neotropical Ericaceae, but in *Disterigma*, the most distal pair (rarely fused into one) are well differentiated in size and shape from the rest, are inserted directly at the apex of the short pedicel, and clasp the calyx. Differentiated apical bracteoles are a putative synapomorphy of *Disterigma* and display taxonomically useful characters.

The term bracteole has sometimes been used incorrectly in the Ericaceae literature (e.g., Stevens et al., 2004) instead of prophyll, which makes reference to the first or the two first leaves of a lateral bud that are distinguishable in their shape and arrangement from other leaf organs (Weberling, 1989; Harris & Harris, 1999). Therefore prophylls, unlike bracteoles, appear much earlier in the development, before pedicels are initiated, and in their position corresponds to what in Ericaceae have been called bud scales, axillary bud scales, or pseudostipules [see *Ceratostema rimbachii* (= *Disterigma rimbachii*) (Smith, 1935)]. Additionally, it is necessary to note that recaulescent bracts (displaced bracts that are no longer inserted on the main axis but on the pedicel of the flower) are apparently common in the tribe Ericaceae (Oliver, 2000), but have not been documented in neotropical Vaccinieae.

New species

In the following descriptions, all measurements are based on herbarium specimens and colors are based on field observations. Although no major differences in length have been found between pickled and dried flowers, it has been noted that corolla diameter and shape are not always well translated into herbarium specimens because of shrinking, longitudinal splitting of thick urceolate corollas, or irregular pressing of specimens; thus, a note in parentheses has been added when the dry and pickled diameters differ.

- 1. *Disterigma appendiculatum* Pedraza, sp. nov.** Type. Colombia. Valle del Cauca: Mun. El Cairo, corregimiento El Boquerón, vereda El Brillante, Cerro del Inglés, en la Serranía de los

Paraguas, 4°45'4.5"N, 76°16'24.2"W, 2100 m, 22 Jul 2004 (fl, fr), *P. Pedraza & C. Pedraza*,
1113 (holotype: COL; isotypes: AAU, CUVC, MO, NY). (Fig. 1.)

Folia ovata. Flores vulgo singulares, (4-)5-meri. Bracteae 14-15. Calyx per bracteolas apicalis usque ad apicem (98-100%) velatus; aestivatio imbricata; lobi ovati; sinu ob margines loborum imbricatorum clauso. Corolla urceolata, intus glabrata. Filamenta connata; antherae calcaribus planis ad basem filamentorum contiguorum affixis praeditae atque ad margines interiores connectivi et thecae contigui. Bacca in calyce persistens, lobis conniventibus; semina vivipara.

Terrestrial *shrubs*, scandent or erect, 0.5–1.5 m tall. Young branchlets reddish, relatively smooth, densely villous with hairs simple, eglandular and golden-brown, the mature branches similar but glabrate. *Leaves* 2–3 per cm, spiral; petiole 2.8–4.0 mm long, villous with eglandular hairs; lamina coriaceous, ovate, 1.8–2.8 x 1.1–1.8 cm, basally obtuse or cuneate, marginally entire, not revolute in dry specimens, ciliolate at apex with simple, eglandular hairs, apically acuminate, adaxially glabrate with simple, eglandular hairs, abaxially glabrate with multicellular, glandular hairs, venation 5-plinerved showing on both sides, impressed adaxially and raised abaxially. *Flowers* solitary or rarely in 2-flowered fascicles; bracts green, 14–15, persistent, chartaceous, ovate, elliptic, or suborbicular, 0.7–6.3 x 1.4–6 mm, marginally eciliate, apically obtuse and often splitting, abaxially and adaxially glabrous; pedicel 0.8–2.4 mm long, much reduced and obscured by overlapping bracts and bracteoles, glabrate with hairs simple and eglandular, or multicellular and glandular, with a ring of hairs at its articulation with calyx; apical bracteoles green, 2, distinct, chartaceous, enveloping calyx up to the upper half of the

calyx lobes or the entire calyx (covering 98–100% of calyx), suborbicular, transverse-elliptic, or reniform, 6.3–6.5 x 6.3–7.4 mm, marginally eciliate, apically obtuse, surface smooth, abaxially and adaxially glabrous. *Flowers* 5-merous (rarely 4-merous). Calyx green, campanulate, 5.6–6.5 mm long, aestivation imbricate; tube terete, 2–2.5 mm long, glabrate with eglandular hairs; limb 4.0–4.7 mm long, abaxially glabrate with eglandular hairs; lobes ovate, 2.8–3.2 x 2–3.1 mm, about or as long as broad, marginally entire and eciliate, apically acute, surface striate in dry; sinuses obscured by the overlapping bases of the imbricate lobes. Corolla aestivation valvate, actinomorphic, pink with darker lobes, thick-fleshy, urceolate (distally inflated), 7.1–8 mm long, 4.4 mm diam. (3.5 mm when dry), 3 mm wide at throat (2.2–3.2 mm when dry), abaxially and adaxially glabrate with simple, eglandular hairs; lobes triangular, 1.2 x 1.2–1.6 mm, marginally entire, apically acute. Stamens 10(–12), adherent to corolla, 5.9–6.3 mm long, more than 2/3 or about as long as corolla, included; filaments connate into a tube, straight, 3–3.3 mm long, abaxially glabrate with few hairs, adaxially pubescent distally, all hairs simple and eglandular; anthers distinct; thecae 1.5–1.7 mm long, papillate, without basal appendage, with abaxial small and flat spurs (flap-like) attached to the connate filaments at their base and to the connective and thecae through their inner side; tubules 2, distinct, 2–2.2 mm long, smooth, dehiscing by longitudinal slits, 0.8–1 mm long. Style included, ca. 6.7 mm long, smooth. Nectary glabrous. Ovary 5-locular. *Berry* color unknown, with the persistent calyx lobes converging into a obconic structure; seeds more or less triangular, 1 x 0.7–0.8 mm, viviparous; embryo color not seen.

Distribution. *Disterigma appendiculatum* is only known from the cloud forests of Serranía de los Paraguas, near Cerro del Inglés (Valle del Cauca), between 1850–2100 m.

Etymology. The specific epithet makes reference to the stamen spurs.

Additional specimens examined. Colombia. VALLE DEL CAUCA: Mun. El Cairo, corregimiento El Boquerón, vereda Las Amarillas, Serranía de los Paraguas, ca. 21–25 km beyond El Cairo, 4°45'N, 76°20'W, 1850-2000 m, 25 Apr 1989 (fl, fr), *Luteyn & Giraldo 12677* (CUVC n.v., NY).

Disterigma appendiculatum is the only species in the genus with staminal spurs. Its appendices are flat, contrary to the more common horn-shaped spurs in other spurred Vaccinieae. This species is also characterized by numerous floral bracts, two apical bracteoles enveloping 98–100% of the calyx, 5-merous flowers, imbricate calyx aestivation, ovate and imbricate calyx lobes at anthesis with the sinuses obscured by the overlapping calyx lobe bases, adaxially glabrate corolla, stamen filaments connate into a tube, fruits crowned by the converging calyx lobes, and viviparous seeds. Although *D. appendiculatum* has many characters that separate it from the rest of *Disterigma*, at first glance, its external morphology is similar to that of *D. cryptocalyx* A. C. Sm. (Colombia and Ecuador); however, the differences between these two species are many (see Table I).

2. *Disterigma hiatum* Pedraza, sp. nov. Type. Colombia. Valle del Cauca: Mun. El Cairo, corregimiento El Boquerón, vereda El Brillante, Cerro del Inglés, en la Serranía de los Paraguas, 4°45'4.5"N, 76°16'24.2"W, 2100 m, 22 Jul 2004 (fl, fr), *P. Pedraza & C. Pedraza 1112* (holotype: COL; isotypes: AAU, CUVC, HUA, MO, NY). (Fig. 2.)

Folia obovata vel elliptica, apice obtuso et apiculato. Inflorescentiae e fasciculis 2-11-floris compositae. Flores 5-meri. Calyx aestivatione valvata; lobis deltatis; sinibus rotundis. Corolla urceolata, intus puberula. Tubuli antherarum inconspicui et deminuti, per rimam usque ad basim thecae productam dehiscentes.

Terrestrial *shrubs*, scandent or erect, up to 1.3–1.5 m tall. Young branchlets relatively smooth, generally glabrous or glabrate with hairs inconspicuous, simple, eglandular, and white, the mature branches similar. *Leaves* 1–2(–3) per cm, spiral but sometimes appearing secund; petiole 3–5 mm long, glabrous or glabrate with simple, eglandular hairs; lamina coriaceous, obovate, or elliptic, (1.6–)2.2–4.5 x (0.9–)1.3–2.7 cm, basally attenuate, marginally entire, sometimes slightly revolute in dry specimens, ciliolate at apex with simple, eglandular hairs, apically obtuse and apiculate, adaxially and abaxially glabrate with hairs simple and eglandular or multicellular and glandular, venation 3– or 5-plinerved on both sides, impressed adaxially and raised abaxially. *Inflorescences* in 2–11-flowered fascicles or flowers appearing solitary due to asynchrony of floral bud development; bracts green, 2–3, persistent, chartaceous, ovate, 0.5–1.7 x 0.5–2.5 mm, marginally eciliate, apically obtuse, abaxially and adaxially glabrous; pedicel 0.5–1.5 mm long, much reduced and obscured by the overlapping bracts and bracteoles, glabrous, without a ring of hairs at its articulation with calyx; apical bracteoles green, 2, distinct, coriaceous, enveloping calyx up to the base or the entire calyx tube [covering 39–50(–85)% of calyx], suborbicular, transverse-elliptic, or reniform, 2.2–3.2 x 3.7–4 mm, sometimes marginally ciliolate with minute simple, eglandular hairs, apically obtuse, surface smooth, abaxially and adaxially glabrous. *Flowers* 5-merous (although some calyces are 4– or 6-lobed). Calyx green,

cylindric, 3.3–4 mm long, aestivation valvate; tube terete, 2–2.1 mm long, glabrous; limb 1.4–2.1 mm long, abaxially glabrous; lobes triangular, 0.3–0.5 x 0.5–1 mm, broader than longer, marginally entire and eciliate, apically acute, surface smooth; sinuses rounded (U-shaped). Corolla aestivation valvate, actinomorphic, pale pink or white, very thick-fleshy, urceolate, 5.2–6.4 mm long, 2.6–3.5 mm diam. (2–2.6 mm when dry), 1.8–2.2 mm wide at throat (1.5–1.8 mm when dry), abaxially glabrate with hairs minute, multicellular, and glandular, adaxially puberulous even in the lobes, with simple, eglandular hairs; lobes triangular, 0.8–1 x 0.7–1 mm, marginally entire, apically acute. Stamens 10, adherent to corolla, 4–4.7 mm long, more than 2/3 or about as long as corolla, included; filaments distinct, straight, linear, 3.4–4 mm long, abaxially glabrous, adaxially pubescent distally with simple hairs; anthers distinct; thecae 1.5–1.7 mm long, basally papillate, with basal appendages; tubules 2, distinct, 0.3–0.5 mm long, very reduced and hard to differentiate from thecae, smooth, dehiscing by a cleft that extends almost to base of thecae, 1.4–1.5 mm long. Style included, 4.5–5 mm long, micropapillose. Nectary glabrous. Ovary 5-locular. *Berry* translucent white, the persistent calyx lobes erect or spreading, becoming succulent and the color of the mature berry; seeds elliptic, 1.4 x 0.6 mm, with a mucilaginous coat; embryo color not seen.

Distribution. *Disterigma hiatum* is known from the cloud forests of Serranía de los Paraguas (Valle del Cauca-Chocó border), around Cerro del Inglés and on the road to San José del Palmar.

Etymology. The specific epithet comes from the latin *hio* which means cleft, referring to the dehiscence of the anthers.

Additional specimens examined. Colombia. CHOCÓ: vereda San Antonio, between San José del Palmar and junction road to El Cairo, 1820 m, 12 May 1983 (fl), *Croat 56671* (MO, NY); Ansermanuevo-San José del Palmar road, 19 Mar 1980 (fl), *Lozano & Díaz 3163* (COL), 13 May 1983 (fl), *Luteyn et al. 10428* (AAU, COL, CUVC, E, K, MO, NY, QCA), 15 May 1984 (fl), *Luteyn et al. 10514* (AAU, COL, JAUM, MO, NY); Mun. San José del Palmar, Cerro del Torrá, vertiente oriental, 1920-1950 m, 8 Aug 1988 (fr), *Silverstone-Sopkin et al. 4229* (NY). VALLE DEL CAUCA: Ansermanuevo-San José del Palmar road, km 60-62, 1870-1950 m, 19 Apr 1979 (fl, fr), *Luteyn et al. 7293* (AAU, CAS, COL, CUVC, HUA, K, LPB, MO, NY, QCA, US); Mun. El Cairo, corregimiento El Boquerón, vereda Las Amarillas, Serranía de los Paraguas, along road and beyond Cerro del Inglés, 13 May 1988 (fl, fr), *Luteyn et al. 12298* (NY), 25 Apr 1989 (fl), *Luteyn & Giraldo 12658* (AAU, CAS, COL, CUVC, HUA, K, MO, NY, QCA, US), 23 Jul 2004 (fl, fr), *P. Pedraza, & C. Pedraza 1119* (COL, HUA, NY). CHOCÓ-VALLE DEL CAUCA: justo en la frontera departamental en el sitio conocido como Galápagos, en la carretera que de Albán conduce a San José del Palmar, 4°50'1.9"N, 76°11'3.7"W, 2070 m, 24 Jul 2004 (fl, fr), *P. Pedraza & C. Pedraza 1141* (COL, NY).

Disterigma hiatum is unique within the genus because its anthers have very reduced tubules (0.3-0.5 mm long) and dehisce by a cleft that extends from the tip of the tubules to the base of the thecae (Fig. 2). This particular anther dehiscence, in which the aperture goes along the theca and is not confined only to the tubules, is similar to that of *Lateropora* A. C. Sm. (Costa Rica and Panama). The difference between *Lateropora* and this new species is that in *D. hiatum* the aperture comprises almost all the front of the thecae while in *Lateropora* it is only a latrorse slit

(for illustrations see Luteyn & Wilbur, 2005). *Disterigma hiatum* can also be distinguished from other *Disterigma* in the region by obovate or elliptic leaves that are apically obtuse and apiculate, very reduced calyx lobes with the sinuses rounded, an adaxially puberulous corolla, a micropapillose style, and seeds with a mucilaginous coat.

3. *Disterigma verruculatum* Pedraza, sp. nov. Type. Colombia. Chocó: Mun. San José del Palmar, vereda Río Blanco, Serranía de los Paraguas, en el camino que conduce de El Cairo a Río Blanco, pasando por Cerro del Inglés, 4°44'25.6"N, 76°17'50.7"W, 2150 m, 23 Jul 2004 (fl, fr), *P. Pedraza & C. Pedraza 1138* (holotype: COL; isotypes: AAU, CUVC, HUA, MO, NY). (Fig. 3.)

Caules verrucosi. Folia ovata. Inflorescentiae e fasciculis 2-4-floris compositae. Bractee et bracteolae scariosae, brunneae, et pustulatae. Calyx per bracteolas apicales duas multum quam calycem longiores velatus. Flores 5-meri. Calyx aestivatio valvata, lobis deltatis, sinibus rotundis. Corolla tubularis, intus glabra.

Terrestrial *shrubs*, scandent or erect, 0.5–1.5 m tall. Young branchlets with papilliform outgrowths, puberulous with hairs simple, eglandular, and brown, mature branches similar or sometimes glabrate. *Leaves* 1–3 per cm, spiral, rarely appearing distichous, diffuse; petiole 2.8–3.2 mm long, puberulous with simple, eglandular hairs; lamina coriaceous, ovate or elliptic, 1.6–5 x 0.9–2.8 cm, basally cuneate, marginally entire, sometimes slightly revolute in dry specimens, ciliolate at apex with simple, eglandular hairs, apically acuminate or cuspidate, somewhat glaucescent underneath when fresh, adaxially glabrate with simple, eglandular hairs, abaxially glabrate with minute, multicellular, glandular hairs, venation adaxially 7-plinerved and

impressed, abaxially only the midvein prominent. *Inflorescences* in 2–4-flowered fascicles or appearing solitary due to asynchrony of floral bud development; bracts brown (even in floral buds), 4–5, persistent, scarious, ovate, obovate or suborbicular (some asymmetrical), 1.5–5 x 1.5–4.6 mm, marginally ciliolate with simple, eglandular hairs, apically obtuse, abaxially glabrate with simple, eglandular hairs especially distally, adaxially glabrous; pedicel 0.5–1 mm long, much reduced and obscured by overlapping bracts and bracteoles, glabrous, without a ring of hairs at its articulation with calyx; apical bracteoles brown, 2, distinct, scarious, enveloping 100% of the calyx and extending 2.5–3.8 mm beyond it, elliptic or suborbicular (some asymmetrical), (4–)5–6.7 x (3–)4–6 mm, marginally ciliolate with eglandular hairs, apically obtuse and usually splitting, surface slightly pustulate, abaxially glabrate with simple, eglandular hairs, adaxially glabrate with minute simple, eglandular hairs distally. *Flowers* 5-merous. Calyx green, cylindrical (rarely drying campanulate), 2.2–3 mm long, aestivation valvate; tube terete, (1.1–)1.3–2 mm long, glabrous; limb 0.9–1.1 mm long, abaxially puberulous at apex of lobes with simple, eglandular hairs; lobes triangular, 0.3–0.7 x 0.3–0.7 mm, about or as long as broad, marginally entire and eciliate, apically acute, surface smooth; sinuses rounded (U-shaped). Corolla aestivation valvate, actinomorphic or sometimes slightly zygomorphic with a couple of lobes larger than others, pale pink or white, thin-fleshy, tubular, 7.1–9.1 mm long, 2.4–6.1 mm diam. (2–2.5 mm when dry), 2.3–6.6 mm wide at throat (1.5–2 mm when dry), abaxially glabrate with simple, eglandular hairs, adaxially glabrous; lobes triangular, 1.2–1.8 x 0.8–1.9 mm, marginally entire, apically acute. Stamens 10, adherent to corolla, 5–5.9 mm long, 2/3 to about as long as corolla, included; filaments distinct, straight, long-triangular, 3.8–4.2 mm long, abaxially glabrate, adaxially puberulous distally, all hairs simple and eglandular; anthers distinct; thecae 1.3–1.7 mm long, papillate, without basal appendages; tubules 2, distinct, 1.1–1.5 mm long, smooth, dehiscing by longitudinal slits almost reaching the base of tubules, 0.8–1.1 mm long.

Style included, ca. 6.8 mm long, smooth. Nectary glabrous. Ovary 5-locular. *Berry* translucent white, more or less spherical, 7 mm diam. (mature?), the persistent calyx lobes erect or spreading, becoming succulent and the color of the mature berry; seeds more or less triangular, 1–1.2 x 0.5–0.6 mm, with a mucilaginous coat; embryo white.

Distribution. *Disterigma verruculatum* is known from the cloud forests of the Serranía de los Paraguas (Valle del Cauca-Chocó border), around Cerro del Inglés and on the road to San José del Palmar.

Etymology. Named after the papilliform warts on the stems.

Additional specimens examined. Colombia. VALLE DEL CAUCA: Mun. El Cairo, corregimiento El Boquerón, vereda Las Amarillas, Serranía de los Paraguas, about 21–25 km beyond El Cairo, 1850–2000 m, 25 Apr 1989 (fl), *Luteyn & Giraldo 12648* (AAU, COL, NY), 13 May 1988 (fl, fr), *Luteyn et al. 12303* (CUVC). CHOCÓ-VALLE DEL CAUCA: sitio conocido como Galápagos, en la carretera que de Albán conduce a San José del Palmar, 4°50'1.9"N, 76°11'3.7"W, 2070 m, 24 Jul 2004 (fl, fr), *P. Pedraza & C. Pedraza 1140* (COL, CUVC, MO, NY).

Disterigma verruculatum is unique in the genus due to the papilliform outgrowths on its stems. The species is also characterized by its scarious apical bracteoles that envelope the entire calyx and extend 2.5–3.8 mm beyond it, by its 5-merous flowers with tubular corollas that are adaxially glabrous, and by its white fruits and seeds with a mucilaginous coat. *Disterigma*

verruculatum recalls the large-leaved forms of the variable *D. alaternoides* (Kunth) Nied., but *D. verruculatum* can be easily differentiated by its acuminate or cuspidate leaves (vs. bluntly acute in *D. alaternoides*), brown and scarious bracts and apical bracteoles (vs. green and chartaceous), apical bracteoles that extend well beyond the calyx (vs. mostly clasping up to calyx tube), 5-merous flowers (vs. 4-merous), rounded calyx sinuses (vs. with straight edges), adaxially glabrous corolla (vs. puberulous), ten stamens (vs. eight), and berries that are always translucent white (vs. purple, violet, rarely white in southern Ecuador).

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Literature cited

Font Quer, P. 1953. Diccionario de botánica. Editorial Labor, S. A., Barcelona.

Harris, J. G. & M. W. Harris. 1999. Plant identification terminology: an illustrated glossary, Spring Lake.

- Hermann, P. M. & B. F. Palser.** 2000. Stamen development in the Ericaceae. I. Anther wall, mi-crosporogenesis, inversion and appendages. *American Journal of Botany* 87(7): 934-957.
- Luteyn, J. L.** 1976. A revision of the Mexican-Central American species of *Cavendishia* (Vacciniaceae). *Memoirs of The New York Botanical Garden* 28(3): 1-138.
- , 1983. Ericaceae-Part I. *Cavendishia*. *Flora Neotropica Monograph* 35: 1-290.
- , 1989. Speciation and diversity of Ericaceae in neotropical montane vegetation. In: Holm-Nielsen, L. B., I. C. Nielsen and H. Balslev, (eds), *Tropical forests: botanical dynamics, speciation and diversity*. Academic Press, New York.
- , (ed.), 1995. Ericaceae-Part II. The superior-ovaryed genera (Monotropeoideae, Pyroloideae, Rhododendroideae, Vaccinioideae p.p.). *Flora Neotropica Monograph* 67: 1-560.
- , 1996. Ericaceae. *Flora of Ecuador* 54: 1-404.
- , 2002. Diversity, adaptation, and endemism in neotropical Ericaceae: Biogeographical patterns in the Vaccinieae. *The Botanical Review* 68(1): 55-87.
- & R. L. Wilbur. 2005. *Flora Costaricensis*. *Fieldiana, Botany, new series* 45: 1-107.
- Middleton, D. J. & C. C. Wilcock.** 1990. A critical examination of the status of *Pernettya* as a genus distinct from *Gaultheria*. *Edinburgh Journal of Botany* 47(3): 291-301.
- Oliver, E. G. H.** 2000. Systematics of Ericaceae (Ericaceae: Ericoideae). Species with indehiscent and partially dehiscent fruits. *Contributions from the Bolus Herbarium* 19: 1-483.
- Palser, B. F.** 1961. Studies of floral morphology in the Ericales. V. Organography and vascular anatomy in several United States species of the Vacciniaceae. *The Botanical Gazette* 123(2): 79-111.

- Powell, E. A.** 2005. Molecular systematics of Vaccinieae and a monograph of *Satyria*. Graduate School of Arts and Sciences, Department of Biology, Wake Forest University. Unpublished Ph.D. Dissertation. Winston-Salem.
- Smith, A. C.** 1932. The American Species of Thibaudieae. Contributions from the United States National Herbarium 28: 311-547.
- , 1933. The genera *Sphyrospermum* and *Disterigma*. Brittonia 1(4): 203-232.
- , 1935. Studies of South American plants, IV. New Monimiaceae, Trigoniaceae, and Vacciniaceae. Phytologia 1: 126-132.
- , 1943. *Killipiella*, a new Colombian genus of Vacciniaceae. Journal of the Washington Academy of Sciences 33(8): 242-244.
- Stevens, P. F.** 1970. *Calluna*, *Cassiope* and *Harrimanella*: a taxonomic and evolutionary problem. New Phytologist 69: 1131-1148.
- , 1971. Classification of the Ericaceae: subfamilies and tribes. Journal of the Linnean Society, Botany 64: 1-53.
- Stevens, P. F., J. L. Luteyn, E. G. H. Oliver, T. L. Bell, E. A. Brown, R. K. Crowden, A. S. George, G. J. Jordan, P. Ladd, K. Lemson, C. B. McLean, Y. Menadue, J. S. Pate, H. M. Stace & C. M. Weiller.** 2004. Ericaceae. Pp. 145-194. In: Kubitzki, K., (ed.) The families and genera of vascular plants VI. Flowering Plants. Dicotyledons: Celastrales, Oxalidales, Rosales, Cornales, Ericales. Springer-Verlag, Berlin.
- Vander Kloet, S. P., T. A. Dickinson & W. Strickland.** 2003. From Nepal to Formosa, a much larger foot print for *Vaccinium* Sect. *Aëthopus*. Acta Botanica Yunnanica 25(1): 1-24.
- Weberling, F.** 1989. Morphology of flowers and inflorescences. Cambridge University Press, New York.

Table I

Morphological comparison between *Disterigma appendiculatum* and *Disterigma cryptocalyx*

Character	<i>Disterigma appendiculatum</i>	<i>Disterigma cryptocalyx</i>
Bracteoles extending beyond the calyx	0 mm	2.5–4 mm
Flower merosity	(4-)5-merous	4-merous
Calyx aestivation	imbricate	valvate
Overall calyx length; limb length; lobe length	5.6–6.5 mm; 4.0–4.7 mm; 2.8–3.2 mm	2.8–3.6(–4.5) mm; 1–1.7(–2.5) mm; 1-1.7(–2) mm
Calyx lobe shape	Ovate	Triangular
Calyx sinus	obscured by the overlapping bases of the calyx lobes	with straight edges (V-shaped)
Corolla adaxial indument	glabrate	glabrous
Stamen number	10(–12)	(7–)8

Stamen filament fusion

connate

distinct

Stamen spur presence

present

absent

Fruit calyx lobes

converging into a cone

spreading or erect

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FIG. 1. *Disterigma appendiculatum*. **A.** Branch **B.** Flower with bracts and bracteoles. **C.** Corolla. **D.** Calyx with one bracteole removed. **E.** Calyx with both bracteoles removed. **F.** Adaxial view of connate stamens. **G.** Abaxial view of connate stamens with dorsal flap-like spurs. (Drawn from the holotype.)

FIG. 2. *Disterigma hiatum*. **A.** Branch. **B.** Flower with bracts and bracteoles. **C.** Corolla. **D.** Calyx with bracteoles removed. **E.** Stamen, abaxial view. **F.** Stamen, adaxial view. **G.** Stamen, lateral view. (Drawn from the holotype.)

FIG. 3. *Disterigma verruculatum*. **A.** Branch. **B.** Flower with bracts and bracteoles. **C.** Corolla. **D.** Calyx with one bracteole removed. **E.** Stamen, adaxial view. **F.** Stamen, lateral view. **G.** Mature fruit with persistent bracteoles. (Drawn from the holotype.)

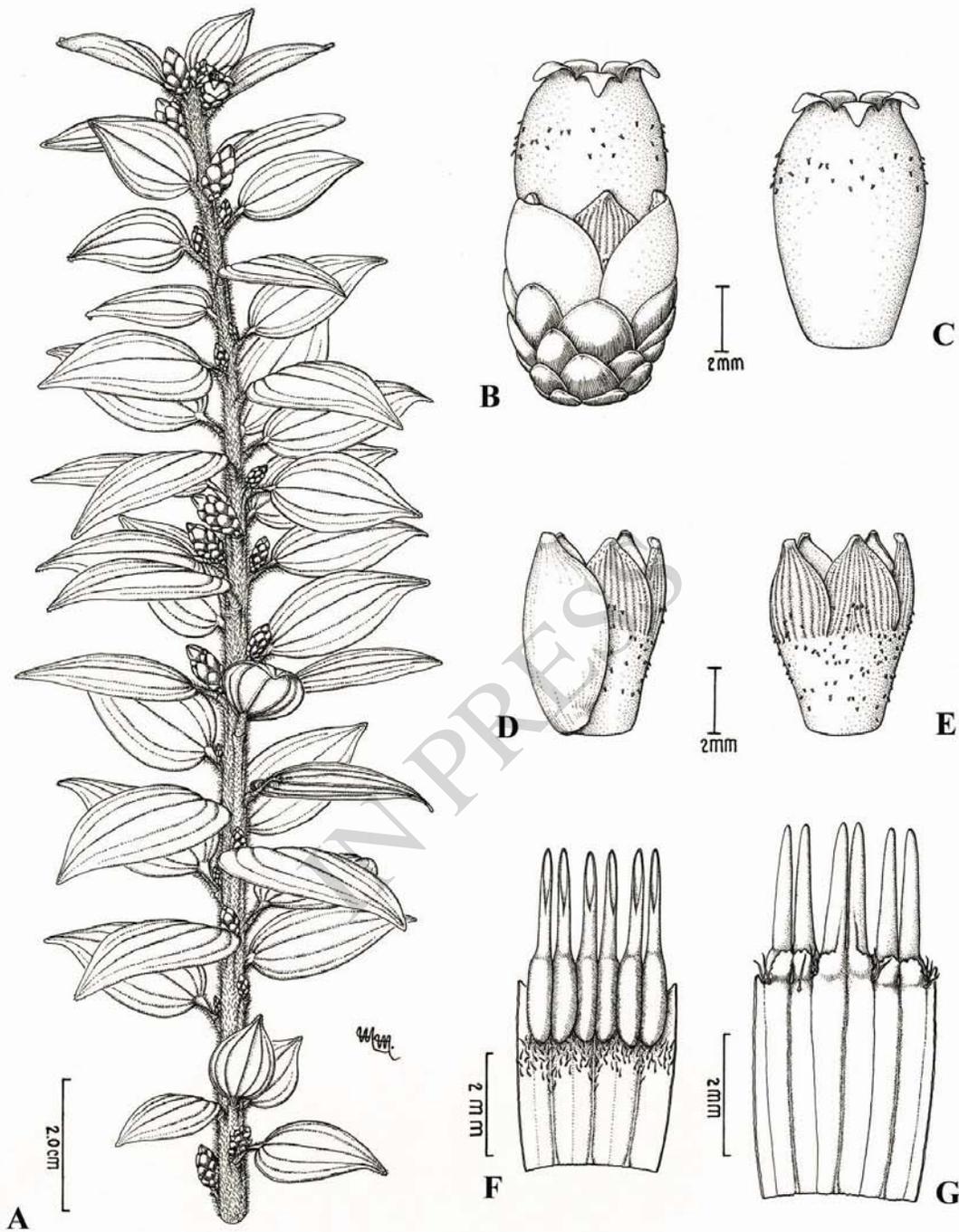


FIG. 1. *Disterigma appendiculatum*. **A.** Branch. **B.** Flower with bracts and bracteoles. **C.** Corolla. **D.** Calyx with one bracteole removed. **E.** Calyx with both bracteoles removed. **F.** Adaxial view of connate stamens. **G.** Abaxial view of connate stamens with dorsal flap-like spurs (*P. Pedraza 1113*, COL).

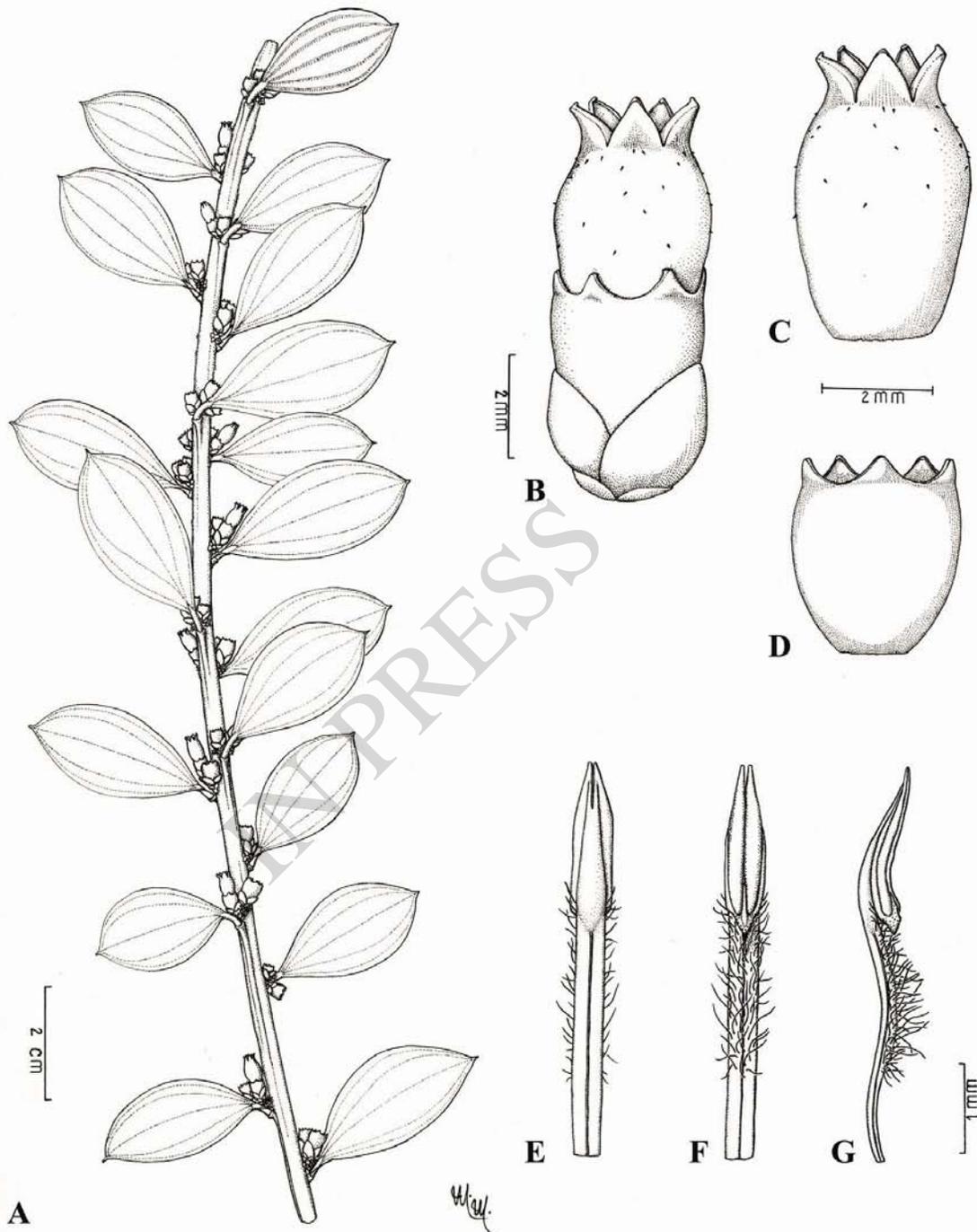


FIG. 2. *Disterigma hiatum*. **A.** Branch. **B.** Flower with bracts and bracteoles. **C.** Corolla. **D.** Calyx with bracteoles removed. **E.** Stamen, abaxial view. **F.** Stamen, adaxial view. **G.** Stamen, lateral view (*P. Pedraza 1112, COL*).

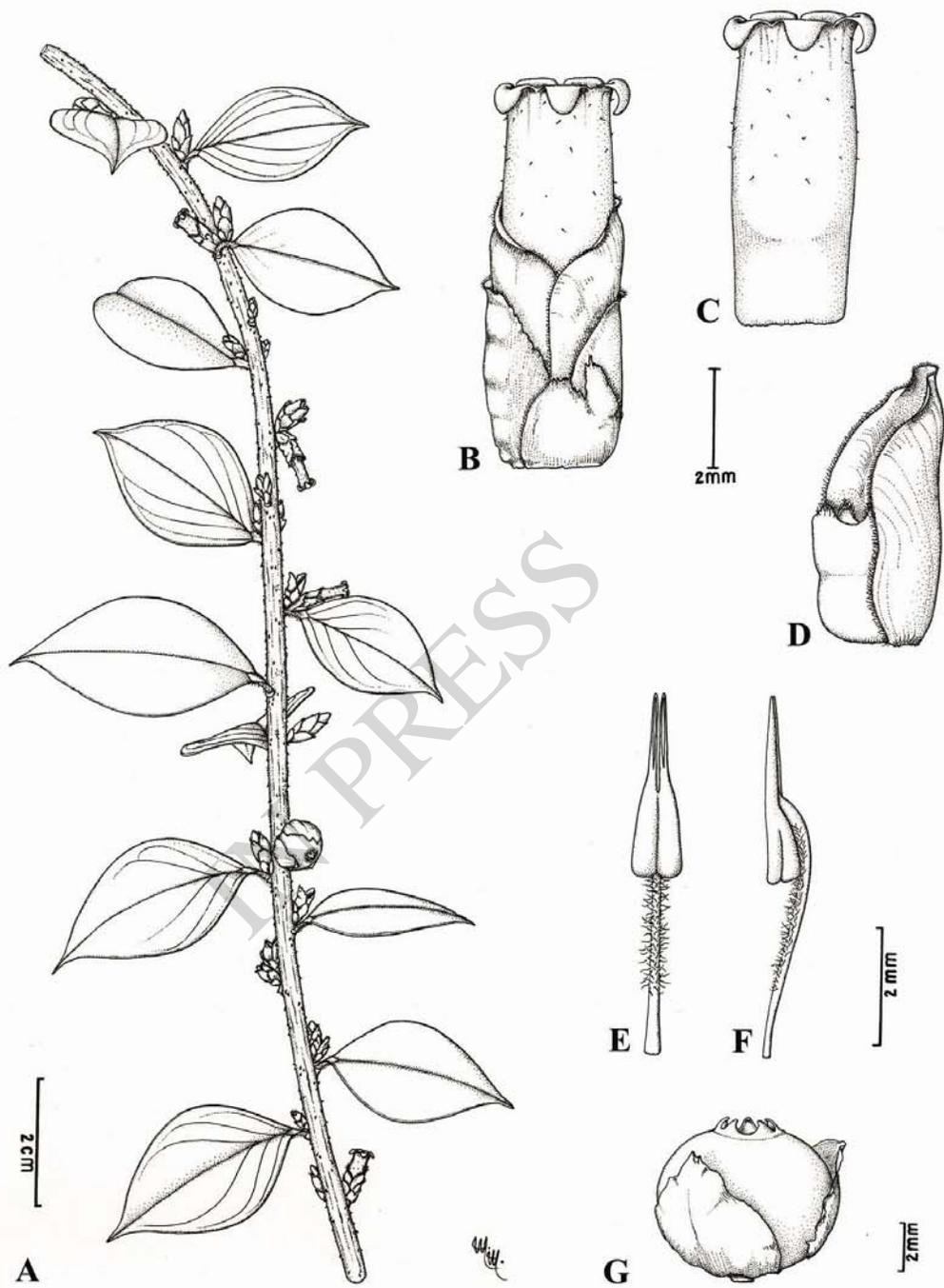


FIG. 3. *Disterigma verruculatum*. **A**. Branch. **B**. Flower with bracts and bracteoles. **C**. Corolla. **D**. Calyx with one bracteole removed. **E**. Stamen, adaxial view. **F**. Stamen, lateral view. **G**. Mature fruit with persistent bracteoles (*P. Pedraza 1138*, COL).

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