SYSTEMATICS AND PHYLOGENY OF THE ANDEAN BLUEBERRY *Disterigma* (Ericaceae: Vaccinieae)

by

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ABSTRACT

SYSTEMATICS AND PHYLOGENY OF THE ANDEAN BLUEBERRY *Disterigma* (Ericaceae: Vaccinieae)

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Disterigma (Ericaceae) is a neotropical blueberry genus that grows in Central and South America. The majority of the species of *Disterigma* are at altitudinally confined to the cold and humid environments of the cloud forests and páramos, few are widespread and many are narrow endemics. The shrubs of *Disterigma* are typically small and have diverse growth forms that include erect, scandent, prostrate or cushion-like shrubs. As the number of species included in *Disterigma* increased over the years, the morphological characters that distinguished it from other inferior-ovaried Ericaceae became less clear; this notion that the morphological circumscription was too wide and that *Disterigma* s.l. might not be a natural group was supported by recent preliminary molecular evidence. In this study, comprehensive phylogenetic analyses incorporating both morphological and molecular data have allowed to identify a diagnosable monophyletic group, *Disterigma* s.s., which is the subject of a monograph. Additionally, here also is investigated the sensitivity of the data and of its derived phylogenetic hypotheses to the variation of analytical parameters. Lastly, the results of two- and one-step phylogenetic approaches (multiple alignment + tree search vs. direct optimization, respectively) are compared. *Disterigma* s.s. is distinguished from other taxa within Vaccinieae by the presence of a pair of bracteoles at the apex of the pedicel, which surround the calyx and which are differentiated in size from other bracts and bracteoles. Thirty-two species are recognized within *Disterigma* s.s., and *D. bracteatum*, *D. pentandrum*, *D. rimbachii*, *D. trimerum*, and *D. ulei* will be segregated from it. The monograph includes changes in the nomenclature and circumscription of three of the most widespread species of *Disterigma* s.s. (*D. acuminatum, D. alaternoides, D. humboldtii*), the resurrection of *D. dendrophilum*, the proposition of seven synonyms and one new combination, as well as the designation of a neotype and a lectotype. Additionally, eight new species from Colombia, Ecuador, and Peru have been discovered during this study.

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DEDICATION

A mi familia, y muy especialmente a mis padres, por todo su amor, apoyo, y dedicación.

Para Mis Viejos.

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CHAPTER I

PHYLOGENETIC STUDIES OF *Disterigma:* A TOTAL EVIDENCE APPROACH EXPLORING TRANSFORMATION COSTS WITH DIRECT OPTIMIZATION AND MULTIPLE ALIGNMENTS

INTRODUCTION

A recent phylogenetic classification of Ericaceae Juss. identified major clades arranged in eight subfamilies and 20 tribes (Kron et al., 2002a). The monophyletic and strongly supported tribe Vaccinieae (blueberries and their relatives) is easily recognized by its characteristic inferior ovary and indehiscent fruits that are usually brightly colored and berry-like (drupes in *Gaylussacia* Kunth); Vaccinieae also has distinctive anther tubules. The vast majority of the tribe Vaccinieae is found in the Neotropics, with 30 genera and ca. 800 species, and of these about 47% of the genera and 92% of the species are endemic to the Tropical Andes (Luteyn, 2002). The Tropical Andes is considered the most biologically rich and threatened region on Earth (Mast et al., 1999). Within the Tropical Andes, and more specifically, within the cloud forest and páramo, Ericaceae is a keystone family not only for contributing to biodiversity, but also for providing food to numerous inhabitants of the highlands such as hummingbirds (Luteyn & Sylva, 1999) and rare and endangered mammals like the Mountain Tapir [*Tapirus pinchaque*] and White-tailed Deer [*Odocoileus virginianus*] (P. Lozano, pers. comm.). Unfortunately, cloud forests are among the most threatened ecosystems of the world (Knapp, 2002) and are being rapidly lost; for example, only 11% of Colombia's original cloud forests remain (Instituto Alexander von Humboldt, 2001). This lost of biodiversity means that many lineages are at imminent risk of disappearing even before base-line information for conservation work is completed.

Vaccinieae is one of the largest clades in Ericaceae, but only a small fraction of the 33 genera and 1267 species in the tribe have been monographed in the last 30 years: *Cavendishia* Lindley with 100 species (Luteyn, 1983), *Didonica* Luteyn & Wilbur with four species (Luteyn, 1991), *Disterigma* (Klotzsch) Nied. with 32 species (Pedraza-Peñalosa, unpubl.), *Satyria* Klotzsch with eight species (Powell, 2005), and *Semiramisia* Klotzsch with four species (Luteyn, 1984). Moreover, the generic limits of the morphologically diverse Vaccinieae are poorly understood, and some of the morphological characters traditionally used fail to clearly differentiate taxa (Kron et al., 2002a; Luteyn, 1996; Smith, 1932; Stevens, 1971). Such view has been corroborated by molecular studies of Vaccinieae (Kron et al., 2002b; Powell & Kron, 2003), in which only 20-40% of the genera sampled were found to be monophyletic. Among the polyphyletic groups is *Disterigma,* a genus with species from Central and South America.

Disterigma groups 36 currently accepted species of terrestrial and epiphytic shrubs. A few species of *Disterigma* are widespread, many are endemics, and the great majority of them have tight ecological affinities, with restricted altitudinal ranges; like many other Ericaceae, the species of *Disterigma* thrive in the humid and cold cloud forests and páramos.

Systematics of Vaccinieae: the Andean Clade and *Disterigma*

Twenty-eight genera (out of 33) of Vaccinieae are native to the Neotropics, and only two genera contain both neotropical and temperate species, as is the case of *Vaccinium* L.*,* the largest genus with ca. 450 species, found mainly in Malesia and the Americas. Historically, some genera have been distinguished by characters of doubtful phylogenetic value and have been treated as a nomenclature dumping ground for highly polymorphic groups (Kron et al., 2002a; Luteyn, 1996; Smith, 1932; Stevens, 1971). Moreover, many of the ca. 30 sections recognized within *Vaccinium* have been considered equally or even more distinct than some genera in the tribe (Camp, 1942; Luteyn & Wilbur, 1977; Stevens, 1971; Vander Kloet et al., 2004; Vander Kloet, 1985).

Phylogenetic studies of neotropical Ericaceae are at an early stage, but solid bases have been laid down by Kron et al. (2002b) and Powell & Kron (2003). Many neotropical Ericaceae are undercollected due to their natural scarcity and high endemism, but slowly, problems in the classification of Vaccinieae are being addressed as more collections are made and incorporated into phylogenetic analyses. The problematic generic relationships within Vaccinieae were phylogenetically tested on a worldwide basis using plastid *matK* and nuclear nrITS sequences for 28 of the 33 genera, sampling 93 species out of the 1267 currently recognized (Kron et al., 2002b). In that study, most of the 22 exclusively neotropical genera sampled clustered together into a novel and well supported Andean clade, sister to a much smaller Caribbean/Mesoamerican clade (trees not shown). Sister to these neotropical clades was an East Malesian clade, but there was no bootstrap support for this relationship. The members of *Vaccinium (*including South American species) were placed within a less derived polytomy, with the exception of *Vaccinium poasanum* (a species from Panama) which was part of the Caribbean/Mesoamerican clade.

In a later study Powell & Kron (2003) addressed the resolution within the Andean clade, using nrITS, *matK*, *rps4* and partial *ndhF* sequences for 55 species; members of the Caribbean/ Mesoamerican clade served as outgroup taxa. With few exceptions, the basal major clades were all composed of several genera, rendering many taxa paraphyletic or polyphyletic.

The five species of *Disterigma* studied by Powell & Kron (2003), were resolved in two different places within the Andean Vaccinieae and once within the Caribbean/Mesoamerican clade. The uniquely 3-merous *Disterigma trimerum* was placed with a 99% bootstrap support next to *Vaccinium poasanum,* with the Caribbean/Mesoamerican taxa. The extra-Andean origin of *D. trimerum* was also found in the study for the entire tribe (Kron et al., 2002b). With regards to the rest of the studied species, *D. rimbachii* was resolved at the base of a clade containing species of *Sphyrospermum* Poepp. & Endl., sister to a clade formed by the remaining *D. alaternoides, D. pernettyoides,* and *D. ovatum*.

Ever since *Disterigma* was elevated from within the subgenera of *Vaccinium* to genus rank (Niedenzu, 1889a), its phylogenetic affinities have been poorly understood and some species have been transferred back and forth between genera (Blake, 1926; Drude, 1889; Hoerold, 1909; Luteyn, 1996; Niedenzu, 1889a; Rusby, 1893; Smith, 1933). Therefore, the significance of the characters that separate *Disterigma* from *Vaccinium*, namely the presence of bracteoles at the apex of the pedicel that envelope the calyx, has been questioned. As for the new relationship suggested by the molecular evidence between *Disterigma* and *Sphyrospermum* (but without bootstrap support above 50%), it is hard to find morphological synapomorphies that fully explain it as the two genera are well differentiated (Table 1).

Table 1. Some morphological differences between *Disterigma* and *Sphyrospermum*

Character	***Disterigma***	***Sphyrospermum***
Pedicel and calyx juncture	Articulate	Continuous
Pedicel appearance and conspicuousness	Cryptic and stout (subsessile), usually up to 2 mm long)	Very slender and filiform, usually greater than 2 mm long
Bracteoles inserted at the apex of the pedicel, embracing the calyx, and well differentiated in size from other bracts and bracteoles	Present	Absent (bracts and bracteoles are alike; the bracteoles are never apical and therefore do not envelope the calyx)

Other than the treatment of *Disterigma* by Smith in 1933, there are no other studies of the entire genus and more recent works address only new species and regional floras (Blake, 1926; Luteyn, 1996; Luteyn & Wilbur, 2005; Wilbur, 1974, 1992). Smith (1933) recognized 15 species and since then, another 25 species have been described, making necessary a new treatment of the genus. However, before a revision of *Disterigma* can be undertaken, its monophyly and its placement within the tribe Vaccinieae need to be tested.

This study addresses the monophyly of *Disterigma* as currently circumscribed. It is hoped that through improved taxon sampling and the integration of molecular and morphological data, a more consistent and robust picture of *Disterigma* will emerge. The main goals of this study are to identify a clade of *Disterigma* species and its accompanying synapomorphies, and for the first time, to test some of the morphological characters traditionally used in Vaccinieae within an explicit phylogenetic framework. Additionally, here also is investigated the sensitivity of the data and of its derived phylogenetic hypotheses to the variation of analytical parameters; this is relevant to the problem of *Disterigma* because preliminary analyses have indicated that certain areas of the topology are may vary with the parameter choice as they are supported by few characters. Lastly, the results of two- and one-step phylogenetic approaches (multiple alignment + tree search vs. direct optimization, respectively) are compared.

BACKGROUND

Static Homologies and Dynamic Homologies

In the two-step phylogenetic approach the construction of the statement of molecular homology, the sequence alignment, and the tree search are performed separately, with different optimality criteria, and under different parameter conditions. For example, while software for automated multiple alignments like Clustal (Thompson et al., 1997; Thompson et al., 1994) optimizes overall similarities and uses a DNA identity matrix, tree search programs like TNT (Goloboff et al., 2000) or NONA (Goloboff, 1999) use parsimony as their optimality criterion and weights molecular character change based on a DNA transformation cost matrix. In Clustal, the resulting alignment (**static homologies**) is dependent on an initial dendrogram (Higgins & Sharp, 1988; Thompson et al., 1994) and some of the parameters used during the construction of the multiple alignment make *a priori* assumptions of evolutionary distances and relationships before the phylogenetic analyses has started. When the multiple alignment and the tree search are conducted in such a disconnected processes, the resulting trees are optimal for one particular alignment, but this alignment may not be the most optimal (or the only optimal) for a given tree or data set (Wheeler, 2001).

To overcome the limitations discussed above with multiple alignments, a different optimization approach, called **direct optimization** (Wheeler, 1996) is implemented in the program POY 4.1908 beta version (Varón et al., 2007b) to calculate **dynamic homologies**. Direct optimization (Wheeler, 1996) is called a one step analysis because it creates optimal cladograms without using pre-aligned sequences (Wheeler et al., 2006a). Here, nucleic acid sequence homologies and cladograms are simultaneously evaluated; in other words, POY 4 revise the sequence homologies as the search proceeds in a way that the program finds the homologies that minimize the cladogram cost (Wheeler, 1996, 1999, 2003a, 2003b). With direct optimization alignment exploration and tree search occur under the same optimality criterion (either parsimony or likelihood) and using the same set of parameters.

Direct optimization is often used and discussed among zoologists to overcome the limitations of manual and automated alignments (e.g., Frost et al., 2001; Giannini & Simmons, 2003, 2005; Giribet, 2001; Giribet et al., 2000; Laurenne et al., 2006); however in plants, this implementation and the implications of using different gap regimes with dynamic homologies is just beginning to be investigated (Aagesen et al., 2005a; Aagesen et al., 2005b; Fernández S. et al., 2006; Gottlieb et al., 2005; Huttunen & Ignatov, 2004). The application of direct optimization to concrete phylogenetic problems is not only interesting because it offers internal consistence and minimization of assumptions, but also because its implementation offers a wider freedom to control analytical parameters that otherwise are not accessible in the programs for multiple sequence alignment commonly used in two-step analyses.

Sensitivity Analyses

It has been shown that different phylogenetic trees may be recovered from different alignments, and that the alignments in turn vary with the parameters we choose. Parameter dependence is a problem that not only affects pairwise-distance-based alignments, but it also affects parsimony-based alignments and maximum likelihood-based alignments (see Giribet 2003). Moreover, sometimes differences are greater when alternative alignments are compared within methods than across methods (Morrison & Ellis, 1997), a case supported in many investigations in which, for example, the results of parsimony and likelihood are highly congruent.

Phylogenetic analyses require arbitrary decisions about cost ratios; however, the accuracy of the cost ratios we choose for our reconstructions cannot be measured without knowing the true phylogeny, and we should here remember that an estimation of the true phylogeny is precisely what we are trying to achieve. Therefore, we are confronted with a circularity problem. Although it is clear that it is not possible to objectively measure the accuracy of the phylogenetic reconstructions and that the tree search is an NP hard problem, we can still compare competing hypotheses using agreement among data (congruence) as the external optimality criterion. With this idea in mind, and not as a way to preclude the simultaneous analyses of different types of data, the sensitivity analysis was proposed by Wheeler (1995) to estimate the sensitivity of a data set to variation in parameter values. The optimal set of parameters that maximize agreement among data is chosen through essays of character congruence; the resistance of the phylogenetic hypotheses (i.e., topologies) to variation in the assumptions, or robustness, is measured in terms of nodal stability or nodal support (Giribet, 2003; Wheeler, 1995).

In sensitivity analyses the ratios of morphological change (MC), indels, transitions (Tr), transversions (Tv), or substitutions as a whole, are typically varied in parallel analyses (Frost et al., 2001; Ogden & Whiting, 2003; Wheeler & Hayashi, 1998). However, the parameter space explored is further expanded if indels are not considered to occur as single events, but rather as strings of gaps. In this case a cost is associated with the opening of a block of indels, or gap opening (GO) [gap opening in POY 4 = affine gap in POY 3, see Varón et al. (2007a)], and another cost is associated with the addition of each individual gap within the block, or gap extension (GE). The rationale for the partition of the gap cost is that insertions and deletions be of all possible lengths and should therefore receive equal cost (i.e., GO) (Aagesen et al., 2005b). However, as now implemented in POY 4, mixed-models with different GO costs can be also chosen.

To investigate the alignments and the analytical parameters through a sensitivity analysis is relevant in terms of implementing a criterion for parameter selection, assessing the robustness of the phylogenetic hypotheses, and also in terms of exploring the constraints that the indels place upon potential nucleotide homologies.

MATERIALS AND METHODS

Taxonomic Sampling

A total of 85 terminals representing 79 species and 13 genera of neotropical Vaccinieae were studied (Appendix 1) and the species were split into two data sets. The first matrix, which contained the entire data set (79 species and 13 genera) and represent the geographic and morphological variation of Andean Vaccinieae, was used to test the monophyly of *Disterigma* s.l. based on molecular data. With regards to *Disterigma* s. l., 31 (out of 36) currently recognized species were included, along with five undescribed new species. Morphologically variable species were broken down into OTUs as follows: five OTUs for *D. humboldtii* (4 from South America, 1 Central America), two for *D. noyesiae* (from Colombia and Ecuador)*,* and two for *D. acuminatum* (from Central and Southern Colombia) (Appendix 1). *Symphysia racemosa* and *Vaccinium poasanum,* both from the Caribbean/Mesoamerican clade, the sister group of the Andean clade according to previous molecular studies (Kron et al., 2002b; Powell & Kron, 2003), were selected as outgroups. The tree was rooted with *S. racemosa*.

The second matrix had 47 species (53 terminals) representing the geographic and morphological variation of *Disterigma* s. l. and it was coded for both morphology and sequence data. The ingroup sampling of the first matrix was maintained in this second data set (31 species and 37 OTUs of *Disterigma* s. l.), but the outgroup taxa was reduced to sixteen species (7 genera) that included at least two representatives from each of the major clades recovered in the most comprehensive analysis. The tree was rooted with *D. trimerum* which in this, and previous studies, is always resolved within the Caribbean/Mesoamerican clade and basal to the rest of the Andean Vaccinieae.

Leaf material and herbarium specimens were obtained during fieldwork in and Bolivia (Convenio NY-LPB 2005), Colombia (DTSA 033 SFF Galeras y otros; Acceso a Recursos Genéticos Res. 734 de 30 de Abril de 2007), Ecuador (021-

IC-FLO-DBAP-MA), Panama (STRI 2002), and Peru (35-2005-INRENA-IFFS-DCB). Additional leaf material came from the greenhouses of The Royal Botanical Garden of Edinburgh and the New York Botanical Garden.

DNA Extraction and Sequencing

Total genomic DNA was extracted from silica-dried leaves and it was later purified using QIAGEN products (QIAGEN, 2000, 2001). When necessary, DNA was extracted from non alcohol-treated and recently collected herbarium specimens; these DNA extractions were not very successful as only partial amplifications were obtained for some regions.

A combination of nuclear and plastid markers were selected according to their estimate number of Phylogenetically Informative Characters (PICs), aligned length, and descriptive tree statistics obtained in previous analyses of neotropical Vaccinieae (Kron et al., 2002; Powell & Kron, 2003) and in exploratory assays for this study. The widely used nuclear marker nrITS (ca. 639 bp) and the chloroplast 5' end of *ndhF* (ca. 1244 bp) has proven to be useful in Ericaceae and have the highest number of PICs so far obtained. Complete sequences of *ndhF* (ca. 1910 bp) were obtained for many of the species sequenced at New York, but since the 3' end of *ndhF* is not available for outgroup taxa (missing in more than 20% of the species here analyzed), the 3' end of *ndhF* was removed from the matrix. The primers used, including newly designed ones, are described in Table 2. The DNA amplifications followed modified standard methods (Clark, 1997) and when difficult amplifications arose, the PCR step-up approach proved to be very effective (Hillis et al., 1996). The material amplified in New York was sequenced on an ABI 377 XL automated sequencer or on a 3730xl Capillary DNA Analyzer. Sequences were edited with Sequencher 4.5 (Gene Codes Corporation).

I generated 80 new sequences for this study, corresponding to 40 species. Two unpublished sequences (1 species) were kindly provided by Dr. K. Kron and were prepared at Wake Forest University. The remaining sequences were published in Kron et al. (2002b) and Powell & Kron (2003) and are available via Genbank.

Table 2. Primers used to amplify the nuclear ribosomal internal transcribed spacer (nrITS) and the chloroplast NADH dehydrogenase gene (*ndhF*). * newly designed

nuclear nrITS	18S-F	CCT TAT CAT TTA GAG GAA GGA G
	5.8S-32F	GCA TCG ATG AAG AAC GTA GC
	26S-25R	TAT GCT TAA AYT CAG CGG GT
	5.8S-32R	GCT ACG TTC TTC ATC GAT GC
chloroplast *ndhF*	1F	ATGGAACAKACATATSAATATGC
	450F *	ACA AGG CCT GTT GCA GCA AG
	477F *	CTG TTG CAG CAA GTG CTT GTC AA
	972F	GTC TCA ATT GGG TTA TAT GAT G
	1318F	GGATTAACYGCATTTTATATGTTTCG
	1347F *	TGT TTC GAA TCT ATT TAC TTA CC
	536R	TCC CCT ACA CGA TTA GTT ACA A
	1318R	CGAAACATATAAAATGCRGTTAATCC
	1603R	GCA TAG TAT TGT CCG ATT CAT RAG G
	1955R	CGA TTA TAT GAC CAA TCA TAT T
	1974R *	ATG ACC AAT CAT ATT TGA TAC

Morphological Data

Fifty-five morphological characters were scored from original observations of herbarium specimens, living plants, and pickled samples, using the dissecting stereoscope. The resulting morphological matrix is provided in Appendix 2. The morphological characters studied for the cladistic analyses (Table 3) were assumed to be independent, putatively homologous, and variable within the group of study. Autoapomorphies were excluded.

All multistate characters were unordered and were mostly discrete. Several continuous characters that showed variation among species and which were thought to be phylogenetically important (i.e., differentiated apical bracteoles coverage of calyx, and length of the calyx, calyx lobe, corolla, stamen, filament, thecae, and anther tubules) were plotted in stock charts and inspected for clear discontinuities. Of these, only the differentiated apical bracteoles coverage of calyx was coded into discrete character states. On the other hand characters traditionally used in taxonomic treatments of Ericaceae, such as the proportion between the length of the stamens and corolla, the length of the filaments and anthers, and the length of the tubules and anthers, were excluded from the phylogenetic analysis because no clear character states were found; moreover, their intraspecific/individual variation made them hard to code unambiguously. Also excluded were the proportion between the length of the filament and anther, and, the length of the tubules and thecae because, although it was possible to define character states for these characters, preliminary analyses showed that they were very homoplasious, with 13-29 steps in the tree, and therefore not informative about phylogenetic relationships.

Characters were not excluded based on the presence of polymorphisms or missing data. In a few cases polymorphism was regarded as characteristic for a species and shared polymorphism potentially informative about common ancestry (e.g., filament fusion and filament shape in lateral view). Nevertheless, the majority rule criterion was used to code certain polymorphic characters (e.g., flower-merosity) in which the variation was considered to be accidental and uncommon, thus not representative of the species (for details, see at the character explanations).

Table 3. Morphological characters used in the phylogenetic analysis

0. Leaf arrangement: apparently distichous [0], spiral [1].

   Although leaves are spirally inserted on the stems of *Disterigma*, the petioles and leaves of certain species are oriented in one plane, making them look distinctively distichous (Chapter 2, Fig. 1, A).

1. Leaf proportions overall: three or more times longer than broader [0], less than three times longer than broader [1].
2. Leaf shape at apex: obtuse [0], acute [1], acuminate [2].

   The apex is the upper ~25% of the lamina. Acute leaves have an apex angle < 90° and straight margins; obtuse leaves have an apex angle between 90-180°; acuminate leaves have an apex angle < 90° and convex apical margins (drip tips) (Leaf Architecture Working Group, 1999; Stern, 1992). Subacute or blunt acute apices are included under acute leaf apices, while acuminate apex do not discriminate between long or short acumens.

3. Leaf apex apiculate: no [0], yes [1].

   The leaves of *Disterigma* could be apiculate at the most apical part of the lamina, whether the apex (the upper ~25% of the lamina) is obtuse or acute (see No. 2).

4. Flowering unit position: axillary [0], axillary and subterminal [1].

   Flowers are typically axillary in neotropical Ericaceae. However, in a few species of *Disterigma* the terminal bud is aborted and reduced to a bristle-like bract, leaving the immediately adjacent floral bud in a terminal position (here called subterminal).

5. Flower arrangement: fascicles [0], flowers solitary [1], racemes [2].

   Although some species of *Disterigma* are polymorphic for this character, there is always an arrangement that clearly dominates over the other and that is the state that was coded. For example, species with fascicles may have a few solitary flowers, or species with solitary flowers may have also a few flowered fascicles (if any).

6. Floral bract size: small (less than 1 x 0.5 cm) [0], large (equal or greater than 1.2 x 0.6 cm) [1].
7. Floral bract color: green, brown or stramineous (i.e., not showy) [0], brightly colored (i.e., red, orange, purple) [1].
8. Pedicel length: flowers subsessile with pedicels less than 2 mm long [0], flowers obviously pedicelate with pedicels usually greater than 2 mm long [1].
9. Pedicel appearance and relative thickness: stout, not filiform [0], very slender, filiform [1].
10. Pedicel articulation with calyx: articulate [0], continuous [1].

    The pedicel and calyx are articulated with a clear constriction between them; however, in some genera the constriction is not apparent and may look more like a line (Chapter 2, Fig. 2, G). The articulation is sometimes more dramatic in fruiting material, when the pedicel is distally swollen.
11. Pedicel exposure: evident or at least a portion exposed [0], obscured by overlapping bracts [1].

    Regardless of the small nature of the pedicels of *Disterigma*, they can be totally obscured by the bracts or subtly exposed. This is not necessarily a function of the size of the bracts since the pedicels of flowers with short bracts are exposed in some species while always obscured in others. The exposure of the pedicel in *Disterigma* also depends of the arrangement and quantity of the bracts.
12. Bracteole insertion: always opposite [0], alternate, subopposite, or opposite on the same plant [1].
13. Bracteole persistence: persistent [0], deciduous [1].
14. Differentiated pair of bracteoles inserted at the apex of the pedicel: absent [0], present [1].

The term bracteole applies to those bracts born directly on the pedicel, thus appearing later in development when compared to the bracts born in the axile at the base of the pedicel or those protecting the floral bud (i.e., bud scales, prophylls). In *Disterigma*, a pair of opposite bracteoles, differentiated from the rest in size and shape, is always present at the apex of the pedicel (Chapter 2, Fig. 1, C-E).

15. Number of differentiated apical bracteoles: 2 [0], 1 [1].

    The number of differentiated apical bracteoles in *Disterigma* is normally two, but in some species a single differentiated apical bracteole can be formed by the fusion of the pair (Chapter 2, Fig. 16, E). Such is the case of *D. pallidum,* where the two bracteoles are fused by one of their ends producing a single differentiated apical bracteole which often has two costae (one from each paternal bracteole) and is obcordate. Exceptionally, among all the material examined, it is possible to find in *D. pallidum* a flower or two with a pair of differentiated apical bracteoles completely distinct; therefore, the majority principle has been employed for coding.

16. Fusion of the differentiated apical bracteoles: bracteoles fused by one of their ends and forming one laminar piece [0], bracteoles fused by both ends and forming a ring-shaped piece [1], bracteoles distinct [2].

    In *Disterigma utleyorum*, a single and ring-shaped differentiated apical bracteole is originated by the fusion of the pair of apical bracteoles at both ends. A notch marks the sites where the fusion of the two pieces occurrs. In the case of *D. pallidum,* where very rarely two distinct bracteoles can be found, the majority principle has been employed to code this character (see No. 15).

17. Percentage of the calyx covered by the differentiated apical bracteoles: < 20% [0], 26 to 92% [1], 96 to 100% [2], bracteoles exceeding the calyx by more than 1 mm [3].

18. Apex of the differentiated apical bracteoles: acute [0], acuminate [1], obtuse [2], truncate [3], more or less flat and with two opposite notches (in ring-shaped bracteoles) [4], emarginate to obcordate [5], cleft [6].

    Truncate leaves have an apex angle of 180°; emarginate or obcordate leaves have a shallow notch or depression that does not reach the mid point of the leaf; cleft leaves are split from the margin to the mid point or more (Harris & Harris, 1999; Leaf Architecture Working Group, 1999; Stern, 1992). For more definitions see character 2.
19. Striation of the differentiated apical bracteoles: absent [0], longitudinally striate [1].

    This character is better appreciated in herbarium specimens and the striation is often also reflected in the calyx lobes.
20. Pustules in the differentiated apical bracteoles: absent [0], present [1].

    In the herbarium specimens the minute pustules look like whitish grains embedded in the tissue.
21. Number of floral parts: 3-merous [0], 4-merous [1], 5-merous [2], 6-7-merous [3].

    Changes in floral merosity is rare and restricted to a handful of abnormal flowers among all the flowers in all the specimens examined; therefore is not representative of the species and the majority rule criteria have been employed to code this character. Deviations in the number of floral parts are often limited to either the calyx or the corolla (e.g., the 5-merous *Disterigma ovatum*, rarely has 4- or 6-merous corollas with 5-merous calyces).
22. Calyx aestivation: valvate [0], imbricate [1].

    Imbricate aestivation includes all the cases in which calyx lobes are overlapping (i.e., quincunx, variations of quincunx, twisted) because sometimes different types of imbrication are present in the species (i.e., *Disterigma stereophyllum*). In the case of valvate aestivation, the parts are applied to each other by the margins only.

23. Calyx shape: campanulate [0], cylindric and rounded at base (never apophysate) [1], urceolate [2], cylindric and basally apophysate [3].

    The calyx outline has been used to define the shape character states. The apophysis, or an enlargement at base of the calyx, is not considered independent of the calyx overall shape. The character definitions are the same employed for corolla shape (see No. 29).
24. Calyx limb vs. calyx lobe: lobes less than half of limb [0], lobes greater than half of limb [1].

    The calyx limb is all the superior part of the calyx that is free from the ovary (Chapter 2 Fig. 2 G); although the limb includes the calyx lobes, it can be longer than the lobes.
25. Calyx lobes shape: triangular [0], ovate [1], elliptic [2], oblong-lanceolate [3].
26. Calyx lobe marginal glands: not marginally glandular [0], marginally glandular [1].

    For a detailed explanation on the various types of marginal glands see Luteyn (1976, 1983).
27. Calyx tube in cross-section: terete [0], angled [1], winged [2].

    Although it is sometimes harder to code in herbarium specimens, the calyx tube is distinctively terete, winged (e.g., *Disterigma dumontii*), or angled in cross-section; in the last case, the angles can be soft and rounded (e.g., *D. alaternoides*) or sharp (e.g., *D.* sp. nov. “ollacheum”).
28. Calyx sinuses shape: acute (V-shaped) [0], rounded (U-shaped) [1], obscured by the overlapping bases of the overlapping calyx lobes [2], more or less flat [3].

    Examples of sinuses types can be seen in Fig. 2 of Chapter 2. Additionally, photos of *Macleania insignis*, with a more or less flat sinus, can be found in the “Neotropical Bluberries” website [photos at http://www.nybg.org/bsci/res/lut Luteyn & Pedraza-Peñalosa (2006); for illustrations see new species in Pedraza-Peñalosa (In press)].

29. Corolla color pattern: of a single color [0], multicolored (usually the lobes or throat of a contrasting color) [1].

    The patchy pink or reddish hue of light colored corollas is regarded as a protection mechanism against intense solar radiation; therefore, it is not considered part of the regular color pattern. Multicolored corollas are like those of some *Macleania* Hook. where the tube is bright orange and the throat and lobes are green

30. Corolla shape: cylindric [0], campanulate [1], urceolate [2], infundibuliform [3].

    The corollas of *Disterigma* are campanulate, cylindric, or urceolate (Chapter 2, Fig. 1, H-K). In the case of the campanulate corollas, the maximum diameter is found at the throat, whereas cylindric and urceolate corollas are slightly constricted at throat; a cylindric corolla has parallel sides below the throat, while an urceolate corolla is inflated below the throat (vase-shaped). Corolla shape was personally confirmed in the field for almost all species since it is sometimes not well translated into herbarium specimens. The urceolate and thick corollas of *D. empetrifolium* can split during the pressing and drying process, thus looking campanulate (see more in the species discussion). Few species are polymorphic for this character, like *D. alaternoides*, which has both cylindric and urceolate corollas.

31. Corolla wing: absent [0], present [1].
32. Corolla hairs adaxially: absent [0]; present [1].
33. Type of corolla indumentum adaxially: glabrate [0], puberulous [1], pilose [2], villose [3].

    All indumentum definitions used in this monograph follow those of Font Quer (1980), Hewson (1998), Stern (1992), and Moreno (1984

34. Stamen number vs. corolla parts: diplostemonous [0], haplostemonous [1], stamens more than corolla parts but not perfectly diplostemonous [2].
35. Length proportion among filaments within a flower: all filaments of equal length [0], short and long filaments alternating [1].
36. Filament fusion: distinct [0], connate [1].

    This character is only polymorphic in *Disterigma styphelioides*, where some flowers have the filaments distinct and others have them connate, but to different degrees.
37. Filament shape in adaxial/abaxial view: elliptic [0], obtriangular [1], linear to long-triangular [2].
38. Filament lateral view: geniculate [0], straight [1].

    The filaments of *Disterigma* are either straight or geniculate (Chapter 2, Fig. 2 D-E), except for those of *D. codonanthum* and *D. empetrifolium,* which exhibit both character states. This polymorphism might be an indication of common ancestry given that these species share many important morphological and habitat features, indicating they might be closely related. Geniculate filaments vary from softly S-shaped to strongly folded.
39. Filament hairs: absent [0], present [1].
40. Filament hair type: eglandular [0], glandular [1].
41. Length proportion among anthers within a flower: all anthers of equal length [0], short and long anthers alternating [1].
42. Number of tubules per anther: 2 [0], 1 [1].
43. Anther tubule fusion degree: distinct [0], partially fused at base [1] (Chapter 2, Fig. 2, A-B).
44. Anther tubule rigidity: flexible [0], rigid [1].
45. Anther distally: narrowing [0], widening [1].

    The anthers of *Satyria* stand out among the rest of the genera because in adaxial view their outline is like an upside-down triangle.

46. Anther tubule aperture: a pore [0], a longitudinal slit [1], a cleft running from the tip of tubules to almost the base of the thecae [2].

    Pores and slits are confined to the tubules, but the dehiscing aperture of *D. hiatum* (Chapter 2, Fig. 2 A, F) is a cleft that extends all the way down into the thecae base. Pores can be perfectly rounded or more or less elliptic (also known as oblique pores).

47. Anther dehiscence orientation: introrse [0], introrse and latrorse [1], apical [2].

    Introrse and latrorse dehiscence is like that of *Satyria* in which the stamens are dimorphic, and the anthers with side-oriented apertures alternate with the ones with center-oriented apertures.

48. Anther ornamentation: papillate [0], foveolate [1].
49. Anther papillae distribution: on thecae [0], on both thecae and tubules [1].

    Generally, the papillae in *Disterigma* are minute and when present in the tubule they are more evident towards its base, otherwise they usually are not very pronounced. Some species may have a few papillae very elongated at the base of the anther or even few short hairs, but this varies within the species.

50. Berry color: white [0], colored (purple, lilac, red, wine-red, yellow) [1].

    Like the corollas, white fruits in *Disterigma* frequently acquire a scattered reddish coloration under intense solar radiation. This red hue is responsible for the ambiguity in the reports of fruit color. Note that fruit color is better determined around maturation time since colored berries can stay pale for a long time (although not quite pure white) before turning colored.

51. Sepal orientation at fruit maturity: erect or spreading [0], converging, tightly overlapping, and forming an obconic structure [1].

    Sepals are always persistent in Vaccinieae fruits, and in some *Disterigma,* they converge and overlap forming an obconic structure on top of the fruit (Chapter 2, Fig. 2 H-I). For some species with fully mature fruits unknown, this state has been coded as sepals erect or spreading, presuming that sepals that are much reduced wont be able to converge to the extent of having overlapping sides.

52. Sepal color at fruit maturity: turning of the same color of the berry or brown [0], remaining green [1].

    Typically, the calyx lobes that crown the fruits turn the same color as the berry and sometimes become fleshy at the base during fruit maturity (like a blueberry). In few species, the lobes remain green and chartaceous.

53. Immature fruit when dry: not brittle (mesocarp developed) [0], brittle (mesocarp very thin and collapsing) [1].

    This character noted by Smith (1933) in his revision of *Sphyrospermum,* has shown to be constant among genera and easily observed in herbarium collections bearing immature fruits. In the dry specimens, the exocarp of immature berries has an eggshell consistency becoming very fragile and brittle. Unfortunately, we lack an anatomical explanation for the phenomenon.

54. Seed embryo color: white [0], green [1].

Analytical Methods

General Methods

The combined analysis of all data partitions provides the greatest possible explanatory power, and therefore it is preferred over individual analyses (Donoghue & Sanderson, 1992; Nixon & Carpenter, 1996). Nevertheless, each data set was separately analyzed to find possible problematic taxa or characters, alignment problems, or incongruence. Because a total evidence approach was used, methods applying the parsimony optimality criterion (Farris, 1983) were favored over other model-based approaches that cannot be applied to morphological matrices (but see Lewis, 2001). Outgroup and ingroup taxa were simultaneously analyzed. Morphological characters were optimized and visualized with Winclada (Nixon, 2002).

Sequence Fragments

Because the second half of nrITS of the rare species *Disterigma leucanthum* was not successfully amplified (ca. 300 bp.), nrITS was divided in two different fragments to alleviate the introduction of ambiguity caused by the missing data. The *ndhF* data was also partitioned in two fragments because the first 400 pb (aprox.) of the 5' end of *ndhF* could not be obtained for *Anthopterus revolutus,* while the same was true for the following 700 bp (aprox.) of *D. leucanthum.* This treatment was performed for both the dynamic and static homologies analyses. The *ad hoc* assumptions that were introduced in the analysis by partitioning the sequences were minimized because the primers were used as cutting points. The primers, as used in the laboratory, assume that the fragments are mutually exclusive and that no homologies are found within those conserved areas, therefore, no further concessions were made when partitioning the sequences at the primers. An additional effect of partitioning the sequences is that the computational efficiency of the phylogenetic analysis is positively affected (Wheeler et al., 2006a).

Initial Phylogenetic Hypotheses, the Position of *Disterigma* within Vaccinieae

The fragments of the 96 species of Vaccinieae were automatically aligned using CLUSTAL X (Thompson et al., 1997) with GO and GE values 1, DNA Transition Weight 0, Delay Divergent Sequences 30% (default), and the Clustal W (1.6) DNA Weight Matrix. A tree search was conducted on the resulting alignment using TNT (Goloboff et al., 2000) with the following parameters: 1000 reps, 10 trees per rep, TBR mult*max*; Bremer subopt 20; Jackknife 1000 reps, 1 random taxa entry, 10 trees saved per rep. Indels were coded as fifth state and all characters were equally weighted. Node support was evaluated with Bremer support –or decay index- (Bremer, 1994) and Jackknife analyses (Farris et al., 1996). From the results of this first analysis the phylogenetic hypothesis of the monophyly and position of *Disterigma* within the tribe were drawn.

Sensitivity Analysis and Parameter Space Using Direct Optimization

A sensitivity analysis was conducted to test the robustness of the phylogenetic hypotheses of *Disterigma* drawn from the larger molecular analysis, under different transformation costs. This analysis also served to find the parameter set at which character congruence was maximized. All the analyses were run in POY 4.1908 beta version (Varón et al., 2007b) in a 256 CPU 3Ghz PIV + Myrinet cluster at the American Museum of Natural History, or in 2 Ghz Intel Core Duo MacBook. For this part of the study I used the matrix with 47 species of Vaccinieae which include both molecular and morphological data.

The possible variations of just one parameter are infinite. However, the lower limits of the parameter space are imposed by the triangle inequality. The triangle inequality is one of the properties of metric spaces and the distances that do not conform to this relation are internally inconsistent because they require unobserved transformations (see Wheeler, 1993). For example, the cost of a Tr must be no more than twice that of a Tv, otherwise it would be less costly to assume two Tv (e.g., T → A → C) rather that one transition (T → C). The same is true for the cost ratio of indels (or GO when in blocks) and substitutions.

The transformation cost matrices used in this study are metric and conform to the triangle inequality. Although there is no theoretical upper bound for either the indel:Tv or the Tv:Tr ratios, further limitations in the parameter space explored in this study lay on the notion that with direct optimization the parameter space is somehow predictable given the tendency of parameters sets located in the close proximity to have similar measures of congruence (Terry & Whiting, 2005). An examination of other sensitivity analyses over a wide range of organisms (Aagesen et al., 2005b; Giribet, 2001; Ogden & Whiting, 2003; Wheeler, 1995) shows that congruence is maximized over a parameter space encompassing relatively small ratios. Contrary to other published sensitivity analyses in which some parameters and parameter ratios were held constant or equally weighted throughout the entire test, all possible parameters were here varied, namely GO, GE, Tr, Tv, and MC. In the total evidence analysis the MC received weights corresponding to different notions of equal weighting (Fig. 1).

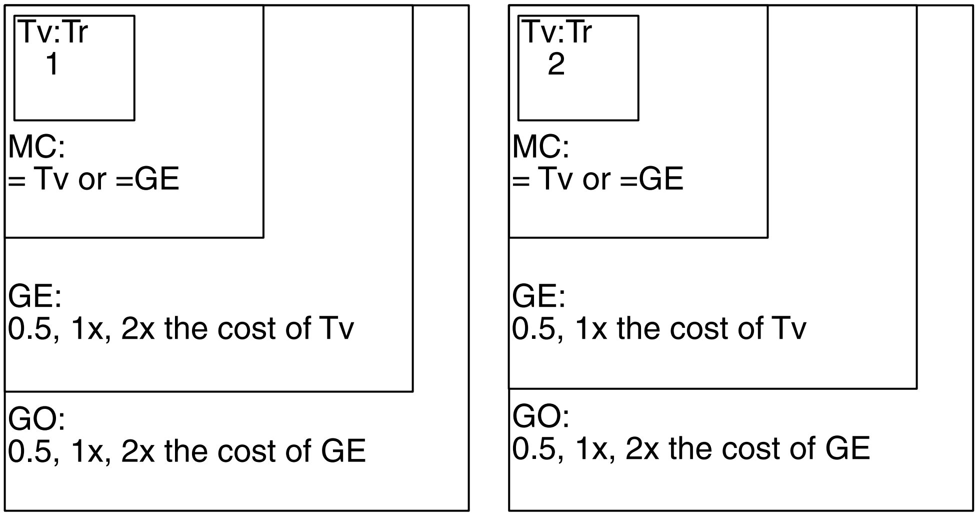


Figure 1. Parameter space explored in the sensitivity analysis. Each big box represent a case of parameter space (Tv:Tr=1 or Tv:Tr=2) with indels considered as blocks. In addition to all the possible parameter combinations described in the figure, also were explored cases in which indels were coded as fifth state with Tv:Tr=1 or Tv:Tr=2, and the rest of the parameters weighted equal to the Tr. Gap opening (GO); gap extension (GE); transitions (Tr); transversions (Tv); morphological change (MC).

In addition to the parameter space summarized in Figure 1, cases in which indels were coded as a fifth state, applying equal weights to all parameters or with the Tv double the cost of the Tr were also explored. All these possibilities rendered 29 different transformation cost matrices (see table 4) that were calculated for nrITS, *ndhF*, molecular, morphology, and total evidence (combined partitions), for a grand total of 128 unique phylogenetic analyses performed. The following is the search strategy used in POY 4.1908, in sequential order: 100 random addition sequences, SPR+TBR keeping one tree per search, select all.

Congruence and Robustness

To evaluate the robustness of the resulting clades and those proposed by the larger molecular analysis, I looked at the consensual support of the topologies of all the Most Parsimonious Trees (MPT) obtained in the 128 phylogenetic analyses. To assess nodal support, Jackknife values were calculated in POY 4.1908 beta version (Varón et al., 2007b) using 1000 reps, 1 random taxa entry, SPR+TBR and saving 10 trees per rep.

Under a congruence optimality criterion, the best parameter set is the one that minimizes character conflict (or maximizes congruence) among multiple data sets. The Rescaled Incongruence Length Difference (RILD) index (Wheeler & Hayashi, 1998) was computed from the tree scores of all 128 different analyses. The RILD is a rescaled version of the ILD (Incongruence Length Difference) of Mickevich & Farris (1981), modified to resemble the Retention Index (RI) of Farris (1989). The RILD measures the number of retained extra steps that may arise due to conflict among data partitions (therefore the lower the RILD the higher the congruence), and it is defined as:

$$RILD = \frac{Combined_{min} - \sum Individual}{Combined_{max} - \sum Individual}$$

For the parameter set with the lowest RILD a more exhaustive search was performed as follows: 1000 random addition sequences, SPR+TBR keeping one tree per search, select all. To escape from a possible local optimum, the data was perturbed using the 2nd and 3rd parameters sets with the lowest RILD values.

Dynamic Homologies vs. Static Homologies

To compare the results obtained using dynamic and static homologies, the conditions of the selected parameter set (the most congruent) were emulated in a two-step phylogenetic analysis. Among all available software for multiple alignment Clustal was chosen to perform the alignments because it is one of the most widely used implementations. The same initial sequence fragments used in POY were aligned with Clustal X (Thompson et al., 1997) and the multiple sequence alignment (no manual editions added) was then analyzed with TNT (Goloboff et al., 2000) using 1000 reps, 10 trees per rep, TBR mult*max*; Jackknife 1000 reps, 1 random taxa entry, 10 trees saved per rep. However, it must be noted that the static homologies and dynamic homologies methods are substantially different and that there is no parameter set that one can select in POY that will give the Clustal alignment and vice versa. Moreover, the range of parameter values available in Clustal (and in similar programs) is much narrower and the initial value of some of the parameters than can be selected by the user, like the GO and GE, are modified by Clustal as the multiple alignment proceeds, every time a new sequence is added to the alignment (see details in Higgins & Sharp, 1988; Thompson et al., 1994). Therefore, the user has no control over the gap penalties during the multiple sequence alignment. Despite the fundamental differences between one- and two-step approaches, I believe it is useful to compare them to not only better understand how they work, but to explore how different the final results may be given a data set.

RESULTS

The Position of *Disterigma* within Vaccinieae

The individual analyses of both nrITS and *ndhF* sequence data from 79 species of Vaccinieae resolve the major clades of Andean blueberries, although with limited resolution (trees not shown). The results of the analyses of the individual markers are in agreement and *Disterigma bracteatum, D. pentandrum, D. rimbachii, D. ulei*, and, *D. trimerum* are placed, by both nrITS and *ndhF,* outside of the main clade containing the the great majority of the species of *Disterigma* s.l. When nrITS and *ndhF* are combined (Fig. 2), the resolution visibly improves and the support values grow or remain about the same. Consequently, the following discussion about the position of *Disterigma* within Vaccinieae will refer to the combined molecular tree. Because *Disterigma* is the subject of this study, only the findings connected with the genus will be discussed at the moment.

The combined molecular analysis retrieved 36 MPT 947 steps long. The consensus tree shows a polyphyletic *Disterigma* s.l. with elements of both Andean and Mesoamerican origin (Fig. 2). As previously found in other studies (Kron et al., 2002b; Powell & Kron, 2003), *D. trimerum* is placed with high support (99% Jackknife; 11 Bremer) within Mesoamerican elements, in a clade basal to the Andean clade. *Disterigma trimerum* is endemic to the montane forest of Panama and Costa Rica, and remains as the only 3-merous taxon within Vaccinieae.

As for the species of *Disterigma* s.l within the Andean clade, they form two clades (Fig. 2). The larger of the two clades, *Disterigma* s.s., includes the genus type species (*D. empetrifolium*) and all but four of the South American species of *Disterigma* sampled (excluding *D. trimerum*); *Disterigma* s.s. is strongly supported (96%;11) and is sister to a clade of *Sphyrospermum.* The rest of the South American species of *Disterigma* sampled, *D. bracteatum, D. pentandrum, D. rimbachii*, and *D. ulei*, form a poorly supported clade (26%; 1) sister to *Disterigma* s.s. + *Sphyrospermum*, but with internal nodes highly supported.

Sphyrospermum, The sister group of *Disterigma* s.s. suggested by this analysis, is a genus easily distinguished from *Disterigma* s.l. (see introduction) with about 22 species distributed in Central and South America. Although this relationship was also found in a previous study of Andean Vaccinieae (Powell &

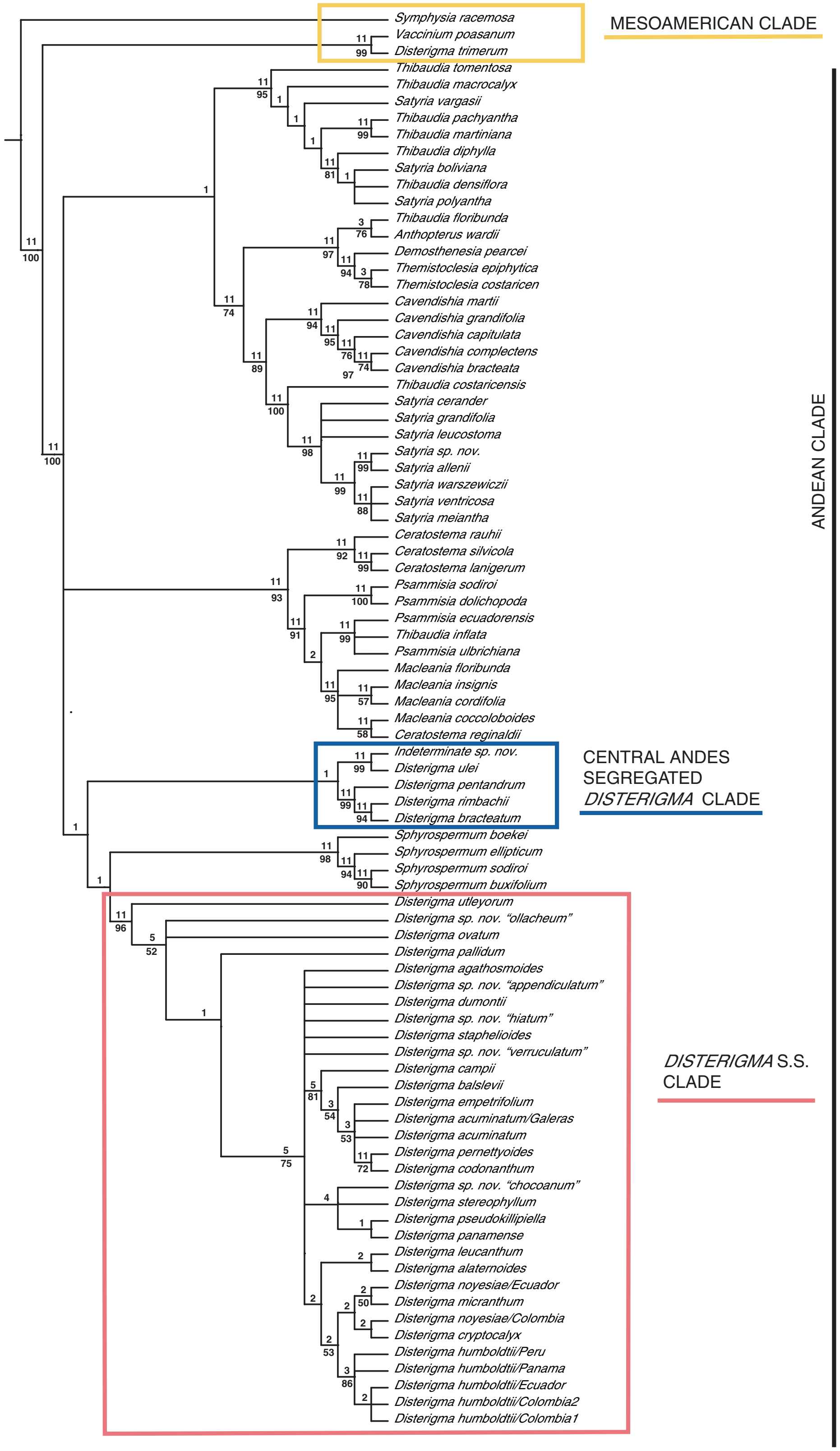


Fig. 2. Strict consensus of 36 MPT found in the analysis of nrITS and *ndhF* data of 79 species of Vaccinieae (L=947, CI=0.47, RI=0.78). Bremer support above and Jackknife support below the lines. See enlarged *Disterigma* clades in Fig. 3.

Kron, 2003), the support for this node remains under 50%. Historically, *Disterigma* was thought to be more closely related to *Vaccinium* given that *Disterigma* was originally described as one of its subgenera (Klotzsch, 1851). However, in a worldwide study of Vaccinieae (Kron et al., 2002b), none of the species of *Vaccinium* sampled were placed in the Andean clade (where *Disterigma* is found); the neotropical species of *Vaccinium* were resolved in much basal grades and only *V. poasanum* (Guatemala-Panama) was placed within the Mesoamerican clade. Therefore, no South American species of the polyphyletic *Vaccinium* are included in the present molecular study.

All the South American species of *Disterigma* s.l. resolved outside of the *Disterigma* s.s. clade (i.e.; *D. bracteatum, D. pentandrum, D. rimbachii*, and *D. ulei)* occur in the central Andes, more specifically in south Ecuador, Peru and Bolivia. All these species form a novel group, here called the central Andes segregated *Disterigma* clade (Fig. 2 and 3), along with a indeterminate new species from Peru that somehow resemble South American members of the polyphyletic genus *Vaccinium*. Although these group of species are similar to *Disterigma* s.s. in having small subsessile flowers, they all lack the characteristic pair of bracteoles which are clearly differentiated from other bracts in size and which are inserted right at the apex of the pedicel and embrace the calyx. Moreover, *D. bracteatum, D. pentandrum,* and *D. rimbachii* can be clearly differentiated from the other species of *Disterigma* s. l. because their flowers are haplostemonous (stamens the same number of floral parts) and not diplostemonous. Because this unusual number of stamens and the presence of undifferentiated and numerous bracts and bracteoles, Smith (1933) recognized *D. pentandrum* as an isolated species within the genus. *Disterigma bracteatum* was described as a new species probably closely related to *D. pentandrum* and *D. rimbachii* (Luteyn, 2005) for they all shared succulent leaves and haplostemonous flowers surrounded by multiple bracts. In the case of *D.*

rimbachii, the species was originally described by Smith (1935a) in *Ceratostema* Juss.; Smith noted that although it resembled certain species of *Disterigma, C. rimbachii* lacked the distinctive “large pedicellary bracts” (bracteoles) and had long “pseudostipules” (prophylls or the bracts of a lateral bud). Afterwards, the generic placement of *C. rimbachii* was much disputed, moving from *Plutarchia* A. C. Sm. to *Pellegrinia* Sleumer, before being finally transferred to *Disterigma* (Luteyn, 1996; Sleumer, 1935; Smith, 1936). The phylogenetic affinities and taxonomic identity of *D. ulei* are not better understood; its holotype (unicate) was destroyed in the fire at the herbarium in Berlin and only a blurred photograph of it

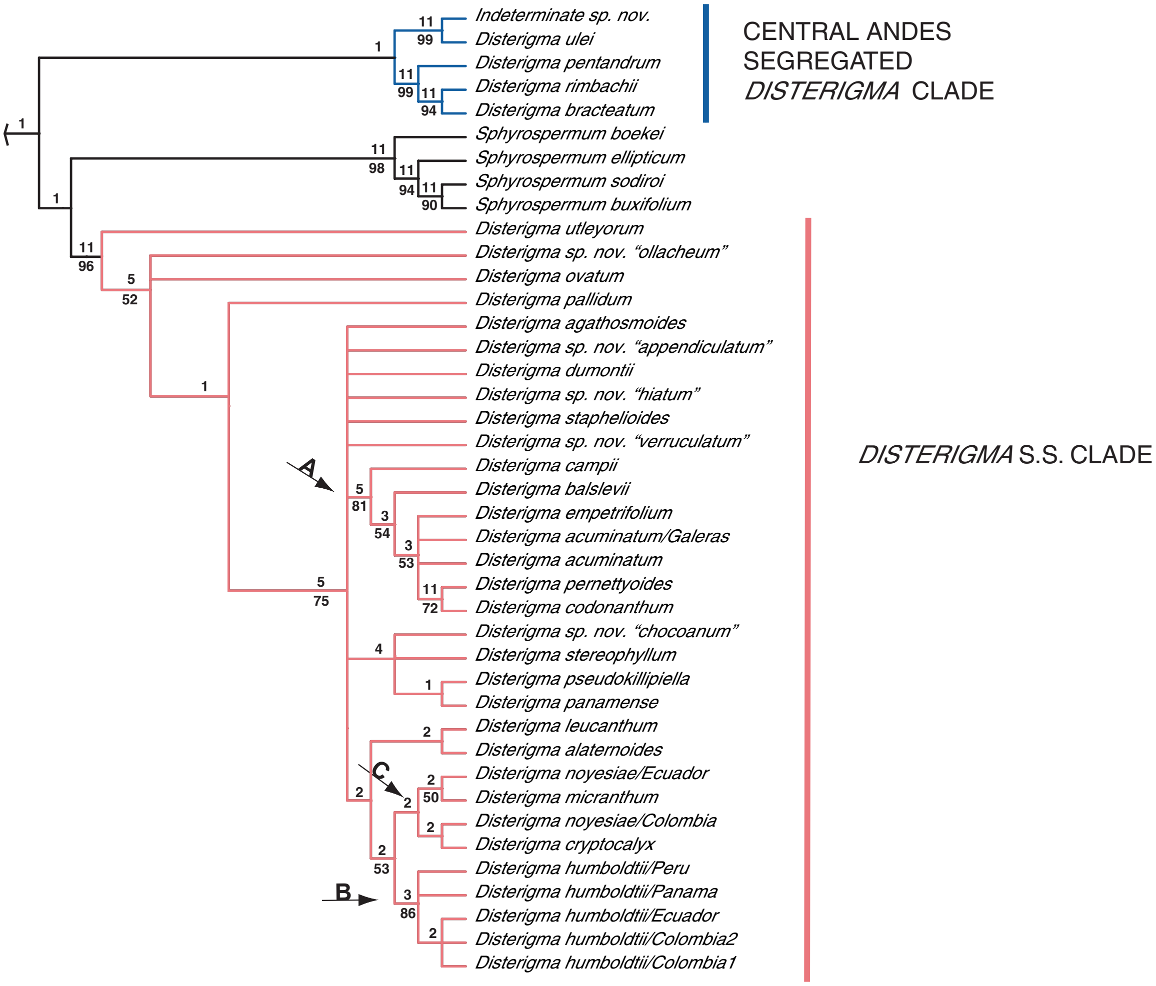


Fig. 3. Detail of Fig. 2 showing part of the strict consensus of 36 MPT found in the analysis of nrITS and *ndhF* data of 79 species of Vaccinieae (L=947, CI=0.47, RI=0.78). Bremer support above and Jackknife support below the lines. See the text for the explanation of the clades highlighted by the arrows.

survived (a neotype has been chosen in Chapter 2). When originally described, *D. ulei*, was placed in *Disterigma* rather than in *Vaccinium* because of its habit and resemblance to *D. pentandrum,* in spite of its reduced “bracts” -here reinterpreted as the absence of differentiated apical bracteoles- (Sleumer, 1941). *Disterigma ulei* is different from *D. pentandrum* and other species in the clade because its flowers are diplostemonous. *Disterigma ulei* is very rare in nature and has only been collected on few occasions; it often grows high in the canopy and all we know about it comes from specimens taken from fallen branches and old trunks on the forest floor.

The resolution within *Disterigma* s.s. in this molecular analysis is rather limited and few major clades have moderate or high Jackknife support values (Fig. 3). The clade formed by *D. campii, D. balslevii*, *D. empetrifolium*, *D. acuminatum* (two OUTs)*, D. codonanthum,* and *D. pernettyoides* (81%; 5) groups species that, with exception of *D. campii,* are typically found in the highest belts of the Andean vegetation (Fig. 3, clade A). These species are abundant in the dry, humid, grassy, or shrubby páramos and subpáramos of the northern Andes, and in the humid puna or yungas (páramo yungeño) of the central Andes. In the case of *D. acuminatum*, although it can be locally abundant in shrubby páramos and punas, overall, it occurs more frequently in the upper montane cloud forest. As for *D. campii,* which grows at lower altitudes (800-1700 m) in the premontane cloud forest, it shares with other members of this clade, like *D. acuminatum,* the presence of small stamens and small, campanulate, and green corollas. Within this clade (A) the only relationship well supported is that of *D. codonanthum,* and *D. pernettyoides* (72%; 11).

The next clade with high support values is that formed by the five OTUs from Central and South America of the polymorphic *Disterigma humboldtii* (86%; 3) which exhibits a lot of variation in the presence of hairs within the corolla and in the size of the leaves and flowers (Fig. 3, clade B). Sister to this group, but with relatively low support (53%; 2), is the clade of *D. cryptocalyx, D. micranthum*, and two OTUs of *D. noyesiae* (<50%; 2) (Fig. 3, clade C); this clade groups species from Ecuador and Colombia with a wide altitudinal range, but perhaps more commonly found in the premontane cloud forests. All these species were described after Smith's revision and *D. micranthum* and *D. noyesiae* were only known from the type specimens for many years. The type collections of *D. cryptocalyx, D. micranthum*, and *D. noyesiae* are quite different from each other, with *D. micranthum* bearing the smallest flowers known in the genus (corollas about 3 mm long) and *D. cryptocalyx* close to the other extreme (corollas about 7-10 mm long). However, the general morphology of the flowers support the close relationship between these three species and this will be further explored in the total evidence analysis.

From the analysis of molecular data it can be concluded that 1) *Disterigma,* as currently circumscribed, is a polyphyletic group with three independent origins; 2) most of the currently recognized species form a well-supported monophyletic *Disterigma* s.s. group, sister to the clade of species of *Sphyrospermum* sampled (but unsupported); 3) *D. trimerum, D. bracteatum, D. pentandrum, D. rimbachii*, and *D. ulei* should be segregated from *Disterigma* s.l.; 4) and, that although the position of *D. trimerum* within Mesoamerican taxa is well founded, the proper placement of the rest of the segregated species remains ambiguous. Even though a clade of *Disterigma* has been identified, some questions remain: What are the synapomorphies of *Disterigma* s.s.? How are the segregated species different? Will the results change if more species are added? Are the results sensitive to the alignment and the analytical parameters chosen? Do different statements of homology support the phylogenetic hypotheses?

Sensitive Analysis and Congruence

This part of the results is based on the analysis of molecular and morphological data of the second matrix which has 47 species of Vaccinieae. In both the total evidence and molecular analyses, character incongruence is minimized when MC, Tr, and Tv are equally weighted, with GE twice the cost of Tv and GO twice the cost of GE [1:1:1:2:4, where GO has the highest cost] (Table 4). A regime in which GO is so strongly penalized will render fewer and shorter indels, and precisely, that is the indel behavior observed in previous alignments produced by Clustal and manually for this group. When comparing morphological data to molecular data, the minimum incongruence occurs when MC and Tr, and, Tv and GE, are equally weighted, with Tv twice the cost of Tr, and GO twice the cost of GE [1:1:2:2:4, where GO has the highest cost] (Table 4).

Robustness of Phylogenetic Relationships

Though the consensus trees obtained for each one of the individual partitions (i.e., nrITS, *ndhF*, molecular, morphology, total evidence) using the transformation cost matrix with the lowest RILD [1:1:1:2:4, where GO has the highest cost] agreed in the composition of *Disterigma* s.s. and the segregation of five species from *Disterigma* s.l., their resolution is in general too poor to draw many more conclusions. Because the total evidence analysis represents the strongest hypothesis of relationships, the following results and discussion will only emphasize those results. The composition of major clades recovered in this analysis of combined morphological and sequence data of 47 species are in agreement with those of the molecular analysis of 79 species.

The most parsimonious tree obtained from the total evidence analysis of 47 species of Vaccinieae using the lowest RILD is 2564 steps long (Fig. 4); even when perturbations are applied to escape from local optimum, the same tree is

Table 4. Results of 128 phylogenetic analyses using 29 different transformation cost matrices, for the sensitivity analysis of Vaccinieae. Tree lengths are shown for individual and combined data partitions. TCM= transformation cost matrix, MC= morphological change, Tr= transitions, Tv= transversions, GE= gap extension, GO= gap opening, Mol= ITS +*ndhF*, Morph= morphology, Total= Mol+Morph, Wmol= maximum length for Mol, Wtotal= maximum length for Mol+Morph, RILD= rescaled inconsistence length difference, RILDMor/Mol= incongruence metric for Morph vs. Mol. * 2nd and 3rd lowest RILDs.

TCM	MC	Tr:Tv:GE	GO	nrITS	*ndhF*	Mol	Morph	Total	Wmol	Wtotal	RILDTotal	RILDMol	RILDMor/Mol
1	2	2:2:2	1	591	1603	2304	408	2780	4362	5206	0.0684	0.0507	0.0273
2			2	636	1688	2434	408	2952	6940	8386	0.0389	0.0238	0.0198
3			4	750	2120	3098	408	3586	24460	25026	0.0142*	0.0106*	0.0037*
4	2	2:4:2	1	706	1948	2807	408	3283	5548	6377	0.0667	0.0529	0.0215
5			2	752	2066	2992	408	3470	7668	9332	0.0400	0.0359	0.0118
6			4	866	2506	3620	408	4124	24980	25760	0.0157	0.0115	0.0044
7	4	2:4:2	1	706	1917	2807	816	3770	5548	7304	0.0856	0.0629	0.0399
8			2	752	2030	2992	816	4040	7668	8760	0.0856	0.0430	0.0468
9			4	866	2442	3620	816	4692	24980	26108	0.0258	0.0144	0.0118
10	2	4:4:2	1	1008	2511	3726	408	4217	7417	8374	0.0652	0.0531	0.0196
11			2	1062	2640	3898	408	4392	10022	11740	0.0370	0.0310	0.0116
12			4	1182	3132	4668	408	5164	28646	27984	0.0190	0.0145	0.0038
13	4	4:4:2	1	1008	2490	3726	816	4698	7417	9260	0.0776	0.0582	0.0331
14			2	1062	2664	3898	816	4886	10022	12234	0.0447	0.0273	0.0229
15			4	1182	3068	4668	816	5676	28646	27780	0.0269	0.0171	0.0086
16	1	1:1:2	1	378	1115	1560	204	1801	2525	3110	0.0736	0.0649	0.0275
17			2	421	1205	1685	204	1936	3193	3555	0.0614	0.0377	0.0282
18			4	526	1591	2316	204	2577	23567	24194	**0.0117**	**0.0093**	0.0026*
19	2	1:1:2	1	378	1070	1560	408	2045	2525	3539	0.1123	0.1040	0.0490
20			2	421	1176	1685	408	2164	3193	4277	0.0700	0.0551	0.0325
21			4	526	1412	2316	408	2838	23567	23445	0.0233	0.0175	0.0055
22	1	1:2:2	1	436	1253	1814	204	2090	3359	3637	0.1130	0.0749	0.0445
23			2	481	1381	1963	204	2200	5384	5969	0.0343	0.0287	0.0087
24			4	593	1719	2598	204	2828	23649	24091	0.0145*	0.0134	**0.0012**
25	2	1:2:2	1	436	1322	1814	408	2301	3359	4092	0.0701	0.0350	0.0422
26			2	481	1412	1963	408	2465	5384	5181	0.0569	0.0201	0.0335
27			4	593	1797	2598	408	3131	23649	23406	0.0162	0.0098*	0.0061
28	2	2:2:2	0	544	1500	2150	408	2642	3892	4754	0.0825	0.0574	0.0383
29		2:4:2	0	656	1836	2638	408	3132	4872	5990	0.0751	0.0613	0.0292

recovered. Marked with stars in the most parsimonious tree are the clades that were common to all the MPT under the 29 different parameter combinations; they are the clades *Anthopterus, Cavendishia, Satyria, Sphyrospermum, Disterigma* s.s., the clade composed by the segregated haplostemonous species of *Disterigma* from the central Andes (*D. pentandrum, D. rimbachii*, *D. bracteatum*), the clade of the OTUs of *D. humboldtii,* the clade *D. ovatum* + *D. sp. nov. "ollacheum"*, and the clade *D. panamense* + *D. pseudokillipiella* (Fig. 4)*.* All these clades are robust, insensitive to parameter variation, and have moderate to high nodal support (71-100%).

The great majority of the species of *Disterigma* s.l. are in the the *Disterigma* s.s. clade, a group that has the same species composition of the equivalent clade obtained in the analyses of molecular data of 79 species (Fig. 2). As for the other Andean *Disterigma* resolved outside of *Disterigma* s.s., *D. ulei* (southern Peru and northern Bolivia), it clustered again with *Indeterminate* sp. nov. (central Peru) with a Jackknife support of 100%. However, this relationship is not very robust because it is sensitive to parameter variation and is present in only 75% of the MPT of the sensitivity analysis. In the case of the rare *D. trimerum* with trimerous flowers, this species is always resolved in isolation of the rest of the genus independent of the parameter combination used.

With the addition of morphological data, a different hypothesis regarding to the sister group of *Disterigma* s.s. emerged [(*Disterigma* s.s. (*Sphyrospermum* (central Andes segregated *Disterigma*)))], marked with an arrow in Fig. 4]; however the robustness and stability of this hypothesis is questionable because its Jackknife support value is well bellow 50% and only 6 of the 29 different parameter sets converged into the same hypothesis. Nonetheless, no other hypothesis is particularly favored by any of the other transformation cost matrices for this node; for example, the sister group of *Disterigma* s.s. favored when all the

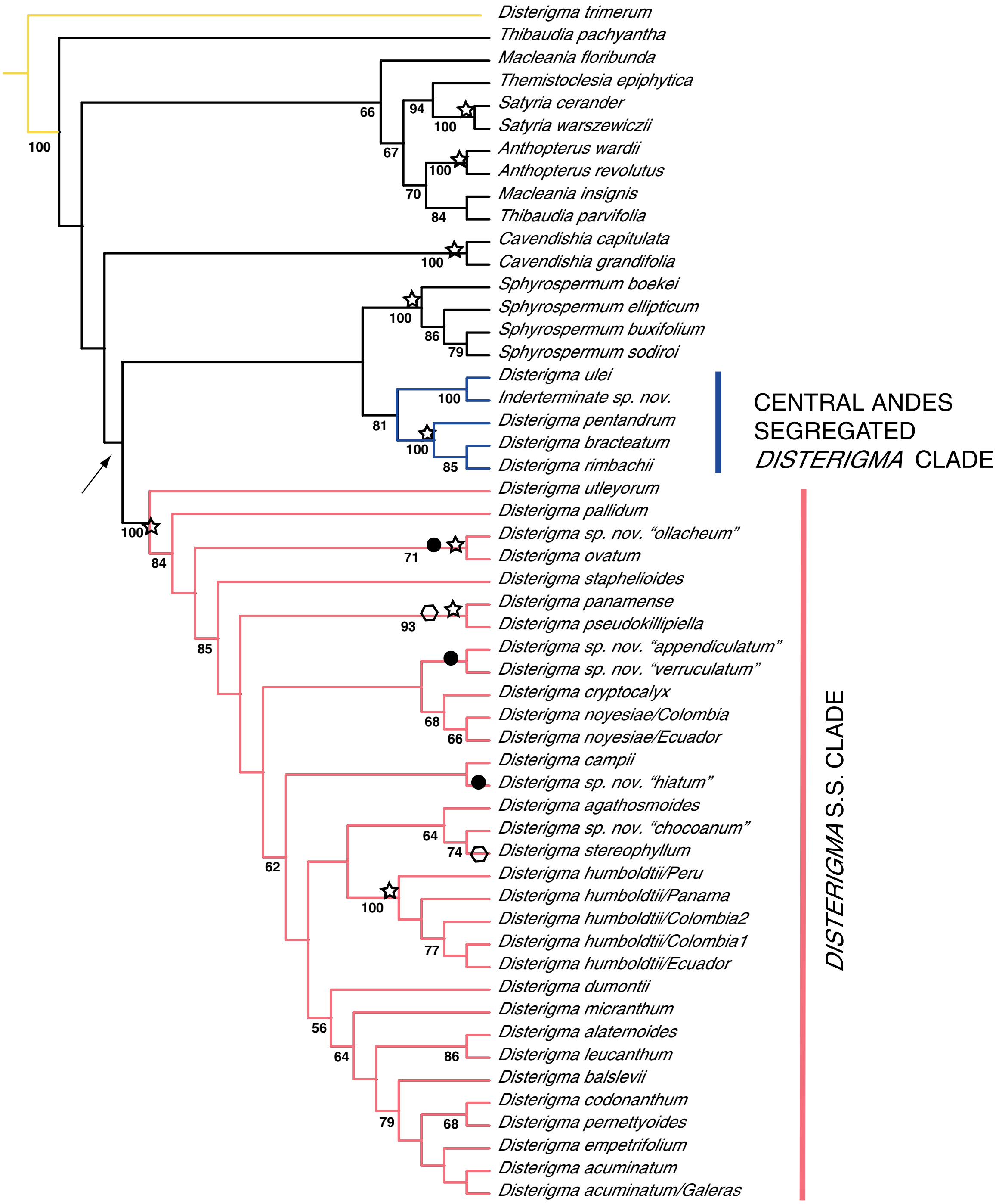


Figure 4. The most parsimonious tree from the total evidence analysis of nrITS, *ndhF*, and 55 morphological characters of 47 species of Vaccinieae (L= 2564), using the parameter combination with the best RILD in POY 4.1908 [1:1:1:2:4, when morphology change:transitions:transversions:gap extension:gap opening]. Jackknife support below the lines. Stars mark the nodes that are common to all the resulting MPT under 29 parameter combinations; closed circles mark 5-merous species; hexagons mark species with subterminal and axillary flowers; see text for explanation of the arrow.

parameters are equally weighted is not supported by any other transformation cost matrix and this node remains unresolved when gaps are coded as a fifth state (Fig. 5).

With exception of the robust clades within *Disterigma* s.s. previously mentioned and for which the support is high to moderate, the position of the remainder of the species of *Disterigma* s.s. is not robust (present in < 50% of all MPT) and their support values are mostly moderate (Fig. 4). When looking at the optimization of individual morphological characters on the tree, it is interesting to observe the levels of homoplasy and the evolution suggested for characters regarded as phylogenetically informative such as flower merosity (ci: 37) and the position and development of subterminal flowers along with the typical axillary flowers (ci: 50). The homoplasy is caused by the placement of *D. stereophyllum* and its implications in the evolution of the rare subterminal flowers (hexagons in Fig. 4), and of the sympatric new species *D. sp. nov. "verruculatum," D. sp. nov. "appendiculatum",* and *D. sp. nov. "hiatum"*, and what their position implies for the evolution of 5-merous flowers (closed circles in Fig. 4) within a largely 4-merous genus. A closer look at all the MPT obtained under the different parameter combinations shows that the placement of these species is less homoplasious when gaps are coded as a fifth state and all parameters are equally weighted (1:1:1:1:0, when GO is 0) (Fig. 6); moreover, the resulting consensus tree is as robust as the single MPT obtained with the parameter set in which overall character incongruence is minimized (lowest RILD) because all the clades insensitive to parameter selection are present. Although nodal support is similar for both analyses, the placement of the sympatric 5-merous species and that of the taxa with both axillary and subterminal flowers is supported in the analysis with gaps coded as a fifth state (Fig. 6), while the position of these species is unsupported or moderately supported by the analysis with the lowest RILD (Fig. 4). Because of the previous results in terms of nodal stability and support, and

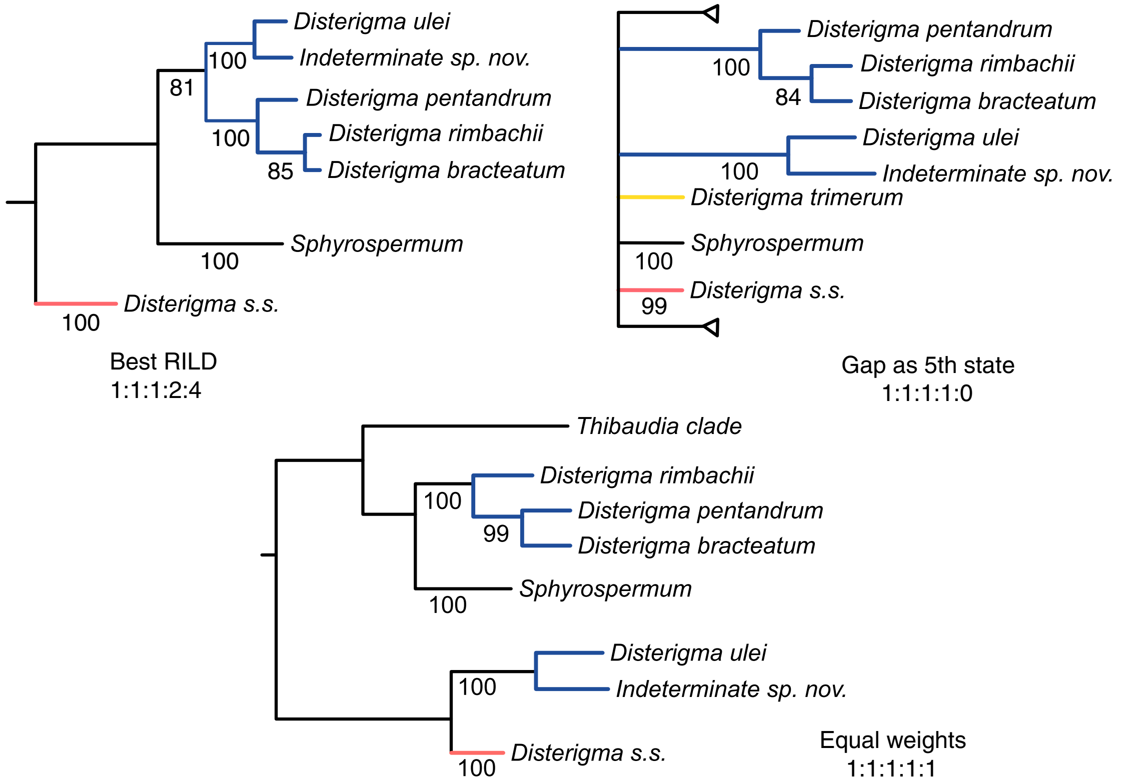


Figure 5. Example of different hypotheses for the sister group of *Disterigma* s.s. obtained in the sensitivity analysis with POY 4.1908. Key: [morphology change:transitions:transversions:gap extension:gap opening]. Jackknife values below lines.

because floral merosity and the position and development of the inflorescence are complex characters, I believe that the most sound hypothesis is the one derived from equally weighting all parameters with gaps coded as fifth state. Moreover, the fact that in the 29 parameter combinations investigated in this sensitivity analysis incongruence is always minimized when the GO is penalized higher or as high as any of the other parameter (Table 4), suggests that perhaps the RILD could be skew as the denominator becomes progressively inflated as the maximum length of the combined data set inevitably grows.

Although one could argue from a theoretical point of view about which is the most appropriate coding scheme for indels (i.e.,. blocks vs. individual gaps), in this analysis, whether one chooses the trees derived from coding gaps as blocks or those from considering gaps as a fifth state, the main outcomes of the test of

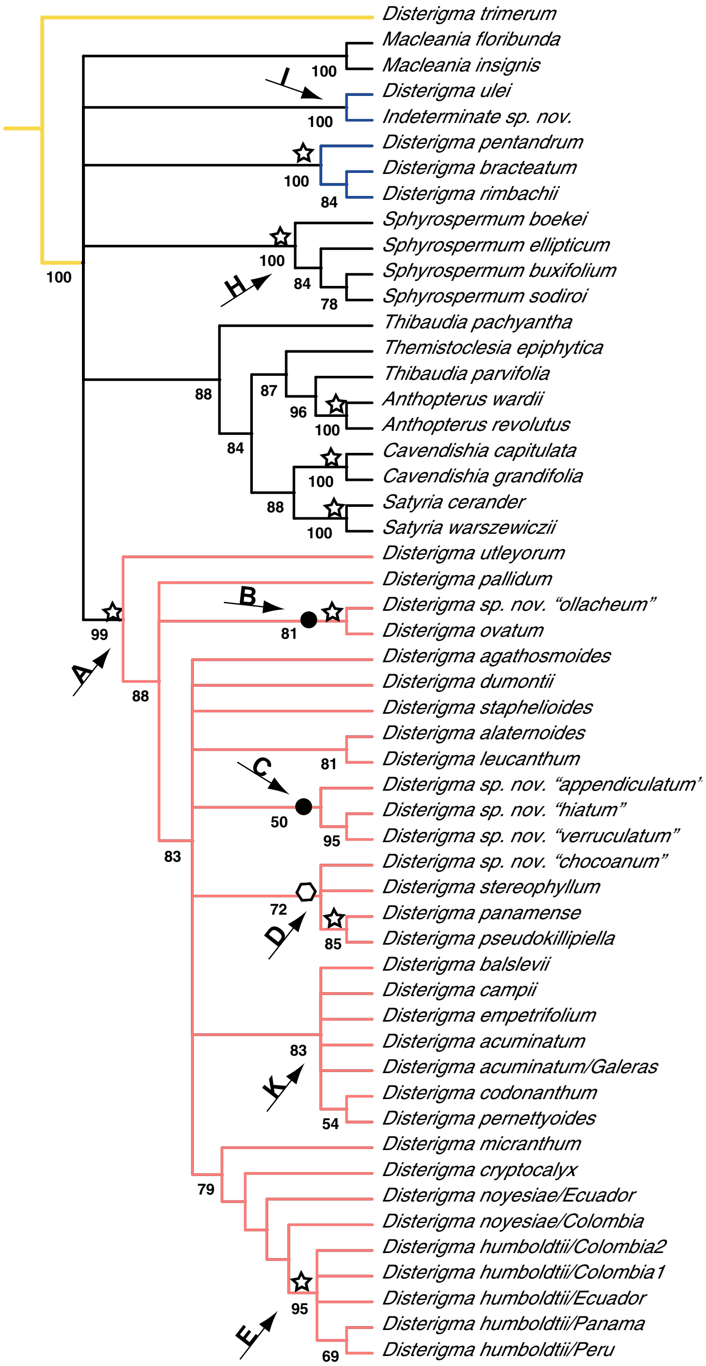


Figure 6. Strict consensus of 71 MPT from the total evidence analysis of nrITS, *ndhF*, and 55 morphological characters of 47 species of Vaccinieae (L= 1319), coding gaps as 5th state and equally weighting all parameters in POY 4.1908 [1:1:1:1:0, when morphology change:transitions:transversions:gap extension:gap opening]. Jackknife support below the lines. Stars mark the nodes that are common to all the resulting MPT under 29 parameter combinations; closed circles mark 5-merous species; hexagons mark species with subterminal and axillary flowers; see text for explanations of the arrows.

Disterigma s.l. (i.e., strongly-supported and non-refuted clades) are not affected.

Dynamic Homologies vs. Static Homologies

The two-step method method with static homologies is applied using the preferred analytical conditions -equal weights and gaps coded as fifth state-. The GO and GE values of Clustal X were set to 1, and the DNA Transition Weight to 0; as already observed by Ogden & Whiting (2003), these values are likely to resemble equal costs. The influence of the Delay Divergent Sequences setting of Clustal X over the alignment is less clear, thus I used the default value (30%) because the program manual notes that when the taxa have a sequence identity < 30% (default), this automatic method for multiple alignments becomes less reliable (Thompson et al., 1994, 1997). To account for the differences caused by using a DNA Identity Matrix [Clustal W (1.6) DNA Weight Matrix, default] instead of a DNA Transformation Cost Matrix, a customized DNA weight matrix was built and fed into Clustal.

After aligning the sequences with CLUSTAL X (Thompson et al., 1997) and conducting the tree search with TNT (Goloboff et al., 2000), the total evidence analysis resulted in 26 MPT 1447 steps long (Fig. 7). The CLUSTAL X + TNT analysis differs from POY 4 (Varón et al., 2007b) analysis in that POY retrieved the most parsimonious trees, which are 1319 steps long (Fig. 6). The results from both analyses also differ in their node support values; not only the Jackknife values in the POY analysis tend to be higher, but also much more nodes have support above 50%.

Regarding the major clades of *Disterigma* that have been discussed in this paper, the CLUSTAL X + TNT analysis (Fig. 7) recovered all the clades found to be stable under different parameter conditions, and here too, *D. rimbachii, D. pentandrum, D. ulei,* and *D. bracteatum* are placed outside of a *Disterigma s.s.* clade. The results of this analyses are also similar to those of POY because here too a polytomy is at the base of the tree and therefore there is no resolution for the sister group of *Disterigma* s.s.

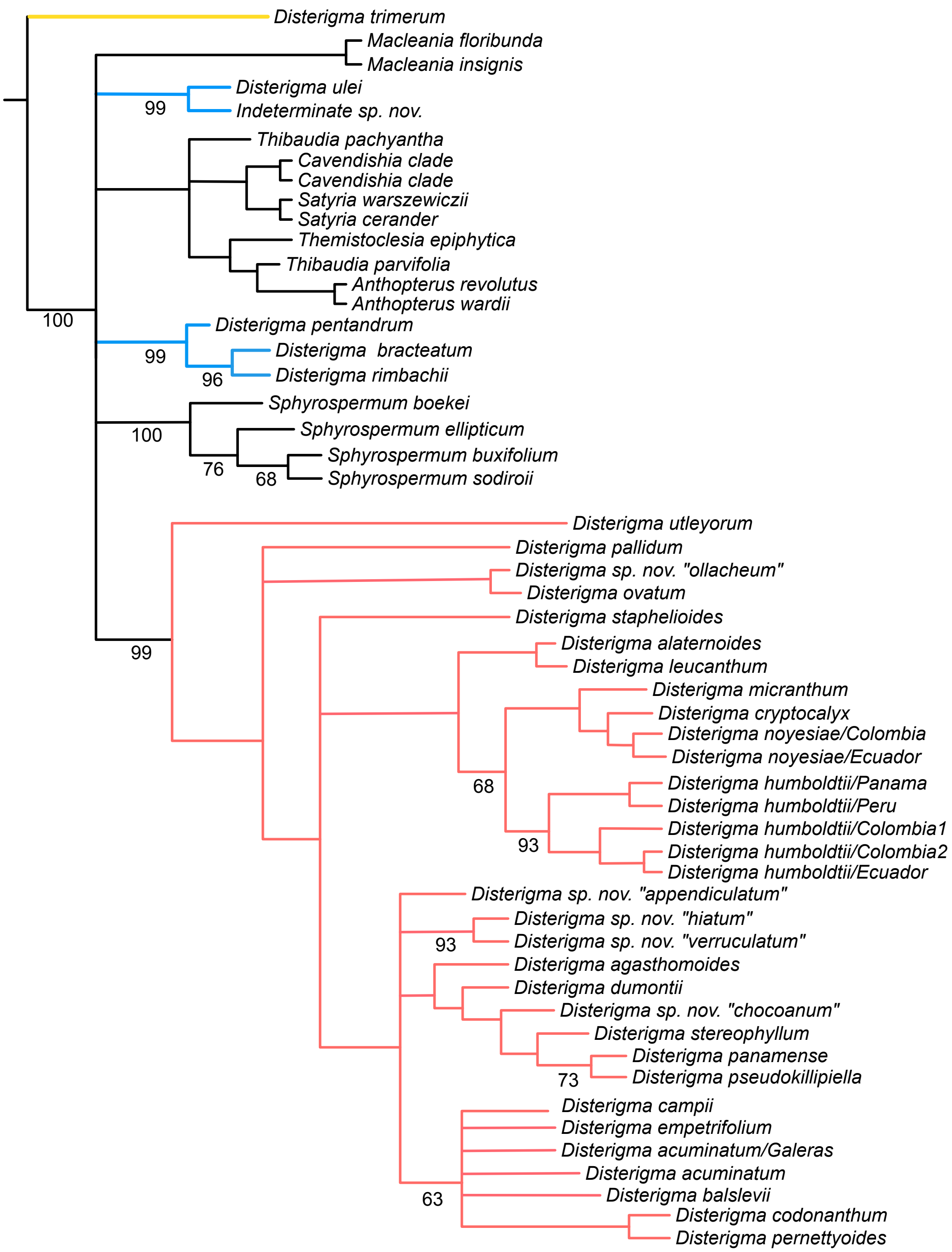


Figure 7. Strict consensus of 26 MPT from the total evidence analysis of nrITS, *ndhF*, and 55 morphological characters of 47 species of Vaccinieae (L= 1447). Tree search in T.N.T. with gaps coded as 5th state and all parameters equally weighted. Multiple sequence alignment in Clustal X, emulating equal weights for all parameters. Jackknife values below lines**.**

DISCUSSION

The presence of a differentiated pair of apical bracteoles (char. 14) (Fig. 8 A) is a homology of the robust and well-supported monophyletic *Disterigma* s.s. (Fig. 6 A); seed embryos white (char. 54) is also among its synapomorphies (Fig. 8 A). Apical bracteoles are largely absent in Vaccinieae, and in *Disterigma* s.s., are clearly differentiated from other bracts and bracteoles in size and position. In the case of the segregated *D. pentandrum*, the most distal bracteoles (apical in position) do not form a distinctive pair and rather are part of a series of numerous similarly looking and sized bracts and bracteoles. Differentiated apical bracteoles are not only diagnostic of *Disterigma* s.s., but also bear several taxonomically and phylogenetically important characters (e.g., fusion, ornamentation, coverage). Other plesiomorphic characters of the genus are pedicels usually less than 2 mm long and obscured by the overlapping bracts, and bracteoles always opposite (non-homoplasic). Although not all the species of *Disterigma* could be sampled for DNA work and therefore are not in the total evidence analysis, the results of the morphological analysis placed them within *Disterigma* s.s.; they are *D. baguense, D. campanulatum, D. dendrophilum, D. hammelii*, and *D. synanthum*.

The following are the clades within *Disterigma* s.s. with moderate to high Jackknife support (above 70 %) (Fig. 6 B, C, D, E) which have diagnostic synapomorphies (Fig. 8 B, C, D, E). The clade *D.* sp. nov. “ollacheum”-*D. ovatum* was supported by 5-merous flowers (char. 21), calyces with sinuses with straight edges (V-shaped) (char. 28), and leaves with apiculate apex (char. 3) (Fig. 8 B). A more derived clade also diagnosed by its 5-merous flowers is that of *D.* sp. nov. “hiatum”- *D.* sp. nov. “verruculatum”-*D.* sp. nov. “appendiculatum” [Fig. 8 C; leaves spirally arranged (char. 0) and apically acuminate (char. 2) are also diagnostic]; although the Jackknife support for this clade is only 50 % (Fig. 6 C), the internal clade *D.* sp. nov. “hiatum”-*D.* sp. nov. “verruculatum” has a 95 % support and synapomorphies such as flowers arranged in fascicles (char. 5), calyx completely cylindric (char. 23) and with the lobes very reduced (char. 24), and corolla internally puberulous (char. 33) (Fig. 8). The clade *D. panamense-D. pseudokillipiella-D.* sp. nov. “chocoanum”-*D. sterophyllum* (Fig. 8 D) is supported by the presence of subterminal flowers mixed with axillary flowers (char. 4) (flowers only axillary in *D. chocoanum*); subterminal flowers are rare within neotropical Ericaceae and are not found anywhere else within the genus. Finally, all the Central and South American OTUs of *D. humboldtii* sampled form a clade (Fig. 6 E). *Disterigma humboldtii* has a variable vegetative and reproductive morphology, and the combinations of the extremes of the variation have been described as different species. For instance, the polymorphism here sampled include South American specimens with short and long corollas internally glabrous or glabrate, along with Central American specimens with corollas long and glabrate; in the case of *D. humboldtii/Ecuador*, the specimen has bracteoles and leaves larger than the average of the species. The *D. humboldtii* clade is supported by their bracteoles covering 26-92% of the calyx (char. 17) (Fig. 8 E).

Even though *Disterigma micranthum* (collected at the type locality), *D. cryptocalyx* and *D. noyesiae* s.l. (two OTUs sampled) are closely related and are in a clade with 79 % Jackknife support (Fig. 6), there is no morphological synapomorphy that diagnose this group which also contains *D. humboldtii*. *Disterigma noyesiae/Ecuador*, collected at the type locality in Carchi, and, *D. noyesiae/Colombia*, from Cauca, only differed in the distribution of the papillae on the anthers (char. 49), the shape of the calyx sinuses (char. 28), and in the shape of the corolla (char. 30), characters that have been found to be polymorphic in other species (Fig. 8). Because the terminals *D. noyesiae/Ecuador* and *D. noyesiae/Munchique* do not have other characters that clearly differentiate them (apomorphies) and both of them have bracteoles exceeding the calyx by more than 1 mm (char. 17), they are not considered two different species. Furthermore,

Figure 8. Character state distribution on one of the 71 MPT from the total evidence analysis of nrITS, *ndhF*, and 55 morphological characters of 47 species of Vaccinieae (L= 1319), coding gaps as 5th state and equally weighting all parameters in POY 4.1908 [1:1:1:1:0, when morphology change:transitions: transversions:gap extension:gap opening]. Fast optimization. Open circles are homoplasious characters, closed circles are non-homoplasious. The characters numbers correspond to the list in Table 2.

molecular analyses do not show signs of hybridization, and the specimens previously identified as potential hybrids between *D. alaternoides* and *D. cryptocalyx*, and, *D. acuminatum* and *D. cryptocalyx* by Luteyn (1996) belong to the polymorphic *D. noyesiae* s.l.

Although in the strict consensus tree of the total evidence analysis there is no resolution at the level of the sister group of *Disterigma* s.s. (Fig. 6), from the character optimization over one of the MPT it is possible to see that *Disterigma* s.s. and the clade formed by the South American segregated *Disterigma* and *Indeterminate* sp. nov. share subsessile flowers (char. 8), pedicels obscured by the overlapping bracts (char. 11), and bracteoles with opposite insertion (char. 12) (Fig. 8 F). In the same tree, the symplesiomorphies that are found at the base node that connected these clades to *Sphyrospermum* are 4-merous flowers (char. 21), calyx lobes longer than half of the calyx limb, (char. 24), and corolla urceolate (char. 30) (Fig. 8 G). The well-supported *Sphyrospermum* clade (Fig. 6 and 8 H) had three non-homoplasious homologies, namely pedicels filiform and very slender (char. 9), urceolate calyces (char. 23), and foveolate anthers (char. 48); its homoplasious homologies included pedicels continuous with the calyx (char. 10) and the mesocarp of the immature fry fruits thin and brittle when dry (char. 53).

Because the behavior of congruence tests within sensitivity analyses needs to be examined in more detail, it has been proposed that the most sensible strategy is to only perform this analyses across a range of models to determine which relationships are robust to the analytical parameters (Dowton & Austin, 2002). Ideally, one would expect that a well-supported node would not be model dependent. But there are cases in which a well-supported node is only obtained under one or few models out of the whole parameter set explored. This lack of stability with high node support could be caused by many reasons, from a limited number of informative characters in the entire data set, the dominance of one of the partitions, to a limited taxon sampling. Is especially in the cases where disagreement exits when sensitive analyses can be a great tool to better understand the data set and detect key areas of the tree that need to be further investigated before introducing changes in the nomenclature. The following are examples of clades that were sensitive to parameter variation (low nodal stability) in spite of having moderate to high node support. The novel clade *Indeterminate sp. nov.-Disterigma ulei* is unambiguously supported by two homoplasious synapomorphies, calyx sinuses with straight edges (V-shaped) (char. 28, very homoplasious with 13 steps) and glabrous staminal filaments (char. 39) (Fig. 6 and 8 I). Because this clade was present in the consensus tree of both the nrITS and ndhF analyses, the results suggest that the lack of stability might be produced by the sampling rather than by the amount of data. Although the node ancestral to *Indeterminate sp. nov.-Disterigma ulei* is unresolved in the strict consensus, in one of the MPT connects to the other segregated *Disterigma* from the Central Andes (Fig. 8 J) and it is supported by the presence of haplostemonous flowers (char. 34), a character with 5 steps in the tree that is lost in *D. ulei* (Fig. 4 I). Within the *Disterigma* s.s., the clade containing high altitude species (with exception of D. campii), has a 83% Jackknife support in the total evidence analysis (Fig. 6 K) and it is unambiguously supported by corollas adaxially glabrous (char. 32) and papillae present on both anther theceae and tubules (char. 49) (Fig. 8 K). However, this clade is not in the strict consensus of the individual molecular partitions and is not present in 75% of the resulting MPT under the different parameters sets (sensitivity analysis), thus being likely that the molecular character sampling is still limited to satisfactorily resolved this closely related species.

As for the behavior of the RILD test observed, although other measurements of congruence exist, and a study of the performance of various tests points out that none of them is obviously preferable over the others (Aagesen et al., 2005b). In mixed-model analyses the ILD and RILD tests are unlikely to be an effective measure of congruence when two data sets differ markedly in size (Dowton & Austin, 2002), but this problem is overcome when enough data is combined (Aagesen et al., 2005b). In the case of this data set of Vaccinieae, the partitioning the molecular markers alleviate the size difference, and given that for this data set indels are not frequent or too long (many are 1-3 bp long), it is unlikely that these factors could have caused the RILD to skew. However, more studies are necessary to further evaluate the performance of RILD and rule out the inflation of the denominator as the cause of the results here obtained. The exploration of other congruence tests, like the recently proposed partition free Meta-Retention Index (MRI) (Wheeler et al., 2006b), in which the maximum cost is in both the numerator and denominator, may be a solution for the possible deviation of the RILD.

CONCLUSIONS

Sensitivity Analysis and Direct Optimization

Regarding to the analytical methods it can be concluded that direct optimization, as implemented in P0Y 4, offer the most parsimonious phylogenetic reconstruction for Andean Vaccinieae when compared with the results of performing an automated multiple alignment with CLUSTAL X followed by a tree search with TNT. The sensitivity analyses make possible the identification of robust and well-supported topologies through the assessment of node support and node stability; it also allow to identification of key areas with complex relationships that need further investigation. Although the RILD is used to find the most congruent parameter scenario, for this data set, this is not the only one that produce a robust hypothesis.

Taxonomic Conclusions

Disterigma s.s. is a robust monophyletic group that is recovered in all analyses despite changes in transformation costs. Additionally, none of the analyses refuted the segregation from *Disterigma* s.l. of the Mesoamerican *D. trimerum* and of *D. ulei, D. pentandrum, D. rimbachii,* and *D. bracteatum*, all from the central Andes. *Disterigma trimerum* seems to be an isolated lineage within the tribe, and its correct placement requires extensive sampling of the poorly understood Mesoamerican/Caribbean clade. As for the segregated species from the central Andes, although they form diagnosable and novel groups, their placement within Vaccinieae is also ambiguous; to resolve their complex generic affinities more evidence is necessary. Both morphological and molecular evidence supports the robust novel clade composed of *D. pentandrum, D. rimbachii,* and *D. bracteatum*, but the inclusion of *D. ulei* and *Indeterminate* sp. nov. within this novel clade needs to be further tested by sampling more South American species with similar morphology or/and distribution. Even though the sister group of *Disterigma* s.s. is unknown, there is strong evidence in the total evidence analysis that support *Sphyrospermum* and *Disterigma* s.s. as two monophyletic and diagnosable clades.

Genus *Disterigma s.s.* Klotzsch

Tree diagnosis: 1) presence of a pair of apical bracteoles, differentiated in size from other bracts and bracteoles; 2) seed embryos white (except in *D. ovatum*).

Comparative diagnosis: symplesiomorphic characters include flowers 4-merous (except in *D.* sp. nov. “appendiculatum”*, D.* sp. nov. “hiatum”*, D.* sp. nov. “ollacheum”*, D. ovatum, D.* sp. nov. “verruculatum”), diplostemonous and subsessile (usually less than 2 mm long), the pedicels obscured by the overlapping bracts (except in *D.* sp. nov. “ollacheum”*, D. leucanthum, D. pernettyoides,* and sometimes *D. humboldtii*) and articulated with the calyx, and the bracteoles with opposite insertion.

Content: *Disterigma acuminatum*, *D. agathosmoides*, *D. alaternoides*, *D.* sp. nov. “appendiculatum”, “*D.* sp. nov “baguense”, *D. balslevii*, *D.* sp. nov. “campanulatum”, *D. campii* , “*D.* sp. nov ”chocoanum”, *D. codonanthum*, *D. cryptocalyx*, *D. dendrophilum*, *D. dumontii*, *D. empetrifolium*, *D. hammelii*, *D. hiatum.*, *D. humboldtii*, *D. leucanthum*, *D. micranthum*, *D. noyesiae*, *D.* sp. nov. “ollacheum”, *D. ovatum*, *D. pallidum* , *D. panamense*, *D. pernettyoides*, *D. pseudokillipiella*, *D. staphelioides*, *D. stereophyllum*, *D. styphelioides*, *D.* sp. nov. ”synanthum”, *D. utleyorum*, *D.* sp. nov. “verruculatum”.

Distribution: from S Mexico through Central America, south to N Bolivia, and east to Mount Roraima at the border of Guyana, Brazil, and Venezuela.

Disterigma trimerum, *incertai sedis*

Tree diagnosis: 1) flowers 3-merous (non-homoplasious); 2) calyx cylindric and never apophysate; 3) corolla infundibuliform.

Distribution: Costa Rica (Limón) and Panama (Chiriquí).

Comments: this species should be excluded from *Disterigma* s.s., however, no new combination is suggested at the moment.

Central Andes Segregated *Disterigma* Clade*, incertai sedis*

Tree diagnosis: 1) haplostemonous flowers (except in *D. ulei*).

flowers 5-merous; 2) calyx aestivation imbricate (except in *D. rimbachii*); 3) staminal filaments geniculate.

Comparative diagnosis: the symplesiomorphies include subsessile flowers, pedicels obscured by the overlapping bracts and articulated with the calyx, bracteoles with opposite insertion, and differentiated apical bracteoles are absent.

Comments: further evidence may support a different placement for *D. ulei* and *Indeterminate* sp. nov, for their placement within this clade is not robust in this analysis.

Content: *Disterigma pentandrum, D. rimbachii, D. bracteatum, D. ulei, Indeterminate* sp. nov.

Distribution: Ecuador to northern Peru.

CHAPTER II

MONOGRAPH OF THE ANDEAN BLUEBERRY GENUS *Disterigma* (ERICACEAE: VACCINIEAE)

INTRODUCTION

Disterigma (Klotzsch) Nied. is a neotropical genus of species that inhabit the cloud forests and páramos of Central and South America. A few species of *Disterigma* are widespread, many are endemics, and the great majority of them have restricted altitudinal ranges and are confined to cold and humid environments.

Disterigma includes species of small shrubs bearing very small and inconspicuous flowers, with the corollas just one centimeter long and pale-colored. However, a closer look reveals that the species within this genus are morphologically diverse and complex, with 44 names published to date. The need of a revision of *Disterigma* has been apparent for many years because the number of accepted species has been doubled since the only revision available for the entire genus; Smith in 1933 recognized 15 species and by 2007 36 names were in use.

As the number of species included in *Disterigma* increased, the characters that distinguish it from other inferior-ovaried Ericaceae became less clear. Morphologically divergent species, often called “isolated”, were included within *Disterigma*, whereas others not necessarily more atypical were moved into its own genus (*e.g.; Vacciniopsis* Rusby). The notion that the morphological circumscription of *Disterigma* was too wide and that the genus might not be a natural group was supported by preliminary molecular evidence (Kron et al., 2002b; Powell & Kron, 2003); there, according to the parsimony analysis of nuclear and plastid sequence data, *Disterigma* had three independent origins.

Morphological and molecular systematic studies including 80% of the species of *Disterigma* s.l., as well as OTU’s representing polymorphic species, were used to identify the monophyletic group *Disterigma* s.s. (Pedraza-Peñalosa, in press; see phylogeny), which is the subject of this monograph. This treatment recognizes 32 species from Central and South America within the monophyletic

Disterigma s.s. group, and from which *D. bracteatum, D. pentandrum, D. rimbachii, D. trimerum,* and *D. ulei* should be segregated. This monograph include changes in the nomenclature and circumscription of three of the most widespread species of *Disterigma,* which account for 40% of the material examined; the resurrection of one species; the designation of one neotype and lectotype; and the proposition of seven new synonyms, one new combination, and eight new species.

This monograph is based in the study of 3018 different collections from 46 herbaria from Central and South America. The majority of the voucher specimens were studied at The New York Botanical Garden [A, AAU, AMES, CAS, CAUP, CGE, CUVC, DS, DUKE, E, F, FMB, G, GB, GH, HEID, HUSA, JAUM, L, LL, MA, MICH, MO, NA, NY, OXF, S, SEL, TEX, UC, US, W, WIS; acronyms as indicated by Holmgren & Holmgren (1998)], but herbaria in Central (PMA) and South America (COL, BOLV, CUZ, HOXA, HUA, LOJA, LPB, MEDEL, PSO, QCA, QCNE, USM), as well as historically important collections from Europe (B, B-W, BM, K, P, P-Bonpl.), were studied in person. I also have been fortunate to study almost all the species in their natural habitat during extensive fieldwork in Panama (2002), Ecuador (2003, 2004), Colombia (2004, 2007), Peru (2005-2007), and Bolivia (2005). Data also came from living collections at The New York Botanical Garden, The Royal Botanical Garden of Edinburgh, and the Botanical Garden in Heidelberg.

Photographs from living plants and species descriptions are being added to the Neotropical Blueberries website (Luteyn & Pedraza-Peñalosa, 2006) and an interactive key for the threatened species endemic to Ecuador has been created and made available at http://www.nybg.org/bsci/res/lut2/SLIKS14/disterigmaecuador.html.

HISTORY

Within the inferior-ovaried genera of Ericaceae, *Disterigma* was described by Klotzsch (1851) as one of nine subgenera of *Vaccinium* L., in the newly described family Siphonandraceae. Subgenus *Disterigma* grouped South American shrubs with persistent leaves; geminate, ternate, or solitary axillary flowers, 4-lobed tubular or conical corollas, bibracteolate calyx, and, anthers without spurs. Within subgenus *Disterigma,* Klotzsch differentiated between creeping shrubs and erect shrubs or trees; however, trees was an incorrect interpretation of tall shrubs and all the creeping species were slightly different variations of *D. empetrifolium* (=*V. empetrifolium*, *V. penaeoides*, and *V. epacridifolium*).

Niedenzu (1889a) raised *Disterigma* to generic rank, but the proper combinations for the species were not published until later in the same year (Niedenzu, 1889b). However, in between the two papers of Niedenzu, Drude (1889) published the new combination for the type species, *D. empetrifolium*.

The genus *Metagonia* was described by Nuttall (1843) after studying material from the United States, the Sandwich Islands, and a single specimen from Peru. He transferred to *Metagonia* species now in *Vaccinium* and *Disterigma*, and except for the presence of spurs in some species of *Vaccinium*, the description of *Metagonia* was identical to that of many species of *Disterigma*.

The genus *Vacciniopsis,* with two species described by Rusby (1893), was synonymized into *Disterigma* by Blake (1926). Although *Vacciniopsis* is identical to *Disterigma,* Rusby circumscribed it solely on its differences with *Vaccinium*. Blake (1926) recognized 22 species of *Disterigma*, and with the description of *D. pentandrum* S. F. Blake, he expanded the genus concept from species with stamens twice as many as the corolla lobes (8 or 10 stamens, diplostemonous) to include species with an equal number of stamens as corolla lobes (5 stamens, haplostemonous).

It was not until 1933 when Smith provided a comprehensive taxonomic revision for the entire genus, the only one previous to this monograph. Of the 22 species proposed by Blake (1926), Smith recognized 15 as distinct, including *D. pentandrum* as an isolated taxon within the genus. Among other characteristics, Smith defined *Disterigma* based on its 4-5-merous flowers, calyx articulate with the pedicel, stamens (5-)8 or 10, and by its short pedicels crowned at the apex with a pair of apical bracteoles embracing the calyx tube.

In a later work, Smith (1943) described *Killipiella* as a striking new genus from the Colombian Chocó region that superficially resembled *Epacris* Cav.*,* in the Epacridaceae (now Ericaceae: Epacridoideae from Australia, New Caledonia, and New Zealand). However, Smith admitted that *Disterigma* was the closest relative of *Killipiella* because they both had apical bracteoles clasping the calyx. In 1996, Luteyn synonymized *K. stereophyllum* (the second species described in *Killipiella*) into *Disterigma*, thus implying that the entire genus is close to, if not equal with *Disterigma.*

Through various publications and floristic works such as the Ericaceae for the Flora of Ecuador (Luteyn, 1996) and *Disterigma* for Central America (Wilbur 1974, 1992), the number of species of *Disterigma* has doubled since A. C. Smith's revision and previous to this monograph 36 names were in use.

MORPHOLOGY

Habit

The species of *Disterigma* can easily shift from a terrestrial to an epiphytic habit, a common phenomenon in very humid habitats, where the abundant masses of epiphytes serve as traps of sediments and as substrates for other species. The rhizomatous stems with caulinar roots of many scandent and prostrate species also facilitate epiphytism. Although all species of *Disterigma* are shrubs and each individual is rather inconspicuous (few centimeters to 3 m tall), they tend to have an aggregate distribution, often forming dense patches of contiguous individuals, or sometimes, compact cushions several centimeters high (i.e., *D. empetrifolium*).

The species of *Disterigma* are not necessarily restricted to one type of growth form and the growth form is not clearly correlated with geographic/environmental factors. Sometimes the same species can be either completely erect or decumbent and forming cushions within feet of each other (e.g., *D. empetrifolium*); however, the cushion forms are only found in the páramos, typically over 3000 m in swampy areas. Similarly, almost all erect species have been observed scandent, climbing several meters up into the trees. Morphological plasticity is not rare in high altitude plants, because they have to adapt to the constantly changing conditions; therefore, subtle micro-environmental conditions may play an important role in triggering vegetative variability. Additionally, it can be hypothesized that given that *Disterigma*, and Ericaceae in general, thrive in gap openings and vegetation edges, where they are not overshadowed by other plants, they are not only more exposed to the elements than plants inside the forest, but they also need to have certain flexibility to rapidly colonize these areas.

Indumentum

Hairs are present throughout all organs of *Disterigma* and are of two types: **simple, unicellular and eglandular**, or, **simple, multicellular and glandular**. In this monograph, they are referred to as eglandular and glandular hairs. The glandular hairs of *Disterigma* are like those of many other neotropical ericaceous genera, they have a stipe that is swollen at the base and a globose multicellular head. Glandular hairs are frequently deciduous and when they fall off they leave behind the base that darkens to form minute punctuations. Glandular hairs are here equivalent to those hairs called “glandular fimbrie” by Luteyn (e.g., Luteyn 1983, 1996); however, the term “fimbria” is not used here because it implies a marginal position (Font Quer, 1980; Harris & Harris, 1994) and glandular hairs occur on any surface. In *Disterigma,* both glandular and eglandular hairs are inconspicuous, 0.1-0.6 mm long, although the eglandular hairs of the young stems are normally over 1 mm long. Glandular and eglandular hairs are usually found together, forming a rather loose glabrate or puberulous indumentum. Given that both types of hairs are inconspicuous and that their occurrence, density, and distribution within species is too variable to be of major significance, no emphasis is put upon describing them in more detail. However, it is important to note that the presence of hairs within the corolla is useful to identify species (see below under corolla). All indumentum definitions used in this monograph follow those of Font Quer (1980), Hewson (1998), Stern (1992), and Moreno (1984).

Leaves

The leaves of *Disterigma* are alternate, simple, shortly petiolate, and in comparison with other neotropical Ericaceae, smaller (less than 5 cm long and 4 cm broad). Although all leaves are spirally arranged on the stems, in the mature branches they are sometimes oriented in one plane giving the appearance of being distichous (Fig. 9 A) as in *D. agathosmoides, D. campii, D. chocoanum, D. cryptocalyx, D. dendrophilum, D. hammelii, D. panamense, D. pallidum,* and *D. staphelioides* . Like other neotropical Ericaceae, the young leaves of new flushes are bright red, possibly a result of anthocyanin production, a compound that provides protection against solar radiation (Luteyn, 1983).

The venation is probably plinervate (acrodromous) in the entire genus, but the coriaceous lamina is often so thick and/or fleshy that the veins are obscured in both fresh and dry material. In herbarium specimens the midvein is almost always visible and the thick secondary veins, arising from near the base of the

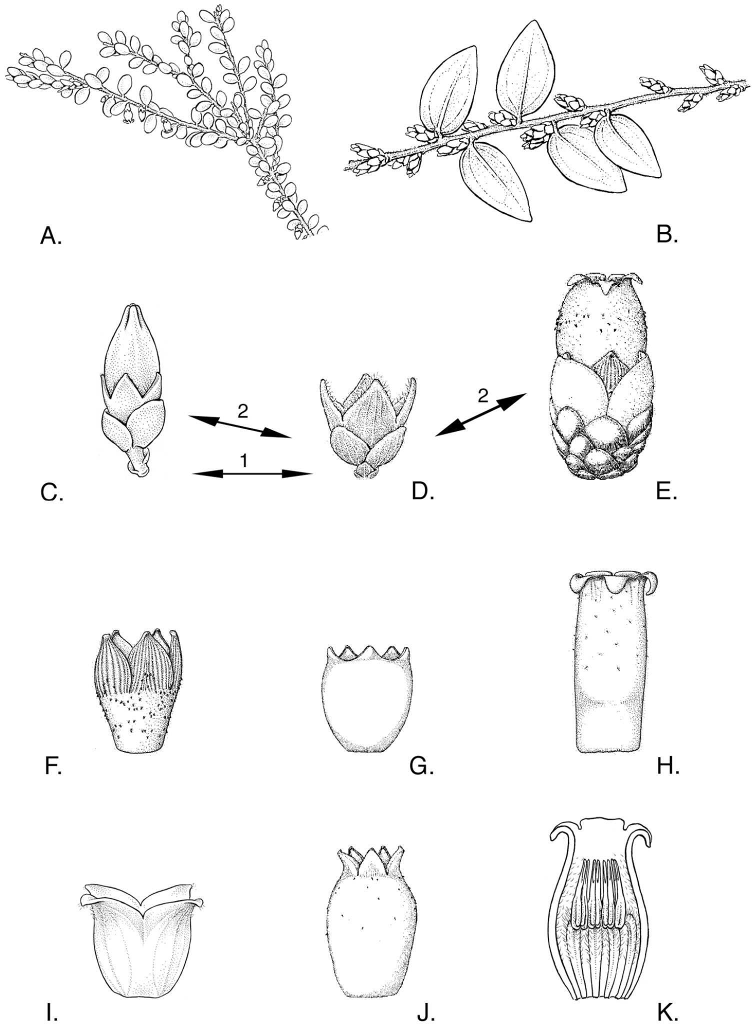


Fig. 9. Examples of external morphology. **A.** Example of leaves with distichous appearance, *Disterigma chocoanum*; **B.** Portion of a branch bearing axillary fascicles and solitary flowers, *D. synanthum*; **C.** Floral bud showing the inconspicuous bracts borne at the base of the pedicel (1) and the differentiated apical bracteoles borne at the apex of the pedicel (2), the calyx sinuses acute (V-shaped), *D. ollacheum*; **D.** Pedicel with inconspicuous bracts at the base (1), the calyx basally enveloped by the differentiated apical bracteoles (2), the calyx sinuses acute (V-shaped), *D. campanulatum*; **E.** Flower with numerous and increasingly conspicuous overlapping bracts, the pair of differentiated apical bracteoles much larger (2) and as long as the calyx, *D. appendiculatum*; **F.** Calyx with the sinuses obscured by the overlapping bases of the imbricate calyx lobes, *D. appendiculatum*; **G.** Calyx with rounded sinuses (U-shaped), *D. hiatum*; **H.** Tubular corolla, *D. verruculatum*; **I.** Campanulate corolla, *D. campanulatum*; **J.** Urceolate corolla, *D. hiatum*; **K.** Longitudinal section of an urceolate corolla adaxially puberulous, *D. chocoanum*.

lamina and obliquely attached to the midvein, are sometimes apparent only in the thinner young leaves. *Disterigma styphelioides* is unique in the genus because it has parallel secondary veins.

A great array of leaf shapes and sizes and, especially of widths, is found among the species; leaves vary from needle-like and just about 2 mm wide [e.g., *Disterigma agathosmoides, D. empetrifolium, D. hammelii, D. panamense,* and *D. pernettyoides*] to suborbicular and several centimeters wide (e.g., *D. alaternoides, D. hiatum,* and *D. ollacheum*) (Fig. 10). Although certain species or groups of species are characterized by the combination of leaf size and shape, size variation can be great within a single species. Such is the case of *D. humboldtii,* in which the extremes of the morphological variation were once regarded as different species. Conspicuous variation within the same individual is also possible given that the leaves of the rhizomatous stems often are either larger or smaller than the average leaf.

Inflorescence

The majority of the species of *Disterigma* have axillary solitary flowers, and within the same plant, the solitary flowers are sometimes accompanied by few-flowered fascicles. Only in a few species does the contrary occur, where the flowers are typically organized in axillary fascicles and the solitary flowers are rare [e.g., *D. alaternoides, D. dendrophilum*, and *D. synanthum*] (Fig. 9 B).

Solitary flowers have been interpreted in different groups of Ericaceae as the product of reduced racemose inflorescences (e.g., Luteyn et al., 1995; Smith, 1943; Oliver, 2000). However, I have found no morphological evidence of such reduction in any *Disterigma*. In the fascicles of this genus, all the flowers emerge directly from the axil, one next to the other (the greater the number of flowers the larger the axillary area), without any trace of a common rachis. In the occasional

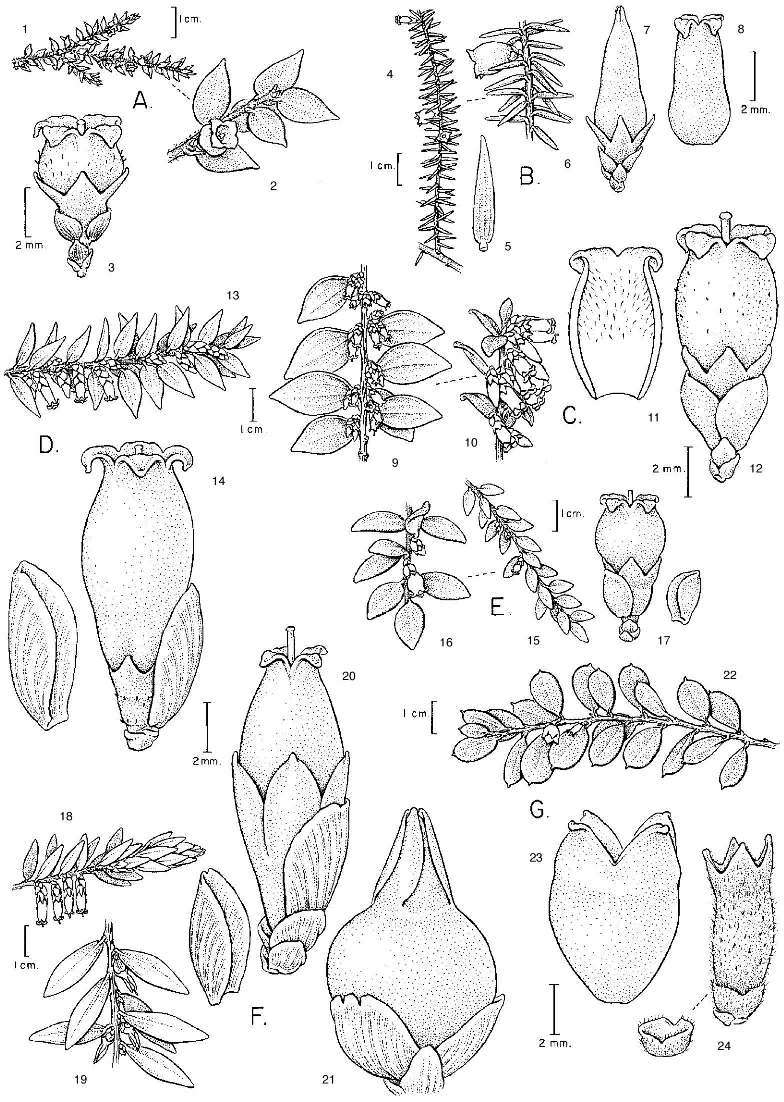


Fig. 10. Exemplary species of *Disterigma* illustrating the overall morphological diversity of the genus. **A.** *D. acuminatum,* branch (1) with an enlarged axillary solitary flower (2) and a detail of a complete flower (3); **B.** *D. agathosmoides,* branch (4) with an enlarged leaf (5) and a mature fruit (6), and a detail of a floral bud (7) and an open corolla (8); **C.** *D. alaternoides,* branch (9) with a zoom of axillary fascicles (10), and a detail of a longitudinal section of a corolla (11) and a complete flower (12); **D.** *D. cryptocalyx,* branch (13) and a detail of a complete flower with a detached differentiated apical bracteole (14); **E.** *D. micranthum,* branch (15) with an enlarged axillary solitary flower (16) and a detail of a complete flower with a detached differentiated apical bracteole (17); **F.** *D. stereophyllum,* branch with flowers (18), branch with fruits (19), detail of complete flower with a detached differentiated apical bracteole (20) and of a mature fruit (21); **G.** *D. utleyorum,* branch (22), corolla (23), and calyx (24) with the differentiated apical bracteole detached (A: *P. Pedraza & C. Pedraza 1121*, NY; B: *P. Pedraza & C. Pedraza 1139*, NY; C: *P. Pedraza & C. Pedraza 1139*, NY; D: *P. Pedraza & C. Pedraza 1139*, NY; E: *P. Pedraza & C. Pedraza 1139*, NY; F: *P. Pedraza & C. Pedraza 1139*, NY; G: *P. Pedraza & C. Pedraza 1139*, NY).

single flowers found in species with fascicles, it is possible to find aborted buds adjacent to the single flower; however, not all single flowers necessarily have adjacent aborted buds. Therefore, it is hypothesized that in *Disterigma* the transformation from multi-flowered fascicles to single flowers is mediated through the suppression or initiation of individual floral buds, rather than through the reduction of a branched and multi-flowered common structure into a solitary flower. Moreover, the flowers of *Sphyrospermum* Poepp. & Endl., a closely related genus (Powell & Kron, 2003), are also either solitary or arranged in fascicles. However, newer analyses have shown that the evidence supporting *Sphyrospermum* as the putative sister group of *Disterigma* is not conclusive (Pedraza-Peñalosa, in press; see phylogeny) and further analyses are necessary to better understand the origin of the inflorescences in this group.

In the case of the fasciculated *Disterigma hiatum* and *D. verruculatum,* they sometimes appear to have solitary flowers instead of fascicles due to the asynchrony of the development of floral buds. A single fascicle may contain fruits that have passed maturity, immature fruits, and some floral buds. Interestingly, in these species the “single flowers” are frequently located distally along the branches.

Solitary flowers and inflorescences are typically axillary in neotropical Ericaceae. However, in the single-flowered *Disterigma panamense, D. pseudokillipiella,* and *D. stereophyllum*, the terminal bud is aborted and reduced to a bristle like bract, leaving the immediately adjacent floral bud in a terminal position (here called subterminal). In young shoots, the surrounding leaves many times hide the subterminal flowers, which until now had passed unnoticed. Vegetative growth is later taken over by a subterminal bud.

Bracts and Bracteoles

Terminology that applies to inflorescences, bracts, and bracteoles has been used inconsistently in Ericaceae. *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 the bracteoles, which come later in the development of the inflorescence and are borne on the pedicel (Font Quer, 1980; Harris & Harris, 1994; Weberling, 1989) (Fig. 9 C, D). Two bracteoles per pedicel is the general rule in neotropical Ericaceae. Nevertheless in *Disterigma,* the most distal pair (rarely fused into one) is distinguishable for being inserted right at the apex of the short pedicel, clasping the calyx, and also for being differentiated in size and shape from the rest of the bracts and bracteoles. 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 and confused with that of prophyll (for an example see Stevens et al. 2004). Prophyll 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 (Harris & Harris, 1994; Weberling, 1989); therefore prophylls, unlike bracteoles, appear much earlier in the development, even before pedicels are initiated, and in their position correspond to what in Ericaceae have been called bud scales, axillary bud scales, or pseudostipules [see *Ceratostema rimbachii =Disterigma rimbachii* in Smith (1935b)]. 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 Ericeae (Oliver, 2000), but has not been documented in neotropical Vaccinieae.

In general, numerous bracts encircle the flowers of *Disterigma*; they are at times small and inconspicuous (e.g., *D. acuminatum)* or large and conspicuously overlapping (e.g., *D. cryptocalyx, D. styphelioides, D. synanthum*) (Fig. 9 D, E). The bracts inserted in the axile are not taxonomically useful, whereas the texture, presence of striation (usually mirrored by the sepals), presence of pustules, and the extent to which the differentiated apical bracteoles clasp the calyx, are all useful characters for species identification. Differentiated apical bracteoles are normally two in *Disterigma*, but a single differentiated apical bracteole can originate by the fusion of the pair. Such is the case of *D. pallidum,* where the single uppermost bracteole is apically obcordate and has two costae, one from each “paternal” bracteole; rarely, it is possible to find a flower or two with the pair of bracteoles completely free. In the case of *D. utleyorum* the fusion occurs at both ends of the two differentiated apical bracteoles, thus forming a single ring-shaped bracteole.

Flowers

The flowers of *Disterigma* are 4-merous, or less often 5-merous, and with the stamens twice the number of corolla parts (diplostemonous). Although polymorphism in the merosity of the flowers has been observed in several species (e.g, *D. appendiculatum, D. campii*, *D. hiatum, D. pernettyoides,* etc.), it is rare and restricted to a couple of flowers among all the examined specimens. There are cases in which the alterations in the number of corolla and calyx lobes are not reflected in the number of stamens, which then remain stable [e.g., *D. ovatum, D. pernettyoides*]. *Disterigma ovatum* typically has 5-merous flowers, and although 4-merous flowers are rarely found, the calyces frequently appear to be 4-lobed because one lobe is reduced and somehow inconspicuous, or because two adjacent lobes are smaller and displaced one next to the other.

Pedicel

The flowers of *Disterigma* are subsessile, with the pedicel usually 1 mm long (ranging from 0.3 to 3 mm long) and obscured by the overlapping bracts and bracteoles; rarely, pedicels 11 mm long are found in *D. empetrifolium*. Although subtle, a portion of the pedicel is not completely hidden by the overlapping bracts in *D. dendrophilum, D. leucanthum, D. micranthum, D. ollacheum,* and *D. pernettyoides*, and occasionally in *D. chocoanum, D. codonanthum, D. dumontii,* and *D. empetrifolium*. The pedicel is terete and it has a clear constriction (articulation) between it and the calyx. From the articulation, a ring of minute glandular and eglandular hairs arises, usually 0.1 mm long.

Calyx

Calyx aestivation is a useful taxonomic character, although it is often overlooked in neotropical Ericaceae. Many times in the literature the aestivation of the calyx and corolla is generalized despite the fact that they are not necessarily equivalent (as in several species of *Disterigma*). Whether the generalized aestivation reported in the descriptions of many Vaccinieae makes reference to the calyx or the corolla is not known. In *Disterigma*, the calyx is valvate when the lobes are applied to each other only by the margins, or is less often imbricate when the lobes are overlapping in various ways one with the other. Imbricate aestivation can be quincunx (typic quincunx in 5-parted calyces, or modified in 5- and 4-merous calyces), or twisted (spiraliter contorta) (Gray, 1875; Stern, 1992). Since different types of calyx imbrication can be observed in one single species (i.e., *D. stereophyllum*), it is the presence of overlapping lobes that seems to be the most meaningful character. Also taxonomically useful is the shape of the calyx sinuses at anthesis.

The calyx shape in this work makes reference to the entire calyx and not just to the calyx tube like in many other studies of Ericaceae (Luteyn, 1976, 1983, 1996; Luteyn & Wilbur, 2005; Wilbur, 1974, 1992). The calyx of inferior-ovaried Ericaceae has two main sections: the calyx tube that is the most basal portion which is adnate to the ovary, and, the calyx limb that is the entire portion free from the ovary (Fig. 11 G); the calyx limb includes the lobes. Although a lot of emphasis has been previously put on the differences of calyx lobe length between species (Smith, 1933; Wilbur, 1974, 1992), after studying the entire genus no significant differences were found. Nonetheless, the proportion of the calyx lobes relative to that of the calyx limb is constant within species.

The shape of the calyx tube in cross-section is also an important character (although sometimes hard to code in herbarium specimens). The shortly winged calyx of *D. dumontii* is well differentiated from angled calyx tubes, like those of *D. ollacheum*, or from terete calyx tubes, like those of *D. hiatum*. Calyx sinuses can be acute, rounded, or obscured by the overlapping bases of the calyx lobes (Fig. 9 C, D, F, G). The last case happens when the calyx remains imbricate even at anthesis; however, it is important to note that calyx lobes initially imbricate in bud, can also flare at anthesis revealing V-shaped sinuses (i.e., *D. panamense*).

Corolla

The corollas of *Disterigma* are usually 4-10 mm long. Although individual corollas vary in their length and width proportions, they still can be classified according to their basic overall shape. They are campanulate when bell-shaped and flaring at the throat, cylindric when the sides are parallel below the throat (whether the throat is slightly constricted or parallel as well), or urceolate when they are obviously constricted at throat and inflated below (vase-shaped) (Fig. 9 H-K). The shape of the corolla is an important taxonomic character, unfortunately, it is not always well translated into the herbarium specimens, sometimes requiring the careful observation of several flowers to confirm the shape. *Disterigma empetrifolium* and *D. codonanthum* share practically identical habit

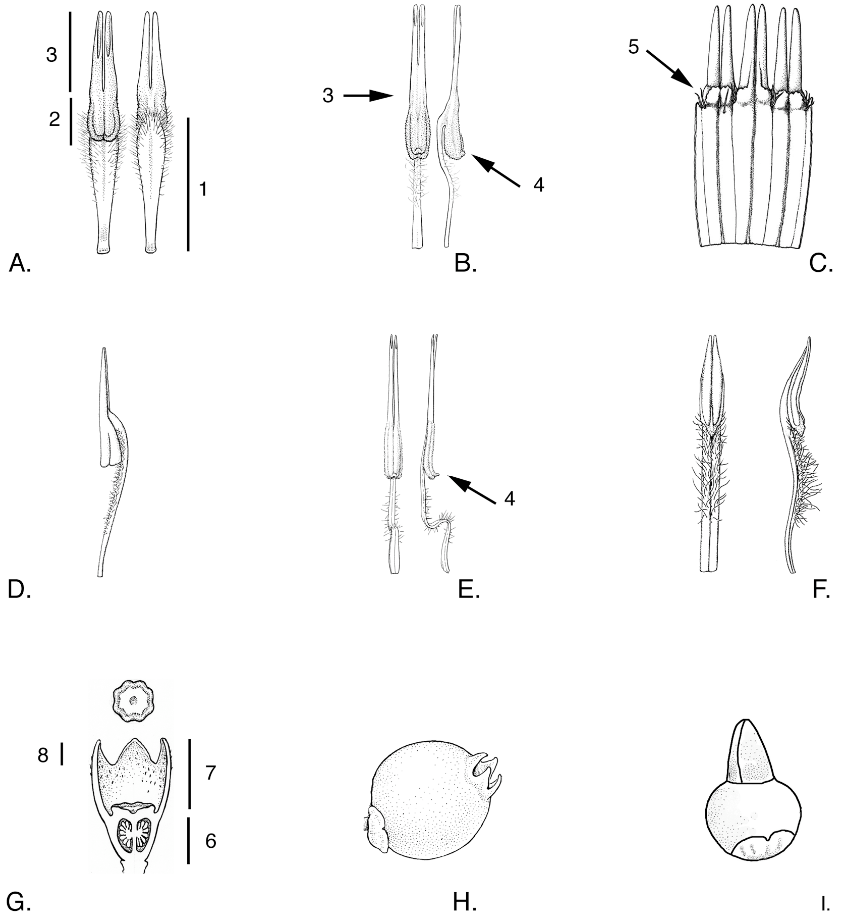


Fig. 11. Examples of external morphology. **A.** Adaxial view of a stamen showing the filament (1) and the anther thecae (2) and tubules (3) dehiscence by longitudinal slits, *Disterigma chocoanum*; **B.** Adaxial and lateral views of the stamens of *D. synanthum* showing tubules fused at base (3) and a basal appendage (4); **C.** Abaxial view of the stamens of *D. appendiculatum* showing abaxial spurs (5); **D.** Lateral view of a stamen without prognathous anthers and with the filament straight, *D. verruculatum*; **E.** Adaxial and lateral views of the stamens of *D. balslevii* showing the prognathous anthers, the basal appendages (4), and geniculate filaments; **F.** Adaxial and lateral views of the stamens of *D. hiatum* showing anthers with the tubules almost completely lacking and anthers dehiscing by a longitudinal cleft going from the top of the tubules to the base of the thecae; **G.** Longitudinal section of the calyx and inferior ovary highlighting the calyx tube (6), limb (7), lobes (8), and the nectariferous disk, *D. synanthum*; **H.** Fruit of *D. pernettyoides* with the calyx lobes spreading; **I.** Fruit of *D. stereophyllum* with the calyx lobes converging into a cone.

and leaf characters, but can be easily distinguished by their characteristic flowers; however, the thick urceolate corollas of *D. empetrifolium* sometimes split distally when pressed, looking very similar to the flattened campanulate corollas of *D. codonanthum*. Therefore, as an aid to the careful study of herbarium specimens, it is strongly advised to explicitly take note of the corolla shape in the field, along with the other color and shape features that are reported on the specimen labels (this applies to other neotropical genera as well). The color of the corolla is an extremely important field character that when combined with other vegetative/floral characters, is diagnostic. Most of the species have corollas white, pink, or red, but *D. acuminatum, D. campii, D. codonanthum, D. ollacheum*, and *D. pseudokillipiella* have green corollas (although not exclusively). All the species have the color pigments evenly distributed in the corolla, but when not completely red, the corollas are very often suffused with a reddish or pink hue, probably as a protection against solar radiation. This change in color shade is usually patchy, it is not considered part of the regular color pattern, and occurs in buds and during or after the anthesis. Additionally, the pink hue of the corollas is not related with anthesis and does not have any known function in pollination.

The presence of eglandular hairs within the corolla (Fig. 9 K) and the type of indumentum they form are important taxonomic characters in *Disterigma*. However, the indumentum within the corollas of neotropical Vaccinieae is not usually described and it could be useful for species identification in other groups. The hairs within the corolla have never been recorded for *Disterigma* and earlier descriptions only mention the external indumentum, which is apparently largely influenced by environmental factors and thus, non-informative. Although these hairs are typically about 0.5 mm long, they can be easily observed in the field with the help of a hand lens in *D. alaternoides,* where they are most conspicuous and abundant. In *D. agathosmoides, D. appendiculatum, D. chocoanum, D. panamense,* and *D. pseudokillipiella* the hairs are thinner, shorter, and less abundant than they are in D. *alaternoides*, being easier to observe them in dry or fresh material. In the case of *D. hiatum, D. ovatum,* and *D. leucanthum*, hairs can be found sometimes even on the corolla lobes.

Androecium

The stamens of *Disterigma* are all equal in size, 8 or 10, double the number of corolla parts (diplostemonous), and sometimes with the tips exerted. Characters such as stamens one-half or two-thirds the length of the corolla has been traditionally used in many genera of neotropical Ericaceae to either distinguish among groups or describe species (see Luteyn, 1996; Luteyn & Wilbur, 2005; Smith, 1933). However, the stamens of *Disterigma* vary in length, from 1.8 to 13.5 mm long, and no significant correlation was found between their length and the length of the corolla. Generally speaking, the gross morphology of the stamens of *Disterigma* is not very different from that of other Vaccinieae genera such as *Vaccinium*, *Sphyrospermum,* and *Themistoclesia* Klotzsch. But, before discussing the morphological features in greater detail, it is important to clarify the terminology here employed to describe the staminal appendages.

Appendages

Awns, tubules, and spurs occur in both temperate and tropical Ericaceae. The elongations at the functional apex of each mature anther half are developmentally and morphologically similar. They are called **awns** when they are bristle-like and sit above the dehiscence aperture, and **tubules** when they are hollow extensions of the thecae that bear the aperture distally, through which pollen is shed. Awns can be single (as in *Enkianthus campanulatus* Nichols.) or bifurcate (as in *Pernettya* Gaudich.), whereas tubules are one per theca (as in almost all *Disterigma*) but can occasionally fuse laterally to become one per anther (as in some *Macleania* Hook.*,* and *D. utleyorum*) with its cavity double, lobed, or single (Hermann & Palser, 2000; Palser, 1961). 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, they look like horns in many *Satyria* Klotzsch, fish tails in *Erica australis* L., threads in *Vaccinium stamineum* L., and flaps in *Disterigma appendiculatum* (for illustrations see Hermann & Palser, 2000; Luteyn & Wilbur, 2005; Pedraza-Peñalosa, in press). 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,* 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. (Hermann & Palser, 2000; Luteyn & Wilbur, 2005; Palser, 1961; Smith, 1943). It is important to not confuse the basal appendages with **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 (Fig. 11 E).

To summarize, the hollow extensions at the functional 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, which is the only species in the genus with such appendages (Fig. 11 C). 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 (Fig. 11 B, E).

Filaments

In *Disterigma* the filaments are all equal, usually bear hairs distally, and are adherent to the corolla at their bases. All species have distinct filaments, except for *D. appendiculatum* and *D. styphelioides* which have filaments connate into a tube; in the case of *D. styphelioides* the filaments are either distinct or connate within the same plant. When completely free, the filaments are usually straight but S-shaped (geniculate) filaments are found in *D. balslevii*, *D. codonanthum, D. empetrifolium, D. pernettyoides,* and *D. synanthum* (Fig. 2). The curvature of the filament can be slight, as in *D. pernettyoides,* to strikingly folded as it happens in many populations of *D. empetrifolium* from the northern Andes. When the curvature is not exaggerated, the physical effect of pressing the plants can make it difficult to observe this character in herbarium specimens. It is interesting to note that the few cases in which polymorphism was recorded are those of two closely related species, *D. empetrifolium* and *D. codonanthum*; the polymorphism can either be manifest in the same plant or even within the same flower.

The filament shape in front view is also informative because although the great majority of the species have filaments with sides more or less parallel or slightly widening towards the base, the filaments are distinctively elliptic in *D. dumontii* and *D. utleyorum*, and obtriangular in *D. chocoanum* and *D. stereophyllum*.

Anthers

In *Disterigma* the anthers are all equal, bilocular, without disintegration tissue, and are dorsally attached to the filaments near the base. Their outline is elliptical and *D. balslevii* and *D. dumontii* are the only species with prognathous anthers (pronounced J-shape in side view) (Fig. 11 E). The anther surface is covered by minute papillae and sometimes few of those located at the very base of the thecae elongate like hairs. Anthers are always distinct except in *D. synanthum*, in which they are loosely connate and separating the stamens involves tearing the anthers walls. This has never been observed in *Disterigma* before, and occurs rarely in Ericaceae (e.g., *Coleanthera* Stschegel: Styphelieae, Epacridoideae).

Tubules and Dehiscence

The tubules of *Disterigma* are two, distinct, hollow, and more or less as long as the anthers. They are also soft and their bases are as broad as each anther half. The small papillae that are always present on the anther thecae may sometimes extend to the tubules where they are relatively inconspicuous. The dehiscence aperture is located introrsely in the tubules, usually in the form of a longitudinal slit or an apical pore; the pores are a little oblique in *D. codonanthum,* and rounded in *D. campii, D. dumontii,* and *D. utleyorum*.

Exceptions to the general scheme just discussed are: *Disterigma utleyorum* which has only one tubule per anther and the tubule has a single cavity, and *D. synanthum* in which the tubules are partially fused at their bases (Fig. 11 B). Also atypical is the case of *D. hiatum* that has the tubules almost completely reduced and with the dehiscence aperture extending from the top of the tubules to the base of the theca (Fig. 11 F); dehiscence apertures running into thecae and extending to approximately the entire length of the anther are rare in Ericaceae and have been described only in *Lateropora* A. C. Sm. (Costa Rica and Panama) within Vaccinieae, and scattered in Monotropoideae, Ericoideae, and Enkianthoideae.

Gynoecium

The ovary of *Disterigma* is inferior and 4-5-locular, and each locule has numerous ovules with axile placentation (Fig. 11 G). The nectariferous disk is a conspicuous structure on top of the ovary that surrounds the style (Fig. 11 G); it is quadrangular or annular, (0.5-)1-2.4 mm in diam., and very rarely has inconspicuous eglandular hairs (i.e., in a few collections of *D. staphelioides*). The style is filiform and completely smooth except for *D. hiatum,* which is the only species with the surface micropapillose. The stigma is truncate, but it may occasionally flare a little at anthesis. Besides the number of locules and the presence of papillae on the style, there are no other diagnostic or phylogenetically important characters associated with the gynoecium.

Fruits and Seeds

In general, the berries of *Disterigma* are not very different from the berries of many other Vaccinieae (blueberries, mortiños). They are spherical, fleshy, often colored, and contain multiple seeds. Several diagnostic and phylogenetically useful characters are associated with the fruits and seeds of *Disterigma,* but because the fruits of several species are either unknown or are poorly collected, poorly documented on labels, or poorly understood, their distribution through the entire genus remains uncertain. Additionally, some of these characters, such as the color of the seed embryo or the color of the calyx lobes at fruit maturity, are cryptic or not obvious to untrained eyes. Therefore, it cannot be emphasized enough the importance of carefully recording in the field all the features of the plant that are lost after pressing, even those that are considered quite common or unimportant (e.g., corolla shape, orientation of calyx lobes in the fruit, etc. See more under “Notes on Descriptions, Terms, and Collecting”).

The presence or absence of pigments in the fruits of the species of *Disterigma* is diagnostic, with the color of the fruits varying from white to solid purple, violet, wine-red, or even almost black. White fruits may be somewhat translucent, sometimes to the point that it is possible to discern from the outside where the seeds are clustered. Other interesting characters are related to the persistent calyx lobes that crown the fruits. While in the great majority of the species the calyx lobes are spreading or erect and somehow embedded within the fruit, becoming succulent, and the same color of the mature berry (like any blueberry), in other species of *Disterigma* the calyx lobes are convergent, with their sides overlapping thus forming a cone (Fig. 11 I). When convergent, the calyx lobes preserve their texture and apparently remain green at fruit maturity (color unknown in *D. appendiculatum*). Converging calyx lobes have apparently appeared independently in *D. appendiculatum, D. stereophyllum,* and *D. styphelioides* (see phylogeny, chapter 1).

When Smith (1943) described the genus *Killipiella* (herein considered a synonym of *Disterigma*), he differentiated it from related genera by only having 1-3 seeds developed instead of numerous seeds. However, in all the dissected fruits from herbarium and pickled collections of species previously described in *Killipiella,* I always found numerous seeds developed (if not all). In this and many other ways *Killipiella* is not different from *Disterigma* (see discussion under *D. styphelioides*) and the small number of seeds reported by Smith could have come from an immature or anomalous fruit.

The seeds of *Disterigma* are ellipsoid, 1-1.5 x 0.5-0.8 mm, and have the testa reticulate. Although seeds covered by a mucilaginous coat (in *D. hiatum* and *D. verruculatum*) and viviparous seeds (in *D. appendiculatum*) are rare, these special characteristics are scattered in other Vaccinieae (e.g., *Cavendishia, Macleania, Sphyrospermum*) and could be more frequent and widespread than is actually known. The external morphology of the testa of various species was studied and little variation was found, thus rendering no phylogenetically or taxonomically useful characters.

SPECIES CONCEPT

Species are defined according to the “Phylogenetic Species Concept” (Nixon & Wheeler, 1990), which recognizes species as the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals. Here species are defined by constantly distributed characters, which do not need to be autopomorphic, and without precluding the occurrence of variable traits in the populations. Populations formerly considered as different species based on characters either highly variable or quantitative, were considered the same species when no clear gaps were observed.

HYBRIDIZATION

The understanding of hybridization in *Disterigma* is superficial. Hybrids are thought to occur between *Disterigma alaternoides* and *D. noyesiae* Luteyn (Cauca) and *D. balslevii* and *D. acuminatum* (Putumayo, Nariño, and Cauca), where the species grow sympatrically. Fieldwork in the regions where these populations grow was not feasible; therefore the evidence of their hybrid nature is derived from their morphologies, which are intermediate between their putative parental species. A detailed discussion of the morphology is found under each species.

The concept of *Disterigma noyesiae* has been expanded in this work and now embraces a wider morphological variation and distribution. *Disterigma noyesiae* is a relatively abundant species that includes specimens previously identified as potential hybrids between *D. alaternoides* and *D. cryptocalyx*, and, *D.*

acuminatum and D. cryptocalyx in Ecuador (Luteyn, 1996). No evidence that would suggest of hybridization between these groups was found during molecular work.

DISTRIBUTION AND ECOLOGY

The genus *Disterigma* is found in the mountains of Central America from southern Mexico to Panama, except for Belize, El Salvador, and Nicaragua. In South America it is restricted to the Andes from Colombia to central Bolivia, reaching its easternmost point on Mount Roraima, at the limits of Venezuela, Guyana, and Brazil.

Like other neotropical Vaccinieae, species of *Disterigma* are more abundant in secondary vegetation of forest gaps and edges, and along roads and trails with remnant vegetation. The species tend to have an aggregate distribution and easily colonize open areas sending rhizomatous stems with adventitious roots or shifting from terrestrial to epiphyte form of growth; the sediments and decaying matter trapped on masses of liverworts and mosses in the cloud forests and páramo are a perfect substrate for epiphytes to root. Species with life forms primarily decumbent and prostrate can form large clones, as in the case of *D. empetrifolium* HBK (Luteyn, 2002), *D. codonanthum,* and *D. pernettyoides*, and the same has been observed in species frequently scandent like *D. acuminatum* or *D. campii*. Clonal growth through runners is typical of the great majority of the pioneer species that are present during the first stages of succession in natural landslides in Ecuador (Ohl & Bussmann, 2004). Ericaceae are among the most important plant families present during the first stages of recolonization, with *D. acuminatum* among the common species.

The plasticity in life forms has influenced the taxonomy; thus, the erect, prostrate, and cushion-like forms of *Disterigma empetrifolium* were described as different species (see Smith, 1933). But perhaps the most dramatic example of plasticity is that of the leaves and flowers of *D. humboldtii* in which all the possible combinations between small and large leaves and corollas are found; the variation occurs throughout the entire geographic distribution and the extremes of the variations have been described under different names (i.e., *D. mayanum, D. pilosum,* and *D. pachyphyllum*). Although it is hypothesized that perhaps environmental trends are responsible for the variation within a single species (Luteyn, 2002), after extensive field work no conspicuous patterns have been found and divergent life forms have been found even a few meters apart.

Regarding habitat preference, species of *Disterigma* are found in low and high elevation cloud forests, with few species distinctively restricted to the páramos or to the transitional belt between the lowland rain forest and the premontane forest. The ecosystem preferences are not different from those of any other Vaccinieae and detailed summary of them and the adaptative mechanisms of neotropical Ericaceae can be found in Luteyn (2002).

Little is known about dispersal in tropical alpine environments, but because of the fleshy and sometimes colorful condition of the berry fruit of *Disterigma*, it is reasonable to expect that birds disperse them. In Colombia, the fruits of *D. alaternoides* are eaten by several bird species (*Repizzo & Calle 214;* Cundinamarca) and the fruits of *D. stereophyllum* are eaten by *Tangara arthus* and *Euphonia xanthogaster* (Navarro et al., 2007). The berries of *D. bagua* from Amazonas, Peru, are reported to be eaten by the shiny grass-green tanager (*Barbour 4102*) and the páramo species *D. empetrifolium* is mentioned as an endozoochorous (Frantzen & Bouman, 1989). The fruits of *Disterigma* could also be a source of food for small mammals given that the rare and endangered Mountain Tapir [*Tapirus pinchaque* (Roulin, 1829)] and White-tailed Deer [*Odocoileus virginianus* (Zimmermann, 1780)] (P. Lozano, pers. comm.) also eat Ericaceae fruits.

CONSERVATION

The Tropical Andes harbor approximately 72% of the neotropical Ericaceae, and there, endemism is estimated at 47% at the generic level and 95% at the species level (Luteyn, 2002). These elevated levels of endemism are also evident in *Disterigma*, where out of the 32 species here recognized, 15 species have a restricted distribution. Unfortunately, the cloud forests and páramos where the species of *Disterigma* grow are among the most threatened ecosystems of the world (Knapp, 2002) and are being rapidly lost; for example, only 11% of Colombia's original cloud forests remain (Instituto Alexander von Humbol, 2001). This loss of biodiversity means that many unique lineages are at imminent risk of disappearing even before base-line information for conservation work is completed.

Of the 15 species of *Disterigma* with restricted distribution, 12 can be considered narrow endemics because they only grow in very small geographic areas, which correspond to what one would call one or two adjacent localities. The quality of the habitat where these species grow is either been rapidly loss over human activity (e.g., logging, opening of roads, hunting) or it is threatened by their proximity to growing human settlements. The narrow endemics of *Disterigma* are *D. appendiculatum* (Serranía de los Paraguas, Colombia), *D.* baguense (Bagua, Peru), *D. campanulatum* (La Bonita, Ecuador), *D. campii* (Mera, Ecuador), *D. hammelii* (Cerro Pate Macho, Panama), *D. hiatum* (Serranía de los Paraguas, Colombia), *D. leucanthum* (Cordillera Cutucú and Cordillera del Cóndor, Ecuador), *D. ollacheum* (Ollachea, Peru), *D. styphelioides* (Corcovado, Colombia), *D. synanthum* (Anchicayá, Colombia), *D. verruculatum* (Serranía de los Paraguas, Colombia), and *D. pallidum* (Valle del Zongo, Bolivia). Within the regions occupied by this group of species, it is important to highlight the outstanding floristic richness of the Colombian western cordillera, and more specifically of the Serranía de los Paraguas, where three endemic *Disterigma* are found, along with another probable new species.

As for *Disterigma micranthum* (Pichincha and El Oro in Ecuador), *D. balslevii* (Macizo Colombiano and Colombia-Ecuador border), and *D. pernettyoides* (La Paz, Cochabamba, Cusco, and Junín), although they also have a restricted geographic distribution, their localities form a general area much larger than the one of a species considered a narrow endemic. However, for the assessment of the conservation status of these last group of species it must be also taken into account the number of collections known; for example, *D. micranthum* is only known from three collections made in two distant localities.

The majority of the species of *Disterigma* that have restricted distribution are known from very few specimens, some only from the type collection, and grow in areas with deteriorating environmental conditions and growing human pressure. In an initial step to address their conservation status, the Ecuadorian species of *Disterigma* were categorized according the IUCN parameters and included in the red list of plants endemic to Ecuador (Pedraza-Peñalosa et al., in press). Excerpts of relevant information collected and published on conservation is included for the threatened species *D. campii, D. leucanthum,* and *D. micranthum.*

FLORAL BIOLOGY

The pollination and floral biology of the genus is poorly known. However, the literature (Navarro et al., 2007) and my own field observations agree in that the flowers of *Disterigma* are not strongly specialized for a particular type of pollination, and that both bees and hummingbirds visit their flowers. A closer examination of the flowers shows intermediate characteristics between entomophily and ornithophily, as illustrated in the following examples. Snow and

Snow (1980) reported that *Disterigma* sp. (Colombia) with corollas white, 8 mm long, and a nectar concentration of 22-41%, was visited by the hummingbirds *Adelomyia melanogenys*, *Boissoneaua flavescens*, and *Heliangelus amethysticollis*. The sugar concentration of this species of *Disterigma* is higher than that preferred by hummingbirds (averaging 20%) and in fact bees were observed among the frequent visitors. In the area studied, *Adelomyia* fed from flowers also visited by insects, mostly Hymenoptera; it appeared to be trap-lining over considerable distances, mainly to flowers with small amounts of relatively concentrated nectar like *Disterigma* sp., which would be uneconomic for larger birds. Interestingly, the feeding habits of the other two short-billed hummingbirds recorded were not specialized and insects were an important part of their diet.

Another example of mixed pollination is that of the *Disterigma stereophyllum*, which despite having corollas 7-10 mm long, white, and urceolate, is pollinated by trap-lining hummingbirds attracted by its large amounts of diluted nectar (Table 5). However, *D. stereophyllum* retains the ability to self-pollinate (with a cryptic

Table 5. Sugar concentration of the nectar of several species of *Disterigma*

Species	Nectar concentration % Average (Range)	# Flowers measured	Reference or specimen
D. agathosmoides	18 (8)	1	P. Pedraza 1001
D. alaternoides	23 (11-33)	4	P. Pedraza 1009, 1024, 1050, 1058
D. codonanthum	62 (62)	2	P. Pedraza 966, 1041
D. humboldtii	49	1	P. Pedraza 1075
D. cryptocalyx	23.3 (20-25.6)	7	Luteyn & Sylva, 1999
D. noyesiae	29.6 (24-37)	4	P. Pedraza 973, 974, 1008, 1077
D. pseudokillipiella	22	1	P. Pedraza 999
D. staphelioides	21.3 (18.7-23)	6	P. Pedraza 1062, Luteyn & Sylva, 1999
D. stereophyllum	21.2 (14.6-27.8)	25	Navarro et al. 2007
Disterigma sp.	27.8 (22-41)	Unknown	Snow & Snow, 1980

self-incompatibility) and profits from bumblebee visitors. Therefore it is hypothesized that the mixed floral traits may enhance the species ability to colonize secondary vegetation, where it is more abundant. The lack of specialization of this species favors pollen transfer by any of a wide range of pollinators available in the area, while the capacity of selfing may serve to assure reproduction in case of pollinator scarcity of poor efficiency (Navarro et al., 2007). Studies of the disturbance and predictability of flowering patterns in bird-pollinated cloud forest plants found that most of the plants studied were self-compatible and that although the species with long corollas and relatively specialized for attracting long-billed hummingbirds were more abundant in cutovers areas, the species with short corollas compensated being outnumbered with nectar traits that attracted many hummingbirds and some insects as well (Linhart et al., 1987).

Although extended and rigorous studies are necessary throughout the entire genus, the estimations of the energy content of the nectar of several species of *Disterigma* shown in Table 5 are comparable with those of the species just mentioned with mixed pollination systems. However the high concentration of nectar in *D. codonanthum* is well within the range preferred by bees, much higher than the 20% preferred by hummingbirds (see Hainswort, 1976; Snow & Snow, 1980), and may suggest that there is also space for some specialization. My nectar concentrations presented in Table 5 were measured in the field in different locations with two Milton Roy Company hand refractometers, one calibrated for 0-32% and the other for 28-62%. Values from Luteyn & Sylva (1999) studies on Ericaceae from Antioquia and from the work of Snow and Snow (1980) and Navarro et al. (2007) also in the Colombian Andes, are included.

Species of *Disterigma* with poricidal anthers (*D. campii, D. codonanthum, D. dumontii*, and *D. utleyorum*) could be pollinated by bees using a vibration technique called “buzzing”, a mechanism documented elsewhere in the family (e.g., Cane et al., 1985; Knudsen & Olesen, 1993). Although bees often visit the flowers of *Disterigma*, it is not known if they harvest nectar or pollen, nor is there evidence that they buzz the anthers to extract pollen grains. Moreover, the great majority of the species of *Disterigma* dehisce by introrse longitudinal slits. It has also been suggested that buzz pollination probably works best when the pollen is shed in monads and not in tetrads like in *Disterigma*, where it is more likely it

Table 6. Plant/animal interactions of *Disterigma.* Specimen identified in the original reference as **D. acuminatum* and ***D.* aff. *acuminatum.*

Species	Hummingbirds	Insects	Nectar robbing birds	Reference
D. alaternoides (or possibly *D. cryptocalyx*)	*Adelomyia melanogenys*, *Boissoneaua flavescens*, *Doryfera ludoviciae*, *Heliangelus amethysticollis, Metallura tyrianthina*	Bees		Snow & Snow, 1980
D. chocoanum		Bumblebee		P. Pedraza pers. observ.
D. cf *dendrophilum*	*Eriocnemis nigriventris*		*Diglossa lafresnayii*	Bleiweiss & Olalla, 1983*
D. empetrifolium	*Chalcostigma stanleyi*			F. Ortíz, pers. comm. to J. L. Luteyn
D. humboldtii	*Aglaeocercus*[1] *coelestris*	*Centris gavisa*[2]	*Diglossa duidae*[2]	[1] *Sperling & Bleiweiss 5053* [2] Renner, 1989
D. noyesiae	*Eriocnemis* [3] *nigriventris*	Bumblebee[4] butterflies	*Diglossa* [3] *lafresnayii*	[3] Bleiweiss & Olalla, 1983 [4] P. Pedraza pers. observ.
D. ollacheum	Hummingbirds	Bumblebee		P. Pedraza pers. observ.
D. ovatum		Bumblebee		P. Pedraza pers. observ.
D. stereophyllum	*Ocreatus underwoodii* *Chlorostilbon mellisugus*	Bumblebee		Navarro et al. 2007

would get stuck due to the shape and diameter of the pollen grains (King & Buchmann, 1995). A summary of the field observations and literature reports of animal visitors is given in Table 6.

USES

Although the family Ericaceae has a remarkable role in temperate zones as ornamentals and edible plants (e.g., rhododendrons, azaleas, cranberries and

Table 7. Vernacular names and uses registered for *Disterigma*

Species	Vernacular name (region)	Uses
Disterigma sp.	Piquisique (Colombia)	
D. acuminatum	Buze-ievcheshaj (Colombia); Mortiño, Pipisiki (Ecuador)	Fruits edible (Ecuador)
D. alaternoides	Chite, Mortiño, Capulí silvestre, Mata de caballo (Colombia); Albricias, Borrachera (Venezuela); Zchirpe, Perlillo, Tira, Motilón (Ecuador); Piku-mullaca (Peru)	Fruits edible (Ecuador)
D. balslevii	Pipisiki (Ecuador)	
D. dumontii	Los Reales (Ecuador), Chaquilulo (Colombia)	Los Reales (Ecuador), Chaquilulo (Colombia)
D. empetrifolium	Chirimote, Joyapa, Orco mote, Uvilla de monte (Ecuador); Pushgay blanco (Peru)	Fruits edible (Ecuador, Peru). The infusion of leaves and flowers is used as a postpartum purger. The crushed leaves are scrubbed over the legs of children, preparing them to walk in Ecuador
D. humboldtii	Muras (Ecuador)	
D. noyesiae	Mortiño (Ecuador)	Fruits edible (Ecuador)
D. panamense	Pasino (Ecuador)	Plant crushed into a paste and placed on forehead against fever in Ecuador
D. pernettyoides	Perla-perla (Peru)	
D. stereophyllum	Chaquilulo (Colombia)	

blueberries), in the Neotropics there are very few reports of uses of native Ericaceae and their potential has not yet been explored (Luteyn, 2002). The ethnobotanical information of highland species is not very rich and medicinal uses have been mentioned for only a few species (Luteyn & Pedraza-Peñalosa, 2006). Local uses of *Disterigma* have been recorded only from Ecuador, while vernacular names are known from Colombia, Venezuela, Ecuador, Peru, and Bolivia; the findings are summarized in Table 7.

NOTES ON DESCRIPTIONS, TERMS, AND COLLECTING

Key morphological characters were studied in both dried and pickled material, and with the exception of the flowers, there is no significant shrinkage upon drying. Therefore, except when noted in parenthesis, all measurements apply equally to fresh or herbarium-preserved specimens. In the corollas, although length is not dramatically altered when dried, the diameter and shape are not always well translated into herbarium specimens due to shrinking, irregular pressing of specimens, or longitudinal splitting of thick corollas. Corolla shape was personally confirmed in the field for nearly all species, and a note appears when it is only known from pressed material. The corollas of *Disterigma* are campanulate, cylindric, or urceolate, and their diameter at both its throat and widest point are always reported as a way to avoid ambiguous adjectives such as narrow or broad. In the case of campanulate corollas, the diameter and throat are the same and only one measurement is given.

Colors reported were based on field observations and rarely from label data; this is especially important for light-colored corollas and fruits, which when exposed to high solar radiation acquire a pink or reddish, patchy coloration. This reddish hue on white fruits and corollas is due to environmental factors and by no means resemble the true solid red or purple coloration of some species;

however, its occurrence accounts for most of the ambiguity on label data. Unless otherwise stated, floral bracts and bracteoles are green, the calyx is green, the anthers are yellow, orange, or reddish, and the filaments are white.

All measurements are taken over extended structures. This means that structures with a tridimensional shape like the corolla (including its reflexed lobes), bracteoles, or staminal filaments (when geniculate) are straightened out.

To describe the insertion angle of the leaves with the stem the term "reclinate" is used when it is >100°, "patent" when it is about 75 to 100°, "diffuse" when it is 46 to 75°, and "ascending" when it is 16 to 45° (Moreno, 1984). Given the thick and fleshy nature of the leaves of *Disterigma*, the venation patterns here described correspond to what is visible on dry specimens, and it should not necessarily be read as a statement of the true venation pattern. Marginally revolute leaves were not observed in living material, but some species characteristically dry this way and then this is indicated the description . Inflorescence and floral bracts are undifferentiated, and all are described under the category of bracts. The calyx limb is regarded as the part free from the tube and includes the lobes.

"Specimens examined" indicates that all collections seen are cited; "Representative specimens examined" indicates that only a portion of the specimens seen are cited, either for space reasons, or to include only those that convey particularly well the species concept. When a specimen has not been seen it is indicated by "n.v." following the citation. In the locality data, the following abbreviations have been used: Mun. =Municipio, Prov. =Provincia, PN =Parque Natural, PNN =Parque Nacional Natural, and SFF =Santuario de Fauna y Flora.

The following diagnostic characters are important for species identification; however, they can be hard to code once the plants are pressed and dried or they are completely lost. Therefore, it is strongly advised to include among the field notes bracteole color (e.g., stramineous, green), corolla shape, fruit color, color of the calyx lobes at fruit maturity, orientation of the calyx lobes at fruit maturity (e.g., converging into a cone or erect/spreading), and seed color.

SYSTEMATIC TREATMENT

DISTERIGMA (Klotzsch) Nied., Bot. Jahrb. Syst. 11: 160, 209. 1889. *Vaccinium* L. subgen. *Disterigma* Klotzsch, Linnaea 24: 57. 1851; Smith, A. C., Brittonia 1(4): 216-232. 1933; Macbride, J. F., Flora of Peru, Field Mus. Nat Hist., Bot. Ser. 13(1): 69-73. 1959; Standley, P. C. & T. Williams, Fieldiana, Botany 24: 101-102; Wilbur, R. L., Bull. Torrey Bot. Cl. 101(5): 245-249. 1974; Wilbur, R. L. & J. L. Luteyn, Ann. Missouri Bot. Gard. 65: 77-84. 1978; Wilbur, R. L., Bull. Torrey Bot. Cl. 119(3): 280-288. 1992; Luteyn, J. L., Flora of Ecuador 54: 253-286. 1996. Luteyn, J. L., Flora of the Venezuelan Guayana 4: 741-742. Luteyn, J. L. & R. L. Wilbur, Ericaceae, Flora of Costa Rica, Botany New Series 45: 55-60. 2005. Lectotype: *Disterigma empetrifolium* (Kunth) Drude (Smith, 1933).

Metagonia Nutt., Trans. Amer. Philos. Soc., n.s., 8: 263. 1843. [*Disterigma* p.p., *Vaccinium* p.p.]

Vacciniopsis Rusby, Bull. Torrey Bot. Club 20: 433. 1893. Type: *Vacciniopsis ovata* Rusby [=*Disterigma ovatum* (Rusby) S. F. Blake].

Killipiella A. C. Sm., J. Washington Acad. Sci. 33(8): 242. 1943. Type: *Killipiella styphelioides* A. C. Sm. [=*Disterigma styphelioides* (A. C. Sm.) Pedraza].

Terrestrial or epiphytic **shrubs**, erect, scandent, sometimes prostrate and spreading through rhizomatous stems with caulinar roots and bract-like leaves (these either larger or smaller than normal leaves), or occasionally forming compact cushions in páramos; branching usually fastigiate, forming clumps at the end of long shoots; young branches usually ridged and somehow flattened; mature branches terete, the bark grayish to brown, longitudinally fissured. **Leaves** alternate, spirally arranged, but sometimes oriented in one plane then appearing distichous; petioles short; lamina coriaceous, often fleshy (but rarely drying wrinkled), less than 5 cm long, the margin entire or rarely minutely crenate, the venation mostly plinerved but often obscure on both surfaces. **Inflorescence** an axillary fascicle, with 2-4(-11) flowers, or flowers solitary, mostly axillary but rarely subterminal; inflorescence and floral bracts persistent, undifferentiated, usually inconspicuous, gradually growing in length and width centripetally, cuculate, frequently chartaceous, adaxially glabrous; pedicel inconspicuous and hidden by overlapping bracts (subsessile flowers), or occasionally up to 3(-11) mm long and with a portion not completely obscured, articulate with calyx, often with a ring of minute glandular or eglandular hairs at articulation; bracteoles persistent, the most distal pair inserted directly at apex of pedicel and enveloping calyx to various degrees or rarely exceeding it by several millimeters, differentiated in size and shape from other bracts, in some species this differentiated pair of apical bracteoles are fused by one of their ends forming one bracteole, or rarely fused at both ends and giving rise to a ring-shaped bracteole (*D. utleyorum*), the surface completely smooth, striate, or pustulate in herbarium specimens (striation usually also evident in fresh material but sometimes lost in pickled samples), usually adaxially glabrous. **Flowers** 4-merous or less often 5-merous. **Calyx** aestivation valvate or imbricate; tube in cross-section 4-5-angled or terete, seldom shortly winged (*D. dumontii*), rarely abaxially pustulate; lobes mostly triangular, rarely ovate or oblong-lanceolate. **Corolla** aestivation valvate, urceolate, cylindric, or campanulate, bistratose or not, rarely abaxially pustulate, glabrous or with indumentum adaxially, the hairs eglandular; lobes triangular. **Stamens** equal in length, 8-10(-12), adherent to corolla base, the tips sometimes exserted; filaments equal in length, distinct or less often connate, straight or geniculate, rarely spurred (*D. appendiculatum*), with or without indumentum, the hairs eglandular; anthers equal in length, dorsally attached near the base, rarely connate (*D. synanthum*); thecae straight in lateral outline or rarely basally prognathous, papillate, with or without a basal appendage that sometimes bears papillae or hairs; tubules (1-)2, dehiscing introrsely or apically by pores, slits, or rarely a cleft that runs from tubule tip to theca base (*D. hiatum*), lacking disintegration tissue; pollen lacking viscin threads. **Ovary** inferior, 4-5-locular, the placentation axile; style filiform, the tip sometimes exserted, smooth and rarely micropapillose (*D. hiatum*); stigma truncate; nectariferous disc annular or quadrangular, pulvinate, usually glabrous. **Fruits** a fleshy berry, red, purple, violet, wine-red (almost black), white, or translucent white, crowned by persistent calyx lobes, these usually spreading or erect but sometimes converging into a cone; seeds numerous per locule, ellipsoid, 1-1.5 x 0.5-0.8 mm, sometimes with a mucilaginous coat, rarely viviparous, the testa reticulate.

Disterigma is a neotropical genus of 32 species, ranging from S Mexico through Central America, south to N Bolivia, and east to Mount Roraima at the border of Guyana, Brazil, and Venezuela.

Key to the Species of *Disterigma*

1. Leaf apex obtuse and mucronate; differentiated apical bracteole 1, forming a continuous ring-shaped structure; anther tubules 1 .... …..**31. *Disterigma utleyorum***

1'. Leaf apex acute, acuminate, or if obtuse then rounded or apiculate; differentiated apical bracteoles 2 and distinct, or when 1, free on one side; anther tubules 2 ……………………………………………………………..2

2. Differentiated apical bracteoles 1 ..………………………………………………3

2'. Differentiated apical bracteoles 2 ………………………………………………...4

3. Differentiated apical bracteoles cordiform, extending beyond the calyx, with the surface pustulate and longitudinally striate; anthers connate ....**30. *Disterigma synanthum***

3'. Differentiated apical bracteoles ovate or transverse-elliptic, enveloping up to the calyx tube, with the surface smooth and sometimes with 1 or 2 diffuse keels; anthers distinct ………………………………..**23. *Disterigma pallidum***

4. Venation abaxially parallely-nerved; calyx lobes oblong-lanceolate; corolla 5-6.2 mm long ……….....................................**29. *Disterigma styphelioides***

4'. Venation abaxially obscure, hyphodromous, or 3-5-nervate; calyx lobes ovate or triangular; corolla 1-2.5(-3.5) mm long ....…5

5. Flowers 5-merous ……………………………………………………………….6

5'. Flowers 4-merous ……………………………………………………………...10

6. Calyx aestivation imbricate; filaments connate; anthers with flap-like dorsal spurs ………………….................……..…**4. *Disterigma appendiculatum***

6'. Calyx aestivation valvate; filaments distinct; anthers without spurs ....………7

7. Stems with papilliform outgrowths; leaf apex acuminate or cuspidate; differentiated apical bracteoles scarious, finely pustulate, and extending

beyond the calyx at least 2.5 mm; corolla tubular .... …..**32. *Disterigma verruculatum***

7’. Stems without papilliform outgrowths; leaf apex obtuse and apiculate; differentiated apical bracteoles green and chartaceous, smooth, and enveloping up to the calyx tube; corolla urceolate ……………………………8

8. Calyx lobes reduced (0.3-0.5 mm long); anther tubules inconspicuous (0.3-0.5 mm long), dehiscing by a cleft that runs from tubule tip to theca base; fruits white ...……...………………...........................……...**16. *Disterigma hiatum***

8’. Calyx lobes developed (1.3-2.5 mm long); anther tubules developed (1.7-2.6 mm long), dehiscing by a slit confined to the tubule apex; fruits violet to almost black or purple …..………………………............................………………..9

9. When dry, leaf margin revolute towards base and lamina not wrinkled; pedicel reduced (0.9-1.5 mm long) and hidden by overlapping bracts; calyx tube terete; corolla adaxially glabrate (sometimes even in the lobes); anthers papillate on thecae; seed embryo green …..………..**22. *Disterigma ovatum***

9’. When dry, leaf margin not revolute and lamina wrinkled; pedicel (1.5-4.5 mm long) with at least a portion of it evident; calyx tube sharply angulate (angles may look like short wings in dry material); corolla adaxially glabrous; anthers with papillae on thecae and tubules; seed embryo white ………………..….. ……………………………………..……………...…**21. *Disterigma ollacheum***

10. Calyx aestivation imbricate ……..……………………………………................11

10’. Calyx aestivation valvate ....……………………….....13

11. Flowers axillary only; bracteoles minutely pustulate; calyx lobes ovate ………...………**18. *Disterigma leucanthum***

11’. Flowers subterminal and axillary; bracteoles not pustulate; calyx lobes elliptic or triangular ..………………..….......12

12. Calyx lobes obtuse and apiculate at apex, their bases overlapping at anthesis and obscuring the sinuses (rarely, few flowers with the lobes flaring and then

the sinuses V-shaped); fruit with the persistent calyx lobes converging and overlapping into a cone; leaves elliptic, oblanceolate or rarely ovate, 0.9-2.9 X 0.3-1.3 cm ....**28. *Disterigma stereophyllum***

12’. Calyx lobes acute at apex, their bases not overlapping, the sinuses V-shaped; fruit with the persistent calyx lobes spreading; leaves obtrullate or oblanceolate, 0.9-1.5 X 0.2-0.4(-0.5) cm ……… **24. *Disterigma panamense***

13. Differentiated apical bracteoles striate and the corolla campanulate ………….
……………………………………………………………………………………14

13’. Differentiated apical bracteoles smooth with the corolla campanulate, urceolate, or tubular, or when the bracteoles are striate then the corollas are urceolate or tubular …..……………..………………..…………..………16

14. Leaf apex obtuse ....……………….....…………**7. *Disterigma campanulatum***

14’. Leaf apex acute, blunt acute or acuminate ....…………………………………15

15. Calyx (4-)4.5-5.5 mm long; corolla (5.2-)6.7-10.5 mm long; stamens (4.7-)5.3-7.5 mm long; leaves minutely crenulate, apex acute or blunt acute ....…..
…...**10. *Disterigma codonanthum***

15’. Calyx 2-3.5 mm long; corolla (2.8-)3.0-5.5(-6) mm long; stamens 1.8-2.8(-3.9) mm long; leaves entire (a handful of specimens inconspicuously crenulate), apex acute, acuminate or long acuminate ….….**1. *Disterigma acuminatum***

16. Differentiated apical bracteoles striate; corolla urceolate or tubular ……….17

16’. Differentiated apical bracteoles smooth; corolla campanulate, urceolate, or tubular ………………..…………………………………………………...…….20

17. Corolla (2.8-)3-5.5 mm long; stamens 1.8-2.8(-3.9) mm long …………………
….……………………………….……………...………**1. *Disterigma acuminatum***

17’. Corolla 6.6-12 mm long; stamens 6.4-8.3 mm long ……..……………..……18

18. Leaves elliptic or lanceolate, ciliolate at apex with minute eglandular hairs (≤ 0.5 mm long); flowers axillary and subterminal; calyx sinuses V-shaped;

corolla white or light green with the lobes pink …………………………………… ……………………………………………**26. *Disterigma pseudokillipiella***

18’. Leaves ovate, ciliate the entire length (especially young leaves) with long and curly eglandular hairs (0.5-1.5 mm long); flowers axillary; calyx sinuses U-shaped; corolla white or red …………..……………………………………..19

19. Calyx 3.5-3.6 mm long, tube terete; corolla tubular and white; filaments straight ..………………………….........……….**5. *Disterigma baguense***

19’. Calyx 4.3-6 mm long, tube angulate; corolla narrowly urceolate and red; filaments geniculate (note that the hybrids between *D. balslevii* and *D. acuminatum* have flowers smaller than a typical *D. balslevii* and filaments straight or geniculate) ….....................………………**6. *Disterigma balslevii***

20. Corolla campanulate …………………………………………………….....21

20’. Corolla urceolate or tubular …..…………………………………………..…24

21. Leaves obtuse; anther dehiscence by pores ……………….……….……..22

21’. Leaves acute or subacute; anther dehiscence by longitudinal slits or pores ……………………………………………………………………………..23

22. Corolla light green, the lobes more than half the corolla length and strongly reflexed as to expose the stamens half of their length; calyx tube angled ….. ………...……………………………………………..…**8. *Disterigma campii***

22’. Corolla dark red, the lobes less than half the corolla length and straight or just spreading; stamens included; calyx tube shortly winged …..………….. …………………………………………………..…**13. *Disterigma dumontii***

23. Leaves entire; calyx tube shortly winged; corolla dark red, 6.4-8.8 mm long; stamens dehiscing by pores ……………………..…**13. *Disterigma dumontii***

23’. Leaves crenulate; calyx tube more or less terete; corolla white, (10-)11.5-17 mm long; stamens dehiscing by longitudinal slits ....**25. *Disterigma pernettyoides***

24. Filaments obtriangular; leaves apically obtuse, mostly obovate ……...……...
…………………….………………..........……….**9. *Disterigma chocoanum***

24’. Filaments long triangular or with parallel sides; leaves subacute, acute, or acuminate, or if obtuse, then rarely obovate ....….…..…25

25. Lamina lanceolate, linear, or sometimes elliptic, 0.06-0.2(-0.3) cm wide, margin entire ……..………………26

25’. Lamina usually ovate or elliptic, (0.2-)0.4-1.9(-3.5) cm wide, margin entire, or when the lamina is as long and narrow as above then the margin is crenulate ....………...…..........28

26. Leaves spirally arranged; corolla 5-5.5(-6.5) mm at the widest point, urceolate, bright red, usually thick …............ **14. *Disterigma empetrifolium***

26’. Leaves apparently distichous; corolla 2-3 mm at the widest point, tubular or narrowly urceolate, white, pink, or red, chartaceous ....…...27

27. Calyx lobes 2.5-3.1 mm long; corolla 11-14.3 mm long, adaxially glabrous; stamens 12-13 mm long ……………………………..**15. *Disterigma hammelii***

27’. Calyx lobes 1.2-1.7 mm long; corolla 5-7(-9) mm long, adaxially glabrate towards base; stamens 5-7.5 mm long ……..**2. *Disterigma agathosmoides***

28. Corolla with hairs adaxially (hybrids between *D. alaternoides* and *D. noyesiae* look like typical *D. alaternoides* but have flowers adaxially glabrous) 29

28’. Corolla without hairs adaxially ……........………………………….…………..30

29. Flowers in 3-9-flowered fascicles sometimes combined with solitary flowers; corolla adaxially puberulous with conspicuous hairs; leaves mostly acute to blunt acute, (0.4-)0.5-1.9(-3.5) cm wide ………..**3. *Disterigma alaternoides***

29’. Flowers solitary sometimes combined with 2-3-flowered fascicles; corolla adaxially glabrate with minute hairs; leaves obtuse, subacute, or rarely blunt acute, (0.2-)0.3-0.8(-1.3) cm wide …...…………..**17. *Disterigma humboldtii***

30. Bracts 8-11, conspicuous (up to 4.4 mm long); differentiated apical bracteoles (5.2-)6-9 mm long, covering the entire calyx and extending beyond it 2.5-4 mm ……...........……...**11. *Disterigma cryptocalyx***

30’. Bracts 3-8, inconspicuous (usually up to 2 mm long); differentiated apical bracteoles shorter than or equalling the calyx, or when longer than the calyx then extending beyond it 0.5-2 mm ..………….........................….………..31

31. Corolla tubular ....………...............................………......32

31’. Corolla urceolate ....……...............................….…….….... 34

32. Differentiated apical bracteoles as long or longer than calyx and extending beyond it 0.5-2 mm; calyx sinuses V- or U-shaped ..…................................ …................................……................................**27. *Disterigma noyesiae***

32’. Differentiated apical bracteoles shorter than the calyx, covering up to the lower calyx lobes; sinuses V-shaped ....………..............………....33

33. Leaves apically acute to long acuminate, lamina (0.5-)0.7-1.2 cm long; corolla 4.4-5.6 mm long …………………….............**12. *Disterigma dendrophilum***

33’. Leaves apically subacute, obtuse, or rarely blunt acute, lamina 0.6-2(-2.5) cm long; corolla 6.5-13.5 mm long ……........…......**17. *Disterigma humboldtii***

34. Corolla 3-4.5 mm long; stamens 3-3.5 mm long; calyx sinuses V-shaped ....……………………………………………... **19. *Disterigma micranthum***

34’. Corolla (4-)4.5-13.5 mm long; stamens (3.6-)4-11.8 mm long; calyx sinuses V- or U-shaped ....…………….......………..…………………….35

35. Differentiated apical bracteoles as long or longer than calyx and extending beyond it 0.5-2 mm..…......................................…......**27. *Disterigma noyesiae***

35’. Differentiated apical bracteoles shorter than the calyx, covering up to the lower calyx lobes ...………….......……………..………........…………36

36. Corolla white; calyx lobes (2.8-)3.6-5.2 mm long, the sinuses U-shaped ...... ………………………………….....……………..**27. *Disterigma staphelioides***

36’. Corolla pink or red; calyx lobes (1-)1.2-2.5 mm long, the sinuses V-shaped...

.......................………..…..…..….... 37

37. Corollas bright red; filaments usually geniculate, sometimes combined with straight filaments in the same plant or flower; plants prostrate forming dense cushions or sometimes erect; leaves crenulate ....………...……............... ……..…………………………......…...........……**14. *Disterigma empetrifolium***

37’. Corollas white, white-light green, or light pink; filaments always straight; plants scandent or erect, not forming cushions; leaves entire .... ……………………………….....…………………….. **17. *Disterigma humboldtii***

1. **Disterigma acuminatum** (Kunth in Humb., Bonpl. & Kunth) Nied., Bot. Jahrb. Syst. 11: 209. 1889. *Vaccinium acuminatum* Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. Pl. 3: 264, pl. 249. 1818. *Metagonia acuminata* (Kunth in Humb., Bonpl. & Kunth) Nutt., Trans. Amer. Phil. Soc. N. S. 8: 266. 1843. Type. Colombia. Cauca: Páramo de Almaguer and near Pansitara, 3100-3300 m, s.d. (fl), *Humboldt & Bonpland 2065 p.p.* (holotype, P-Bonpl.; isotypes, fragment F ex P, fragment L ex P, P). Photo F neg. 38234 ex P-Bonpl., photo NY s.n. ex P-Bonpl. Note that the type specimen is a mixed collection and *Humboldt & Bonpland 2065 p.p*. at B-W is the type of *Disterigma humboldtii;* a few leaves of the later species can be found in the package of *Disterigma acuminatum.*

Gaylussacia microphylla G. Don, Gen. Syst. 3: 859. 1834. *Disterigma microphyllum* (G. Don) Luteyn, Fl. Ecuador 54: 261. 1996. *Thibaudia microphylla* Ruiz & Pav. in Dunal, Prodr. 7: 576. 1839, pro. syn., nom. illegit. *Vaccinium microphyllum* Ruiz & Pav. in Sleumer, Notizbl. XII: 282.1935, pro. syn., nom. illegit. Type. Perú. Huánuco: Pillao, 1787 (fl, fr), *Ruiz & Pavón s.n*. (holotype, BM; isotypes, BC?, fragment F ex MA, G-DC ex Herb. Thibaud, K, fragment L, MA (x2), NY, OXF, P). Photo NY neg. 13018 ex NY. Another sheet in P was annotated by Sleumer in 1958 as possible isotype, but I am not considering it a type nor a Ruiz & Pavón collection; the label only reads "*Pernettya serpyllifolia* DC, (Ego.), D. Magellan, Herb. Maire".

Disterigma elassanthum S. F. Blake. J. Wash. Acad. Sci. 16(13): 362. 1926, **syn. nov.** Type. Colombia. Huila: Balsillas, on Río Balsillas, 2100-2200 m, 3-5 Aug 1917 (fl, fr), *Rusby & Pennell 827* (holotype, US; isotype, F, GH, NY). Photo F neg. 59450 ex F, photo NY neg. 9889 ex NY.

(Fig. 10 A, 12)

Epiphytic or terrestrial **shrubs**, scandent or erect, 0.3–3 m tall. Young branchlets ridged, more or less smooth, villosulous, the hairs eglandular and brown, the mature branches indumentum similar but glabrate or villosulous. **Leaves** 4–9 per cm, apparently distichous or spirally arranged, patent; petiole 0.4–1.2 mm long, puberulous, the hairs eglandular; lamina ovate or rarely elliptic, 0.3–1.1 x 0.2–0.6 cm, basally obtuse or less often cuneate, marginally entire or very rarely inconspicuously crenulate, the teeth apically setaceous and glandular, often revolute towards base, sometimes apically ciliolate with eglandular hairs (especially in young leaves), apically acute, acuminate, or long-acuminate, adaxially glabrous or glabrate with eglandular hairs, abaxially glabrous or glabrate with eglandular and glandular hairs, the venation obscure on both sides or sometimes 5-nerved abaxially. Axillary **solitary flowers** and rarely 2-flowered fascicles; bracts 3–6, chartaceous, ovate, 0.5–1.8 x 0.6–2.3 mm, marginally ciliolate with eglandular hairs (especially at apex), apically obtuse, abaxially glabrous; pedicel (0.8–)1–2 mm long, much reduced and hidden by overlapping bracts, glabrous or glabrate with eglandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping entire calyx tube, covering 40–60% of calyx, transverse-elliptic or reniform, 1.2–2.5 x 2–3.6 mm, marginally ciliolate with eglandular hairs, apically obtuse, the surface longitudinally striate, abaxially and adaxially glabrous. **Flowers** 4-merous. Calyx aestivation valvate, campanulate, 2–3.6 mm long; tube angled, 0.9–2 mm long, abaxially glabrous; limb 1–2 mm long, abaxially and adaxially glabrous; lobes triangular, 1–2 x 1–2 mm, rarely marginally ciliolate with eglandular hairs, apically acute; sinuses acute (V-shaped). Corolla light green, sometimes with marked pink hue under intense

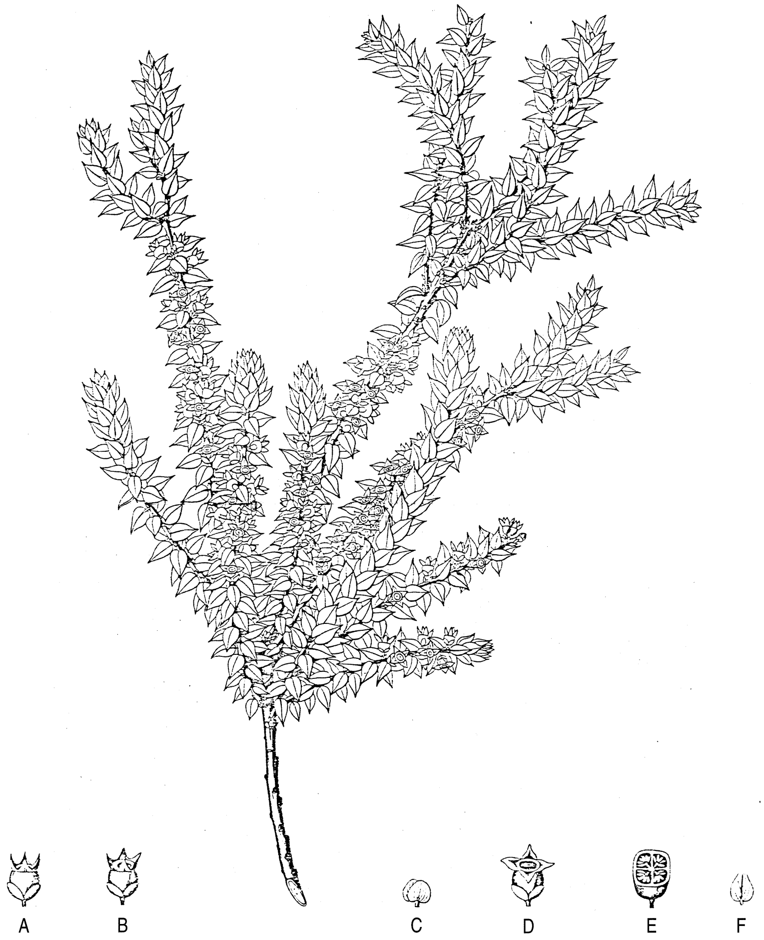
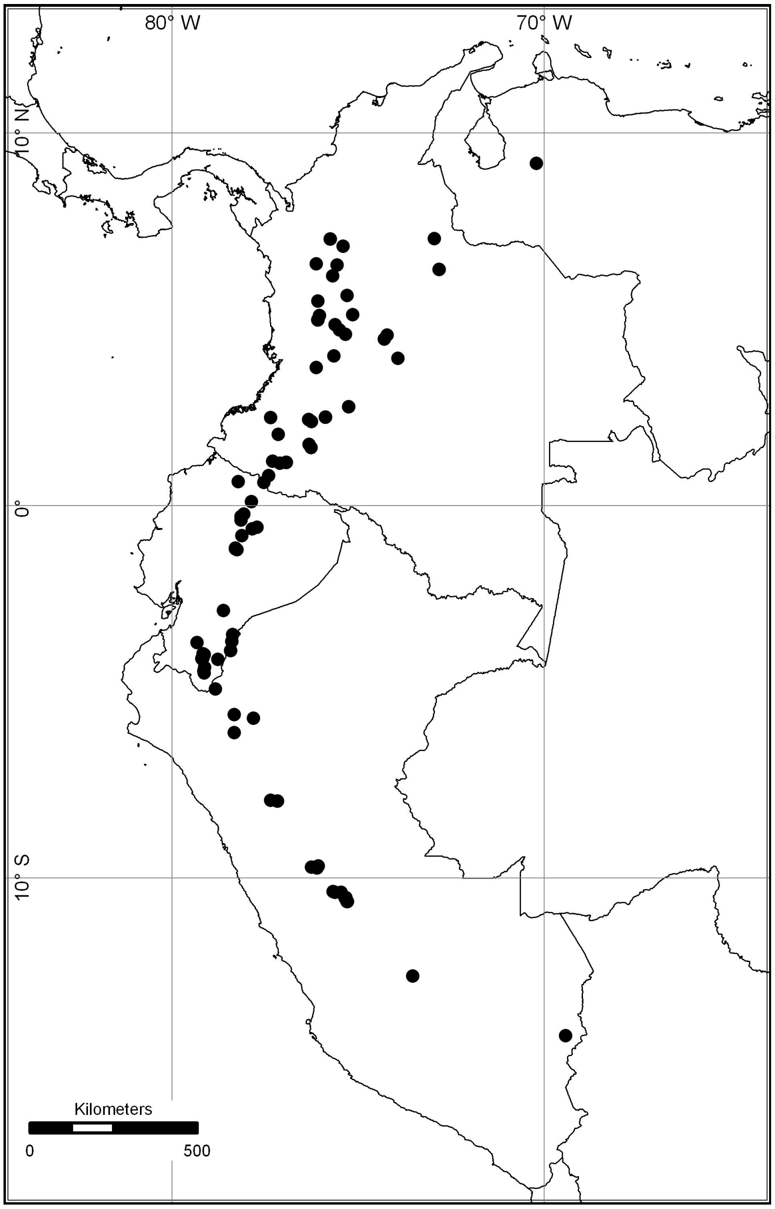


Fig. 12. Illustration of *Disterigma acuminatum.* **A-B, D**. Calyx with differentiated apical bracteoles; **C**. Differentiated apical bracteoles; **E**. Dissected ovary showing axile placentation and multiple seeds; **F**. Leaf. Modified from Nov. Gen. Sp. Pl. 3, pl. 249 (1889).

sunlight conditions and only few unusually large corollas in Peru and southern Colombia are white, thick-fleshy, bistratose, mostly campanulate or sometimes urceolate (inflated at the middle), (2.8–)3–5.5 mm long (up to 6.0 mm in large corollas from Peru and southern Colombia), 3.8–4.5 mm diam. (up to 6.0 mm in large campanulate corollas from Peru and southern Colombia), 2–4.5 mm wide at throat, abaxially glabrate with eglandular or glandular hairs, adaxially glabrous; lobes 1–2.5 x 1.2–3.5 mm, apically acute, or acute and apiculate, adaxially slightly rugose. Stamens 8, 1.8–2.8 mm long (in large corollas from Peru 2.8-3.9 mm, from southern Colombia 4-4.5 mm), included; filaments distinct, straight, broader at base, (0.4–)0.6–1(–1.2) mm long (in large corollas from Peru 1.2-1.8 mm, in southern Colombia 1.6-2 mm), glabrous or rarely glabrate with a couple of abaxial hairs (glabrate to puberulous on both sides in large corollas from Peru and southern Colombia); anthers distinct, papillae on both thecae and tubules; thecae 0.8–1.5 mm long, without basal appendages; tubules 2, distinct, 0.7–1(–2) mm long, dehiscing introrsely by longitudinal slits, 0.4–0.6 mm long. Ovary 4-locular; style (2–)3–3.7 mm long (4.2-5.5 mm in large corollas from Peru and southern Colombia), included. **Berry** white (reported to turn purple in plants with larger corollas from southern Colombia; white in the plants with larger corollas from Peru), more or less spherical or hemispherical, 6–7 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo white (unknown in plants with large corollas from southern Colombia).

Distribution and ecology. *Disterigma acuminatum* is widespread throughout the Andes, from Trujillo (Venezuela) in the north, going through Colombia and Ecuador, and reaching its southernmost distribution in Puno (Peru), where it has been collected only once (Map 1). This species is abundant in Colombia and Ecuador and generally grows in montane cloud forests, subpáramos and less often in páramos, between (1800-)2000-3700. It has been recorded growing in sandy soils, clay soils, or in *Sphagnum* bogs in both primary and secondary vegetation, as well as on roadsides and pasturelands with remnant vegetation. Flowering and fruiting specimens have been found all year-round.



Map 1. Geographic distribution of *Disterigma acuminatum*.

Etymology. The epithet makes reference to the acuminate leaves.

Representative specimens examined. COLOMBIA. Antioquia: Mun. San Antonio de Prado, vereda Potreritos, estribaciones del Alto el Romeral, 2760 m, 12 Jul 2004, *J. C. Betancur & J. Betancur 10909* (COL, NY); Mun. Ituango, camino entre El Retiro y Cerro Paramillo, 3100 m, 25 Feb 1993, *Cuadros 4936* (MO, NY); San José de Cuerquia, camino del páramo, 31 Jul 1958, *Garganta 2170* (US); Sonsón, La Soledad, el camino a Río Toncal, camino antiguo Sonsón y Río verde, 2500 m, 9 Apr 1994 (fl, fr), *Gómez et al. 1012* (COL, HUA, NY); Mun. Belmira, sitio Sabanas, camino viejo a Santa Rosa, 3000 m, 15 Jul 1987 (fr), *Marulanda et al. 461* (HUA); Mun. Urrao, Páramo de Frontino, cuenca alta del Río Anocozca, 3380 m, 6 Sep 2000, *Pérez & Parra 1354* (MEDEL); Mun. Andes, camino desde el Filo del embudo al cerro la Banqueta, 2700 m, 15 Mar 1996, *D. Sánchez & Vanegas 2753* (MEDEL); San Pedro, 2450 m, 25 Mar 1940, *Tomas 751* (MEDEL); Mun. Yarumal, N of Yarumal on road to Cerro Marconi, 2750 m, 29 Nov 1986 (fl, fr), *Zarucchi & D. Cárdenas 4307* (COL, HUA, MO, NY); Mun. Medellín, Cerro del Padre Amaya, 3020 m, 18 Mar 1987, *Zarucchi & Madrigal 4852* (HUA, MO, PSO). **Caldas:** PNN Los Nevados, La Suiza-Cortaderal, 3155 m, May 2004 (fl, fr), *C. Pedraza & Lizcano 15* (COL, CUVC, HUA, NY); carretera entre Manizales y Mariquita, rumbo al PNN los Nevados, después de Padua, 2300 m, 2 Jul 2004 (fl, fr), *P. Pedraza & C. Pedraza 1039* (COL, CUVC, FMB, HUA, NY); Cerro Tatamá, 3500 m, 8-10 Sep 1922 (fr), *Pennell 10507, 10521* (NY). **Cauca:** between Valencia y San Sebastian, 3000 m, 21 Jul 1944 (fl, fr), *Core 1013* (MICH, NY, UC, US); Páramo de las Juntas, 3300 m, 13 Oct 1961, *Cuatrecasas & Willard 26392* (COL, US); PNN Puracé, sector Valencia, 3060 m, 17 Sep 1987 (fl, fr), *Duque 583* (COL); Mun. Puracé, PNN Puracé, cercanias de la laguna de San Rafael, 3300 m, 6 Oct 1984 (fl), *Lozano et al. 4672* (COL); PNN Puracé, road Puracé-La Plata, 3230 m, 4 Mar 1979 (fl, fr), *Luteyn & Lebrón-*

Luteyn 6899 (NY, US). **Cundinamarca:** Bogotá-Fusagasuga road, km 322-34, 2620 m, 15 May 1979 (fl), *Luteyn & Lebrón-Luteyn 7706* (CAS, COL, NY); San Miguel, bei Soacha, 2800 m, 11 Oct 1948 (fl), *Schneider 662* (COL, L, S). **Huila:** Mun. La Plata, vereda Agua Bonita, Finca Merenberg, 2300 m, 21 Jul 1975 (fr), *Díaz-P. et al. 796* (COL); Paramillo Arrabal, Finca La Candelaria, W of Volcán Puracé, 2380 m, 4 Apr 1986, *Gentry et al. 54039* (MO); Mun. Campoalegre, vereda Alto el Roble, 2330 m, 13 Oct 2001, *Llanos et al. 3340* (COL); km 28-32 road Pitalito-Mocoa near divide, 2240 m, 29 Apr 1979 (fl, fr), *Luteyn et al. 7539* (COL, MO, NY, TEX). **Nariño:** carretera Pasto-Mocoa, 15 km de Pasto, Páramo de la Pastora (o Tábano), 3130 m, 11 Nov 1982 (fl, fr), *Albert de Escobar & Salazar de Benavides 2848* (HUA, NY); Pasto, 17 Jun 1876 (fl), *André 2975 p.p.* (K, NY); road Pasto-Río Bobo, 19 Jul 1957 (fl), *H. G. Barclay 4647* (COL); lado S de la Laguna de la Cocha, Páramo de Santa Lucia, 3100 m, 9 Jan 1941 (fr), *Cuatrecasas 11863* (COL, US); road to Buesaco, 10 km NE of Pasto, 2850 m, 11 Jan 1981 (fr), *Gentry et al. 30447* (COL, MO, NY); subpáramo between km 13 and 14 of Pasto, towards, Laguna La Cocha, 3230 m, 25 Jan 1976 (fl), *Luteyn et al. 5018* (COL, DUKE, F, NY, US); Mun. Pasto, bosque de Daza, 17 May 1967 (fl), *López-J. 83* (PSO); Pasto-Sibundoy road, E of El Encano, 2780 m, 9 Oct 1997 (fl), *Luteyn et al. 15207* (COL, NY); 9 Oct 1997, (fl, fr), *Luteyn et al. 15208* (COL, NY); Mun. Pasto, localidad de Cabrera, quebrada Duarte, 2800-2850 m, 3 May 1995 (fl, fr), *B. R. Ramírez 7393* (HUA); Mun. Pasto, trayecto San Francisco-Serranía de Morasurco, 3000-3400 m, 17 Dec 1989 (fl, fr), *B. R. Ramírez 1943* (PSO); Mun. Pasto, corregimiento Aguanoy, SFF Galeras, 2800-3300 m, 17 Jul 2003 (fl), *N. R. Salinas 245* (COL, NY). **Putumayo:** Valle de Sibundoy, 5 km SE de Sibundoy, 2200 m, 3 Apr 1963 (fr), *Chindoy 135, 150* (COL, GH); Pasto-Sibundoy road, 46 km E of Pasto, 20 Feb 1979 (fl), *Luteyn & Lebrón-Luteyn 6803* (CAS, COL, MO, NY, S, TEX); corregimiento El Encano, Páramo de Quilinsayaco, km 29, 3200 m, 25 Feb 1977 (fl, fr) *Salazar de Benavides 926* (PSO); Laguna de la Cocha, Ciudadela, near Páramo de Bordoncillo, 3000 m, 27 May 1946 (fl), *Schultes & Villarreal 7570* (B, COL, F, GH, K, US); Páramo de Quilinsayacu, Valle del Sibundoy, 3300 m, 6 May 1972, *Schultes 26333* (GH, NY). **Risaralda:** Pereira, PNN Ucumarí, entre el Cedral y la Pastora, 2300 m, 14 Jun 1989, *R. Bernal et al. 1653* (COL); Mun. Santa Rosa, vertiente W, entre la Hacienda la Sierra y Termales de Santa Rosa, 3280 m, 27 Jan 1980 (fl), *Jaramillo-M. et al. 5990* (COL); Mun. Santuario, vereda San Rafael, PNN Tatamá, 2950 m, 15 Jul 2004 (fl, fr), *P. Pedraza & C. Pedraza 1098* (COL, CUVC, HUA, NY). **Santander:** alrededores de Bucaramanga, 1500 m, 27 Aug 1948 (fl, fr), *Barkley & Araque 188114* (COL, MEDEL, US); Mun. Tona, en cercanias de Picacho, 3200 m, 7 Apr 2005 (fl), *Galindo & Mantilla 1437* (COL); Mun. Onzaga, alto de Onzaga, entre Soatá y Onzaga, 3450 m, 4 Aug 1958 (fl), *Jaramillo-M. et al. 878* (COL); vicinity of Las Vegas, 3000 m, 21-23 Dec 1926 (fl), *Killip & A. C. Smith 15947* (US). **Tolima:** Mun. Roncesvalles, trocha hacia San José de las Hermosas, 3250 m, 19 Nov 1980, *Camargo 7649* (COL); along divide, near Quindio Highway, 3500 m, 27 Mar 1939 (fr), *Killip & Varela 34589* (COL, NY, US); Mun. Ibagué, camino al Nevado del Ruiz, 2700 m, 30 Jun 2004 (fl, fr), *P. Pedraza & C. Pedraza 1029* (AAU, COL, CUVC, FMB, HUA, MO, NY, US, VEN). **Valle del Cauca:** Cali, Páramo de Socorro, 3000 m, Jul 1938 (fl), *Duque-Jaramillo 4425* (COL); Mun. El Cerrito, Páramo de Pan de Azúcar, 3600 m, 29 Jan 1998 (fr), *W. Vargas 4327* (COL, HUA); Mun. de Riofrío, Páramo del Duende, 3700 m, Aug 1998 (fl), *W. Vargas 6021* (HUA). **Without department:** entre Popayán y Pasto, s.d. (fl), *Triana 2657* (BM, K, L, P).

VENEZUELA. Trujillo: distrito Boconó, Páramo de Guaramacal, 3100 m, 18 Jul 1990 (fl), *Dorr et al. 7372* (CAS, NY), 3000 m, 3 Feb 1987 (fl), *Werff 8815* (MO, NY).

ECUADOR. Azuay: near Páramo del Castillo, Sevilla de Oro-Méndez road, 3300 m, 18 Aug 1945, *Camp E-4810* (NY, US), 3414 m, 31 Aug 1945, *Camp*

E-5173 (NY, US), 3300 m, 28 Aug 1996, *Garmendia & Cisneros 1137* (QCNE). **Carchi:** Tulcán-El Carmelo road, 3200 m, 6-9 Feb 1959 (fr), *Harling 4231* (NY, S), 3450 m, 9 Apr 1979 (fl), *Løjtnant et al. 12070* (GB, NY,) 3200 m, 18 May 1982 (fl, fr), *Luteyn et al. 8461* (NY, QCA); Reserva Guandera, 3400 m, 27 Aug 1997 (fl), *Hughes 19* (QCA), 3400 m, 7 Nov 1998 (fl, fr), *Luteyn & Mogollón 15332* (CAS, NY, QCA). **Imbabura:** Toldadas-Naranjito, E of Volcán Cayambe, 3048 m, 8 May 1944, *Drew E-172* (NY, US). **Loja:** crest of the Cordillera de Zamora, E of Loja, 3000 m, 2 Jul 1944 (fl, fr), *Camp E-75, E-96* (NY, P, US); Fierro Urco road, W of the main Loja-Saraguro highway, 3100 m, 3 May 1997 (fl), *Luteyn et al. 15073* (NY); Páramo de Saraguro, 3050 m, 2 Jan 1979 (fl), *Luteyn et al. 6666* (CAS, COL, MO, NY, QCA); road to Cerro Toledo, E of Yangana, 3323 m, 14 Nov 1990 (fl), *Luteyn et al. 14158* (K, NY, QCA); Vilcabamba-Valladolid road, S of Yangana, 2770 m, 19 Apr 1992 (fl, fr), *Luteyn & Romoleraux 14481* (NY, QCA); PN Podocarpus, 3300 m, 16 Aug 2004 (fl, fr), *P. Pedraza & N. R. Salinas 1245* (COL, MO, NY, QCA, QCNE, USM), 3300 m, 17 Aug 2004 (fl, fr), *P. Pedraza & N. R. Salinas 1217* (QCA). **Morona-Santiago:** Gualaquiza, Cordillera del Cóndor, Campamento Achupalla, 2090 m, 21 Jul 1993 (fl), *Gentry 80308* (MO, NY). **Napo:** Oyacachi, 3110 m, 27 Apr 1996, *Báez 65* (QCA); Cerro Sumaco, 3200 m, 2 May 1979 (fr), *Holm-Nielsen et al. 17679* (NY); Cantón Tena, Cordillera de los Huacamayos, entre Chacana Loma-Sisahua, 2320 m, 9 Aug 1995, *Jaramillo & Tapia 18471* (QCA); Llanganates, N slope to Río Golpe, N of Chosa Aucacocha, 3500 m, 15 May 1982 (fl, fr), *Ollgaard et al. 38649* (F, MO, NY, QCA); Laguna de Papallacta, 3300 m, 12 Dec 2003 (fl), *P. Pedraza & C. Pedraza 968* (AAU, COL, E, MO, NY, QCA, QCNE, US), 3300 m, 12 Dec 2003 (fl), *P. Pedraza & C. Pedraza 967* (COL, E, QCA, QCNE, MO, NY). **Sucumbíos:** Playón de San Francisco-El Mirador trail, 7 Jul 1978, *Boeke & Jaramillo 2380* (MO, NY); carretera El Playón de San Francisco-El Carmelo, 30 Dec 1980 (fl, fr), *Jaramillo & Coello 4011* (QCA); Santa Bárbara-La Bonita, 5 km E of Santa Bárbara, 2750 m, 17 May

1982 (fl), *Luteyn et al. 8434* (NY, QCA, TEX); E of Laguna San Marcos, 3477 m, 6 Nov 1990 (fl, fr), *Luteyn et al. 14048* (NY, QCA, US). **Tungurahua:** Cantón Baños, PN Llanganates, 3500 m, 11 Oct 1998 (fl), *H. Vargas et al. 2714* (NY). **Zamora-Chinchipe:** El Pangui, en la frontera con Perú, Cóndor Mirador, 2000 m, 15 Dec 2000 (fl), *Cerna et al. 424* (MO, NY; road Saraguro-Yacuambi, 2800 m, 26 Oct 1996 (fr), *Eynden 822* (LOJA); Quebrada Honda, en la carretera Yangana-Valladolid, 2580 m, 2 Aug 1996, *Garmendia 965* (LOJA); Nangaritza, Cordillera de Nanguipa, Cerro Colorado, 2740 m, 17 Feb 2002, *Neill et al. 13729* (LOJA, NY, QCNE).

PERU. Amazonas: Prov. Bagua, Cordillera Colán, E of La Peca, 2900 m, 28 Aug 1978 (fl), *Barbour 3233* (MO); Condorcanqui, Cordillera del Cóndor, pared del Cerro Machinaza, 2050 m, 21 Jul 1994 (fl), *Beltrán & Foster 1185* (F, USM), 2160 m, 31 Jul 1994 (fl), *Beltrán & Foster 1517* (F); Prov. Luya, Camporedondo, Tullanya, base Cerro Huicsocunga, 3075 m, 7 Dec 1996 (fl), *Díaz & Peña 8855* (NY, USM); Prov. Bongara, Florida-Rioja, E del Progreso, 2270 m, 14 Jul 1995 (fl), *I. Sánchez-V. & Dillon 8031* (F, MO, NY). **Cajamarca:** Prov. San Ignacio, San José de Lurdes, Santo Tomas, 2200 m, 15 Jun 1995 (st), *Vásquez et al. 20218* (MO, NY). **Cusco:** Prov. La Convención, NE from Hacienda Luisiana and the Río Apurimac, 3400 m, 17 Jul 1968 (fl), *Dudley 11204* (F, NA); Prov. Paucartambo, Kosñipata, 2540 m, 24 Jul 2003 (fl), *H. Qquellón 8* (CUZ, USM); Prov. Paucartambo, distrito Challabamba, PN Manú, Trocha Unión, 3500 m, 8 May 2005 (fl), *Salinas-R. et al. 7637* (AAU, COL, CUZ, F, MO, NY, QCA, USM), *7638* (AAU, COL, CUZ, MO, NY, QCA, USM). **Huánuco:** Prov. Huánuco, Huánuco-Tingo María road, near Carpish tunnel, 3000 m, 26 Feb 1978 (fl), *Luteyn & Lebrón-Luteyn 5459* (CAS, F, GB, MO, NY, USM). **Pasco:** Prov. Oxapampa, PN Yanachaga Chemillén, Abra la Esperanza, 2800 m, 23 Mar 2003 (fl), *Monteagudo et al. 4773* (USM); Prov. Oxapampa, distrito Oxapampa, PN Yanachaga-Chemillén, Chacos, camino hacia la antena, 2380 m, 16 Jun 2006 (fl), *P. Pedraza et al. 1615* (AAU, COL, CUZ, MO, NY, USM); Prov. Oxapampa, distrito Huancabamba, PN Yanachaga-Chemillén, alrededores de la escuela Santa Bárbara, 3430 m, 11 Jun 2006 (fl, fr), *P. Pedraza et al. 1607* (COL, CUZ, NY, USM); Prov. Oxapampa, distrito Huancabamba, PN Yanachaga-Chemillén, Milpo, 2900 m, 13 Jun 2006 (fl, fr), *P. Pedraza et al. 1609* (AAU, COL, CUZ, NY, USM). **Puno:** Sandia hacia Valle Grande, 2200 m, 7 Aug 1957 (fl), *C. Vargas 11854* (CUZ, US). **San Martín:** Prov. Bellavista, distrito Huallaga, valle of river Apisoncho, 30 km above Jucusbamba, 1965 (fl), *Hamilton & Holligan 1120* (K, UC, S); Prov. Rioja, road from Pedro Ruíz to Rioja, between la Esperanza y Nuevo Cajamarca, 2300 m, 21 Oct 2000 (fl), *Weigend et al. 2000/932* (F, NY, USM); Prov. Mariscal Cáseres, Chonchos, NW corner of PN Río Abiseo, 3200 m, 24 May 1986, *Young & Watson 3271* (NY, USM).

Although *Disterigma acuminatum* is among the most common species in South America, because of the small nature of its flowers (Fig. 10 A), it was confused for a long time with *D. dendrophilum* (e.g., Luteyn, 1996; Smith, 1933), which has nearly identical leaves. In the description of *D. acuminatum* Kunth (1818) noted that the flowers were by no means evident and that the floral characters were taken from the label chosen by Bonpland; consequently, the accompanying illustration showed only calyces and very immature fruits (Fig. 5). However, from the best reproductions of the holotype photos it is possible to discern the presence of one corolla, and actually, when examining the type material that was the only mature corolla found. The calyx, 3.6 mm long, the corolla, 3.2 mm long and campanulate, and the stamens, 2.8 mm long, of the holotype specimen are identical to those of *Gaylussacia microphylla* G. Don [*D. microphyllum* (G. Don) Luteyn] and *D. elassanthum* S. F. Blake, which are therefore here synonymized.

Disterigma acuminatum is characterized by its small and usually acuminate leaves (Fig. 10 A); its differentiated apical bracteoles longitudinally striate; its small flowers with the corollas around 3.5-5 long, light green, campanulate or sometimes urceolate, and adaxially glabrous; its small stamens usually up to 3 mm long, with filaments usually shorter than the anthers and around 1 mm long; and by its white berries with white seed embryos. Among the few collections known from Peru, two populations [*H. Qquellón 51* (CUZ) and *Salinas-R. 7636-7* (COL, CUZ, NY, USM)] differed by having corollas white and 6 mm long, which is slightly larger than the average 4 mm long and green corollas of *Disterigma acuminatum* (see description for details). Plants with larger corollas have also been found in southern Colombia (*D. acuminatum/Galeras* in the molecular analysis), but in this case the collections are more numerous and cover the Municipio of Pasto (Nariño) and the nearby Municipio of Sibundoy (Putumayo), where they are reported to be abundant. Besides the size differences in the corolla color and corolla, stamen, and filament lengths (which are the same differenced observed in Peru; see description for details), the berries of this populations are reported to turn dark blue at maturity (*Luteyn et al. 4997*) and not white, which is the fruit color of *D. acuminatum* observed in the field through its entire distribution. Unfortunately, field work was not viable in places where plants with white fruits/small and green corollas, and, plants with blue fruits/large and white corollas grow one next to the other. The molecular and total evidence analyses resolved these OTU's into the same general clade, but the resolution at the species level was too poor to find further evidence regarding the species status [*D. acuminatum* and the large corolla/blue fruit OTU, *D. acuminatum/ Galeras,* only differed in 3 single indels and 1 substitution] (Pedraza-Peñalosa, in press; see phylogeny).

A possible hybrid between *D. acuminatum* and *D. balslevii*, another species that inhabit the same area, is discussed under *D. balslevii*.

Species vegetatively similar to *Disterigma acuminatum* are discussed under *D. staphelioides.* Moreover, *D. acuminatum* can be differentiated from *D. dendrophilum* because of differences in the corolla shape (campanulate or urceolate vs. tubular, respectively), pedicel conspicuousness (hidden by bracts vs. at least partially evident), and in the surface of the differentiated apical bracteoles (striate vs. smooth).

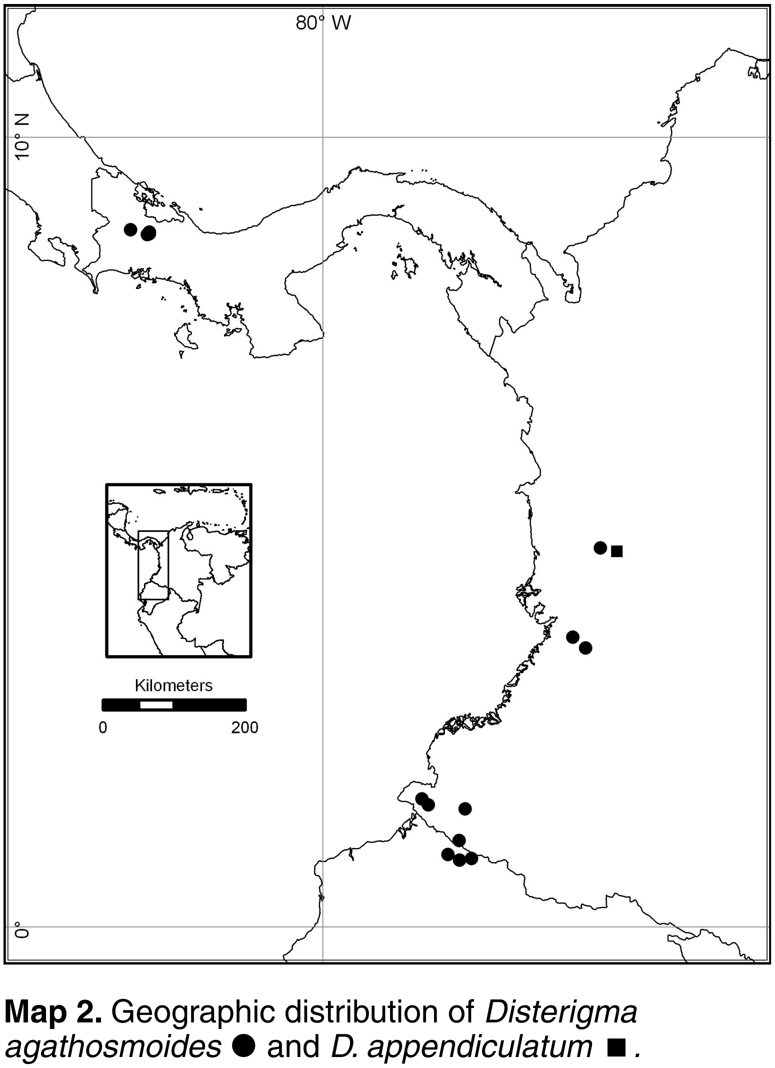
Local names and uses. This species is known as “Mortiño” in Tungurahua and Sucumbíos (Ecuador), and as “Buze-ievcheshaj” in Putumayo (Colombia). In Peru and Ecuador, both humans and birds eat its fruits.

2. **Disterigma agathosmoides** (Wedd.) Nied., Bot. Jahrb. Syst. 11: 224. 1889. *Vaccinium agathosmoides* Wedd., Chlor. And. 2: 179. 1857. Type. Colombia. Nariño: Pasto, Laguna Verde, Volcán de Túquerres, 3300 m, 1851-1857 (fl), *Triana 2661* (holotype, P; isotypes, B†, COL, fragment F ex P (x2), G, K n.v., fragment L ex P, fragment NY ex G). Photo F neg. 26657 ex G. The K sheet was not found.

Disterigma fortunense Wilbur, Bull. Torrey Bot. Club, 119(3): 286. 1992, **syn. nov.** Type. Panama. Chiriquí: La Fortuna Dam area, N of dam, along Quebrada Arena down stream from road crossing, in swampy forest along stream near continental divide, 8°46'N, 82°14'W, 1000 m, 10 Feb 1986 (fl), *Hammel 14429* (holotype, DUKE; isotypes, MO, NY n.v.). The NY sheet was not found.

(Fig. 10 B)

Epiphytic (up to 10–15 m above the ground) or terrestrial **shrubs**, wiry, scandent, or prostrate and decumbent. Young branchlets ridged, relatively smooth, glabrate, pubescent, or puberulous, the hairs eglandular and light brown, the mature branches indumentum similar but glabrate. **Leaves** 15–24 per cm, apparently distichous, patent; petiole 0.3–0.8 mm long, glabrous; lamina lanceolate, linear, or sometimes elliptic, (0.28–)0.32–0.9(–1.1) x (0.04–)0.08–0.2 (–0.26) cm, basally cuneate, marginally entire, apically ciliolate with minute eglandular hairs (especially in young leaves), apically acute, adaxially glabrous or sometimes glabrate with minute glandular hairs, abaxially glabrate with glandular hairs, the venation adaxially obscure, abaxially 3-nerved with the midvein raised. Axillary **solitary flowers**; bracts 4–8, chartaceous, ovate or transverse-elliptic, 0.4–1.6 x 0.4–1.5 mm, marginally ciliolate with eglandular hairs, apically obtuse, obtuse and cuspidate, or acute, abaxially glabrous; pedicel 1–1.2 mm long, reduced and hidden by overlapping bracts, glabrate with eglandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping to part of calyx lobes, covering 50–67% of calyx, ovate, 1.5–2(–2.5) x 1.6–3 mm, marginally ciliolate or ciliate with eglandular hairs, apically obtuse and cuspidate or less often acuminate, the surface smooth, abaxially and adaxially glabrous. **Flowers** 4-merous. Calyx aestivation valvate, campanulate, (2–)2.4–3.3 mm long; tube slightly angled, 0.8–1.3 mm long, abaxially glabrous or glabrate with minute eglandular hairs; limb 1.2–2.2 mm long, abaxially pilulose with eglandular hairs (apically), adaxially glabrous; lobes triangular, 1.2–1.7 x 0.7–1 mm, marginally ciliolate or rarely ciliate with eglandular hairs, apically acute; sinuses acute (V-shaped). Corolla red, pink, or white, chartaceous, bistratose, narrowly urceolate, 5–7(–9) mm long, 2.3–3 mm diam. (2.0 in dry), 1.5–2 mm wide at throat (1.5–1.7 in dry), abaxially glabrate with eglandular hairs, adaxially glabrate towards the base; lobes 0.8–1.2 x 0.8–1 mm, apically acute, adaxially slightly rugose. Stamens 8, 5–7.5 mm long, exserted; filaments distinct, straight, broader at base or more or less linear with parallel sides (in Panama), (2.4–)2.8–4.5(–5) mm long, abaxially and adaxially pilulose or glabrate (especially in Panama); anthers distinct, papillae only on thecae; thecae 0.8–1.2 mm long, with or without basal appendages; tubules 2, distinct, 1.5–2 mm long, dehiscing introrsely by longitudinal slits, 0.8–1.2 mm long. Ovary 4-locular; style 5.5–7.3(–7.8) mm long, exserted. **Berry** white, more or less spherical, 3.8–4.4 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo white.



Map 2. Geographic distribution of *Disterigma agathosmoides* ● and *D. appendiculatum* ■.

Distribution and ecology: *Disterigma agathosmoides* is known from central Panama, and the western mountain ranges of Colombia and of northern Ecuador. The collections of *Disterigma agathosmoides* are relatively few and come from a handful of localities, mainly from the vicinity of Junín, Barbacoas, and Tumaco in Nariño (Colombia), of Reserva Indígena Awá in Carchi (Ecuador), and of Fortuna Dam in Chiriquí (Panama) (Map 2). This species principally grows in very humid areas between 300-1700 m, in the transitional zone between lowland rainforest and premontane forest. However, populations of *Disterigma agathosmoides* between 2430-2950 m have been found in isolated mountain ranges such as Cerro Golondrinas (Carchi, Ecuador) and Cerro Panamá (Chocó, Colombia). This species has been found on both primary and secondary vegetation, as well as on roadsides. Flowering specimens have been collected year-round and fruiting specimens in October and December-April.

Etymology. The reason behind the species name is unknown. However, *agathos* is a Greek word that means good.

Specimens examined. PANAMA. Chiriquí: Edwin Fabrega Dam and reserve in Fortuna, 1075 m, 15 Jan 1989 (fl), *Almeda et al. 6225* (CAS), 1100 m, 5 Feb 1996 (fl), *Luteyn 14808* (DUKE, NY), 975 m, 16 Jan 2003 (fl, fr), *Luteyn & P. Pedraza 15544* (COL, NY, PMA), 975 m, 17 Jan 2003 (fl), *Luteyn & P. Pedraza 15548* (AAU, COL, MO, NY, PMA); primer pico del Cerro Horqueta, desde la cabaña del Dr. Esquivel, 25 Jul 1990 (fl), *Aranda et al. 1492* (MA, PMA); Fortuna valley, N of lake, near oleoducto, 16 Feb 1985 (fl), *Dressler 6104* (NY).

COLOMBIA. Chocó: Mun. San José del Palmar, Cordillera de San Miguel, cumbre del Cerro Panamá (adyacente al Cerro del Torrá), 2470-2510 m, 18 Aug 1988 (fl), *Silverstone-Sopkin et al. 4542* (NY). **Nariño:** near Junín on Tumaco-Tuquerres road, 1100 m, 26 Jul 1986 (fl), *Gentry et al. 55216* (MO, NY), 900 m, 25 Nov 1981 (fl), *Gentry et al. 34949* (COL, MO); km 20-28 Junín-Barbacoas road, 700-800 m, 7 Jan 1989 (fl), *Gentry et al. 64560* (PSO); Mun. Barbacoas, corregimiento Altaquer, vereda El Barro, Reserva Natural Río Ñambi, 1300-1500 m, 1-12 Dec 1993 (fl), *Gómez et al. 980* (COL, NY), 1200 m, 21-22 Dec 2003 (fl), *N. R. Salinas et al. 398* (COL, NY); Mun. Barbacoas, corregimiento El Diviso, hacia Junín, 700-750 m, 25 Aug 1995 (fl), *M. S. González et al. 1085* (PSO); Mun. Barbacoas, vía El Diviso-Tumaco, Altaquer, 680 m, 12 Mar 1995 (fl) *Lozano et al. 6946* (COL); Mun. Barbacoas, NW of Barbacoas, 1185 m, 7 Oct 1997 (fl), *Luteyn et al. 15190* (CAS, COL, NY); Altaquer-Junín road, W of Altaquer, 1250 m, 25 Feb 1979 (fl), *Luteyn & Lebrón-Luteyn 6842* (COL, L, MO, NY, TEX); Mun. Barbacoas, trayecto Junín-Altaquer, El Barro, 1300 m, 10 Dec 1992 (fl), *B. R. Ramírez 5240* (NY); Mun. Tumaco, corregimiento Guayacana, 300 m, 20 Mar 1988, *Salazar de Benavides 9328* (PSO); Mun. Tumaco, 2 km de Tangareal, orillas del Río Mira, 0 m (?), 8 Apr 1978 (fl), *Salazar de Benavides 1384* (MO, PSO). **Valle del Cauca:** carretera vieja entre Cali y Buenaventura, 1200 m, 11 Oct 1982 (fl), *Albert de Escobar et al. 2523* (HUA, NY), 1500 m, 29 Nov 1946 (fl), *Haught 5312* (COL, UC, US), 1300-1750 m, 10 Mar 1979 (fl, fr), *Luteyn & Lebrón-Luteyn 6993* (CAS, COL, NY, US); Mun. Queremal, carretera vieja a Buenaventura, entre Queremal y La Alza, 1600 m, 4 Jul 2005, *J. C Betancur. et al. 11699* (COL, CUVC, HUA, NY); Yatucué, CVC camp at Anchicaya, 700-900 m, 25 Feb 1983(fl, fr), *Gentry et al. 40773* (COL).

ECUADOR. Carchi: Reserva Indígena Awá, 900 m, 18 Feb 1993 (fl, fr), *Aulestia & Grijalva 1089* (MO, NY, QCNE), 1080 m, 10 Apr 1995 (fl, fr), *H. T. Beck et al. 3068* (NY), 1000-1450 m, 14 Jan 1988 (fl), *Hoover et al. 2380* (MO, NY, QCA), 900 m, 21 May 1992 (fl), *Quelal et al. 676* (MO, NY, QCNE), 1600 m, 3 Oct 1991 (fl, fr), *Tipaz et al. 317* (MO, NY, QCNE); Cerro Golondrinas, 2880-2950 m, 24 Jul 1994 (fl), *Boyle et al. 3402* (NY), 2430-2550 m, 5 Dec 1987 (fl), *Hoover 2366* (MO); El Pailón, 45 km below Maldonado along foot path to Tobar Donoso, 800 m, 28 Nov 1979 (fl), *Madison & Besse 7120* (NY, SEL); above San Marcos de los Coaiqueres, trail towards Gualpí Bajo, 1000 m, 7 Feb 1985 (fl), *Ollgaard et al. 57535* (AAU, MO, NY, QCA). **Esmeraldas:** Lita-San Lorenzo road, 800 m, 12 May 1991 (fl), *Gentry et al. 70131* (MO, NY), 600 m, 1 Apr 1994 (fl), *W. Palacios 12210* (MO, NY, QCNE). **Imbabura:** Chota-Paramba, Aug 1904 (fl), *Sodiro s.n.* (L, P). **Imbabura/Esmeraldas:** carretera Lita-Alto Tambo-San Lorenzo, 800-900 m, 20 Dec 2003 (fl, fr), *P. Pedraza & C. Pedraza 1001* (COL, MO, NY, QCA, QCNE).

Disterigma agathosmoides is very characteristic because of its wiry and delicate appearance; its leaves apparently distichous, patent, linear, and less than 3 mm wide; its calyx lobes less than 2 mm long; its corollas narrowly urceolate and adaxially glabrate; and its white berries (Fig. 10 B). Vegetatively, *D. agathosmoides* is similar to *D. hammelii* (Panama) because they share their wiry appearance and narrow leaves. Nevertheless, they can be easily differentiated because *D. hammelii* has corollas adaxially glabrous (vs. glabrate in *D. agathosmoides*) and its leaves are usually lanceolate (vs. linear to lanceolate) and generally wider [(0.1–)0.2(–0.3) vs. (0.04-)0.08-0.2(-0.26)]; additionally, *D. hammelii* also has longer calyx lobes (2.5-3.1 mm vs. 1.2-1.7 mm), corollas [11-14.3 mm vs. 5-7(-9) mm], stamens (12-13 mm vs. 5-7.5 mm), and filaments [8.5-9 mm vs. (2.4-)2.8-4.5(-5.0) mm].

Although *Disterigma fortunense* (type from Panama) was described by Wilbur (1992) as a new species mainly based on its larger leaves and flowers when compared to *D. agathosmoides* (type from Colombia), I found no size difference between the two species, therefore *D. fortunense* is here synonymized. Specimens with smaller leaves and flowers were observed in Central America, while specimens with large leaves and flowers collections were found at Cerro Golondrinas and Cerro Panamá, in South America.

Local names and uses. This species is knows as “Gualbadea”, “Pasino”, and “Téopve-vish” (Coaiquer) in Ecuador, and it is crushed into a paste and placed on forehead against fever.

3. **Disterigma alaternoides** (Kunth in Humb., Bonpl. & Kunth) Nied., Bot. Jahrb. Syst. 11: 224. 1889. *Vaccinium alaternoides* Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. Pl. 3: 265. 1818. *Metagonia alaternoides* (Kunth in Humb., Bonpl. & Kunth) Nutt., Trans. Amer. Phil. Soc. N. S. 8: 265. 1843. Type. Perú. Cajamarca: Ayavaca, 3300 m, Sep (fl), *Humboldt & Bonpland s.n.* (holotype, P-Bonpl.; isotypes, B†, B-W 7354-1, fragment F ex P, fragment L ex P, P). Photo F neg. 4764 ex B-W, photo NY s.n. ex P-Bonpl.

Vaccinium alaternoides Kunth in Humb., Bonpl. & Kunth var. *parvifolium* Benth., Pl. Hartweg. 140. 1844. *Disterigma alaternoides* (Kunth in Humb., Bonpl. & Kunth) Nied. var. *parvifolium* (Benth.) A. C. Sm., Brittonia 1: 220. 1933. Type. Ecuador. Loja: mountains of Saraguro, s.d. (fl), *Hartweg 782** (holotype, K n.v.; isotype, fragment NY ex K). K sheet not found.

Vacciniopsis tetramera Rusby, Descr. New S. Amer. Pl. 77. 1920. Type. Bolivia. Cochabamba: vicinity of Cochabamba, s.d. (fl), *Bang s.n.* (holotype, NY).

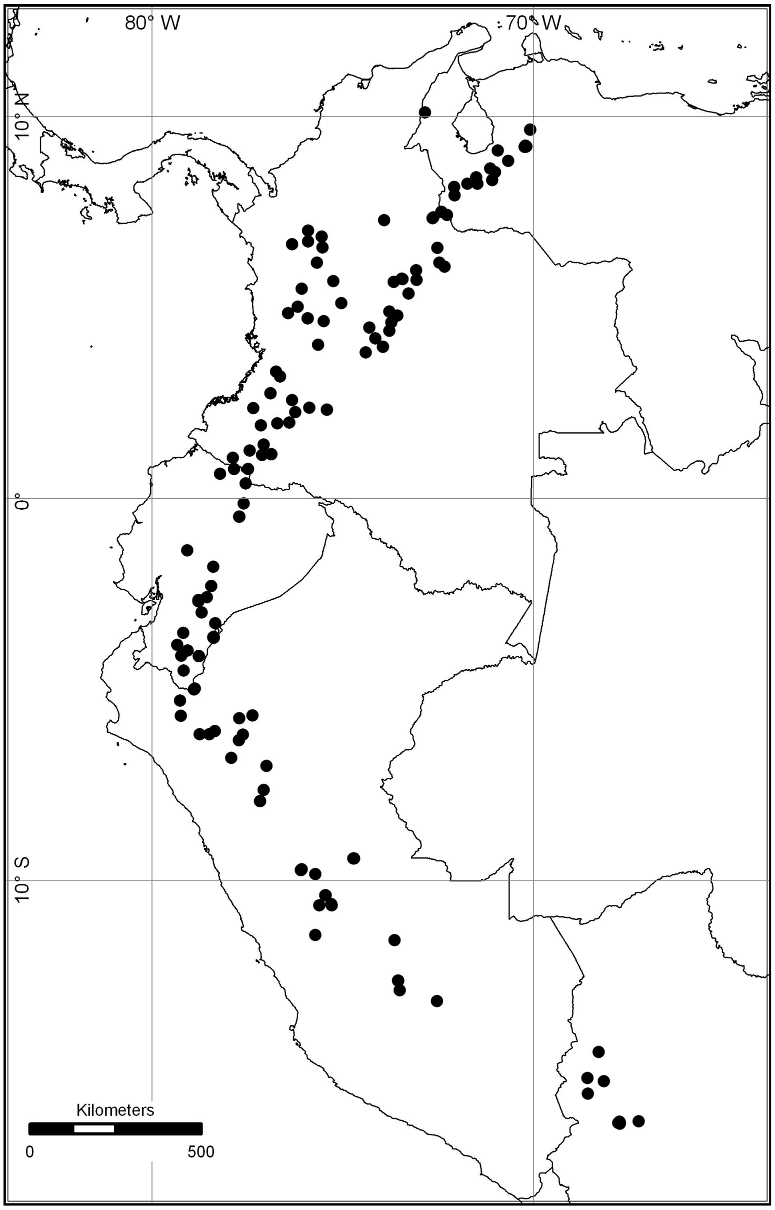
Disterigma popenoei S. F. Blake, Proc. Biol. Soc. Washington 35: 120. 1922. Type. Ecuador. Loja: mountains E of Loja, 2420-2700 m, 11 Apr 1921 (fl, fr), *Popenoe 1323* (holotype, US). Photo NY neg. 9449 ex US.

(Fig. 10 C)

Epiphytic or terrestrial **shrubs**, scandent or erect, up to 3 m tall. Young branchlets ridged, more or less smooth, puberulous or villosulous, the hairs eglandular and white, the mature branches indumentum similar but glabrate. **Leaves** 1–3 per cm, spirally arranged, diffuse; petiole 1.5–3(–3.5) mm long, glabrate, the hairs eglandular; lamina sometimes succulent, ovate or elliptic, (0.8–)1.2–4(–4.7) x (0.4–)0.5–1.9(–3.5) cm, basally cuneate or less often obtuse, marginally entire or rarely crenulate, revolute towards base, apically ciliolate with eglandular hairs (especially in young leaves), apically blunt acute, acute, or rarely obtuse, adaxially glabrate with eglandular hairs (especially over the midvein), abaxially glabrate with glandular and some eglandular hairs, the venation adaxially 3-nerved with the midvein impressed, abaxially hyphodromous or 3-nerved with the midvein raised. **Inflorescence** axillary, of 3–9-flowered fascicles, sometimes solitary flowers also present; bracts 7–10, chartaceous, ovate, 0.8–2 x 0.6–2 mm, sometimes marginally ciliolate with minute eglandular hairs, apically obtuse, abaxially glabrous or glabrate with eglandular hairs; pedicel 1–3 mm long, reduced and hidden by overlapping bracts, glabrous or glabrate with eglandular and glandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping entire calyx tube or to upper half of calyx lobes, covering 51–85% of calyx, ovate or suborbicular, 2.2–4 x 2.3–6 mm, marginally ciliolate with eglandular hairs and inconspicuous glandular hairs, apically obtuse, the surface smooth and often keeled, abaxially glabrous or glabrate with eglandular hairs, adaxially glabrous. **Flowers** 4-merous. Calyx aestivation valvate, campanulate, (2.5–) 3.5–5.5 mm long; tube slightly angled, (1.1–)1.7–2 mm long, abaxially glabrous or glabrate with glandular hairs; limb (1.4–)1.6–3 mm long, abaxially glabrous or glabrate with eglandular hairs (especially apically), adaxially glabrous; lobes triangular, (0.6–)0.9–2 x 1–2.5 mm, rarely marginally ciliolate with eglandular hairs, apically acute; sinuses acute (V-shaped). Corolla pink or white, thin-fleshy, bistratose, tubular or narrowly urceolate (but mostly all drying tubular), 5.3–8.5(–10) mm long, 2.5–5 mm diam., 2.5–3.5 mm wide at throat, abaxially glabrate with inconspicuous eglandular and glandular hairs, adaxially puberulous; lobes 1.5–1.8 x 0.9–2.2 mm, apically acute, adaxially rugose. Stamens 8, 5–7.2(–8) mm long, exserted; filaments distinct, straight, more or less linear with parallel sides or broader at base, 3–4(–5.6) mm long, abaxially and adaxially pilose, the indumentum often dense; anthers distinct, papillae on both thecae and tubules; thecae 0.9–1.5 mm long, basally appendaged; tubules 2, distinct, 1.2–2.3 mm long, dehiscing introrsely by longitudinal slits, 0.5–1.4 mm long. Ovary 4-locular; style 5–8.5 mm long, included. **Berry** purple or violet, rarely reported as white in southern Ecuador (however it is possible this report come from fruits not fully mature), more or less spherical, 8–9.3 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo white.

Distribution and ecology: *Disterigma alaternoides* is known from the Andes in western Venezuela, Colombia, Ecuador, Peru and northern Bolivia, and it is perhaps the most frequently collected taxon of the genus (Map 3).

Disterigma alaternoides is abundant in the cloud forest (montane and premontane) but it can also reach the páramo, with a wide altitudinal range between (1200?)1500-3600 m. This species has been found in both primary and secondary vegetation, as well as on roadsides and pastures with remnant vegetation. Flowering specimens and fruiting specimens have been collected all year-round.



Map 3. Geographic distribution of *Disterigma alaternoides.*

Etymology. It is not evident why Kunth chose this name. Perhaps, this species reminded him of the Italian buckthorn, *Rhamnus alaternus*, which is referred as *Alaternus* in Latin.

Representative specimens examined. COLOMBIA. Antioquia: Mun. San Antonio del Prado, vereda Potreritos, sitio El Silencio, Alto del Romeral, 2600-2760 m, 12 Jul 2004 (fl), *J. C. Betancur 10907* (COL, NY); Mun. Belmira, en la vía a la vereda El Yerbal, sitio Los Patos, margen izquierda del Río Chico, Alto de Sabanazos, 2950-3110 m, 15 Mar 1991 (fl, fr), *Callejas 10077* (HUA, NY); Mun. Santa Rosa de Osos, Llanos de Cuiva, 2700 m, 22 Nov 1978 (fl), *Callejas et al. 965* (NY); Mun. Medellín, El Boquerón, Alto de los Baldíos, 3150 m, 9 Apr 1958 (fl), *Cuatrecasas et al. 24254* (MEDEL, NY, US); Mun. Belmira, Páramo Sabanazo, Estación Ecológica El Refugio, 3080-3280 m, 16 May 1996 (fl, fr), *Fonnegra et al. 6012* (HUA); San Pedro, 25 Mar 1940 (fl, fr), *Hno. Daniel & Hno. Tomás 2246* (MEDEL, US); Mun. Yarumal, 2 km from the Yarumal-Ventanas road junction with Santa Ana-Briceño turn-off, 1800-2000 m, 31 Oct 1996 (fl), *Luteyn et al. 14992* (NY); Mun. Sonsón, carretera Sonsón-Nariño, sitio Arriba-Arriba y el Páramo, 2450-2800 m, 5 Jul 2004 (fl, fr), *P. Pedraza & C. Pedraza 1050* (COL, HUA, MO, NY), *1058* (COL, HUA, NY). **Boyacá:** Villa de Leyva, SFF Iguaque, 2950 m, 14 Dec 2002, *J. C. Betancur et al. 9908* (COL, NY), 2800-3000 m, 22 Apr 1984 (fl, fr), *Pipoly & Monje 6984* (COL, MO, NY); El Alisal, Cañon del Chicamocha, Guacamayas-San Mateo, 2900 m, 1 Oct 1991 (fl), *Etter et al. 506* (COL); Rondón, carretera Cienaga-Rondón, 20 Mar 1996 (fr), *C. Fagua 480* (COL); Cienaga, Laguna La Calderona, 3200 m, 17 Mar 1996 (fl), *G. Fagua 387* (COL); Sierra Nevada del Cocuy, Cobugon, 2900 m, 16 Aug 1957 (fl), *Grubb et al. 543* (COL, MICH, US); Arcabuco, Páramo vecino a la población, 3200 m, 6 Jun 1969 (fl), *Huertas & Camargo 6771* (COL); Mun. Ramiriqui, camino hacia la Laguna Negra, 2900 m, 12 Oct 1965 (fl), *Huertas & Camargo 6237* (COL); valle del Río Cusiana, 2900 m, 22 Jun 1967 (fl), *Jaramillo-M. et al. 2728* (COL); Sutamarchán, Emiliano Alto, 3220 m, 8 Apr 2003 (fr), *C. Prieto et al. 1527* (COL); Mun. Chiscas, vereda Duartes, sector Duartes Arriba, 3200-3650 m, 1 Oct 2003 (fl, fr), *V. Rodríguez et al. 643* (COL); Duitama, en la Hacienda La Rusia, 2700 m, 14 Nov 1945 (fl), *Uribe-Uribe 1074* (COL, US). **Caldas:** Cerro Tatamá, 3200-3400 m, 8-10 Sep 1922 (fl), *Pennell 10508* (NY). **Casanare:** Mun.

Salinas, Quebrada Contadero, 3100 m, 19 Nov 1996 (fl), *Dueñas & Robles 47* (COL). **Cauca:** Macizo Colombano, Páramo de las Papas, alrededores de la Laguna de Cusiyaco, 3360 m, 7 Oct 1958 (fl), *H. G. Barclay & Juajibioy 5931* (COL, US); Páramo de Puracé, S del Volcán, San Francisco, 3400-3450 m, 23 Jul 1943 (fl, fr), *Cuatrecasas 14685* (F, GH); Mun. Silva, about 42 km E of Piendame, 2900 m, 5 May 1984 (fl), *Luteyn et al. 10084* (COL, MO, NY); Puracé, PNN Puracé, bosque hacia el Río Bedón detrás de la cabaña San Nicolás, 2600-2800 m, 12 Oct 1992, *Orozco et al. 1570* (COL); PNN Munchique, Mun. El Tambo, 1700-2640 m, 7 Aug 2004 (fl, fr), *P. Pedraza & Giraldo 1154* (COL, HUA, NY), *1156* (CAUP, COL, CUVC, HUA, MO, NY), 2500 m, 8 Aug 2004 (fl), *P. Pedraza & Giraldo 1163* (CAUP, COL, MO, NY), *1177* (COL, NY), *1179* (COL, HUA, NY); Mun. Puracé, Valle de Paleterá, cerca del Valle de los Frailejones, 9 Aug 2004 (fl), *P. Pedraza & Gómez 1248* (CAUP, COL, NY); Mun. San Sebastián, vereda Loyola, cerca de la Laguna de Cusiyaco, 3200 m, 10 Aug 2004 (fl, fr), *P. Pedraza & Gómez 1183* (CAUP, COL, NY). **Chocó:** Mun. San José del Palmar, Cerro del Torrá, 2730 m, 15 Aug 1988 (fl, fr), *Silverstone-Sopkin et al. 4429* (NY). **Cundinamarca:** Sesquíle, Tierra Negra, Laguna de Guatavita, 2960 m, 16 Jan 1999 (fr), *Acosta et al. 266* (COL); Mun. San Bernardo, verede de Santa Marta, 2400-2500 m, 22 Jul 1981 (fl), *Díaz-P. & Jaramillo-M. 3080* (COL); Sumapaz, corregimiento de Betania, vereda El Raizal, 3170 m, 19 Feb 1997 (fl), *Franco & J. C. Betancur 5642* (COL, NY); La vega-Facatativa road, 2700 m, 6 Sep 1991 (fl), *Haught 6153* (COL, US); Mun. Subachoque, entre La Pradera y Zipaquirá, 2900 m, 29 Mar 2003 (fl), *Hernández-Schmidt 1124* (COL); along road between Bogotá to Choachí, 3110 m, 4 Jan 1976 (fl, fr), *Luteyn et al. 4724* (COL, DUKE, NY, US), 9 May 1980 (fr), *P. A. Palacios 56* (COL); Bogotá- Fusagasuga road, 2450-2620 m, 15 May 1979 (fl), *Luteyn & Lebrón-Luteyn 7693* (COL, MO, NY); Mun. Granada, vereda Los Amarillos, 2600-2800 m, 19 Jun 1987 (fl), *G. Morales et al. 1024* (COL); PNN Chingaza, 2983 m, May 2004 (fl, fr), *C. Pedraza &*

Umaña 1 (COL, NY), *4* (COL, HUA, NY), *5* (COL, CUVC, HUA, NY), *12* (COL CUVC HUA NY); Sibaté, 3000-3100 m, 13-15 Oct 1917 (fl), *Pennell 2487* (GH MO NY US); Mun. Junín, Reserva Biológica Carpanta, 2500 m, s.d. (fl, fr), *Repizzo & Calle 214* (COL); Bogotá, Cerro de Monserrate, 3200-3300 m, 22 Aug 1948 (fl), *Schneider 632* (S); Finca Carpatos, Reserva Forestal Río Blanco, 2900-3000 m, 16 Nov 1991 (fl), *Stiles & Rosselli 669* (COL). **Huila:** Mun. La Plata, vereda Agua Bonita, Finca Merenberg, 1200-1300 m, 21 Jul 1975 (fr), *Díaz-P. et al. 788* (COL); Paramillo Arrabal, Finca La Candelaria, W of Volcán Puracé, near Santa Leticia, 2380 m, 4 Apr 1986 (fl), *Gentry et al. 54036* (MO); Mun. San José de Isnos, vereda El Marmol, 9 km del límite del PNN Puracé, 2860 m, 22 Jul 1980 (fl), *Lozano 3355* (COL, NY); km 28-32 along Pitlito-Mocoa near divide, 2100-2240 m, 29 Apr 1979 (fl, fr), *Luteyn et al. 7541* (COL, NY). **Huila:** Gigante, Reserva Natural Ventanas, cerca del plantio de Aliso, 2500-2600 m, 14 Oct 1993 (fr), *Orozco et al. 2821* (COL). **Meta:** El Calvario, Inspeción de policía San Francisco, 2900 m, 4 Mar 1981 (fl), *Camargo & Huertas 7854* (COL); confluence of Río Arroz with Río del Nevado, S slope of Páramo de Sumapaz, 2650 m, 31 Aug 1943 (fl, fr), *Fosberg 20929* (NY, US). **Nariño:** Mun. Santiago, Páramo Quilinsayaco, km 30 Pasto-Mocoa, 3000 m, 11 Nov 1982 (fl), *Albert de Escobar & Salazar de Benavides 2872* (HUA); cuenca alta del Río Putumayo, Páramo de San Antonio del Bordoncillo, 3250 m, 4 Jan 1941 (fl), *Cuatrecasas 11707* (COL, F, US); Mun. Ipiales, carretera Victoria-Río San Francisco, 3100 m, 5 Sep 1972 (fr), *Hernández-A. et al. 320* (PSO); Mun. Barbacoas, Reserva Natural del Río Ñambi, 1440-1500 m, 5-6 Oct 1997 (fl), *Luteyn et al. 15188* (COL, NY); Mun. Consacá, faldas del Volcán Galeras, cuenca Río Azufral, 2600 m, 9 Oct 1994 (fl, fr), *B. R. Ramírez 6612* (PSO); Mun. Pasto, corregimiento El Encano, vereda San José Alto, 2900 m, 19 Jan 1991 (fl), *B. R. Ramírez 3029* (PSO); Mun. Mallama, trayecto Piedrancha-Cabeceras de la Quebrada La Chorrera, 2300-2500 m, 17 Oct 1993 (fr), *B. R. Ramírez & Jojoa 5756* (NY, PSO); Laguna La Cocha, ciudadela, near paramo de Bordoncillo, 2800-3000 m, 27 May 1946 (fl), *Schultes & Villareal 7580* (COL). **Norte de Santander:** Páramo de Fontibón, 2500 m, 20 Feb 1939 (fl), *Alston 7177* (A, BM, COL, F, L, US), 2600-2750 m, 15 Oct 1941 (fl, fr), *Cuatrecasas et al. 12297* (COL, US); Páramo de Tamá, 3000-3200 m, 28 Oct 1941 (fl), *Cuatrecasas et al. 12696* (COL, GH, F, US); Páramo del Hático, in road from Toledo to Pamplona, 2900 m, 12-13 Mar 1927 (fl), *Killip & A. C. Smith 20678* (A, NY, US); Cucutilla, Vereda El Carrizal, sector Sisavita, 3200 m, 26 Mar 2002 (fl, fr), *Mendoza et al. 14709* (COL). **Putumayo:** Mun. Sibundoy, km 82 Pasto-Mocoa, Páramo del Fraile, 2800 m, 24 Feb 1984 (fl), *Salazar de Benavides & B. R. Ramírez 4478* (HUA); Valle del Sibundoy, 2300 m, 29 May 1946 (fr), *Schultes & Villarreal 7718* (COL, US). **Quindio:** Salento, La Marina, Alto del Puma, 3120 m, Aug 1993 (fl), *W. Vargas 1148* (HUA). **Risaralda:** Mun. Santuario, vereda San Rafael, PNN Tatamá, 2500-2950 m, 15 Jul 2004 (fl, fr), *P. Pedraza & C. Pedraza 1094* (COL, HUA, NY). **Santander:** W slope of Páramo Rico, 3600 m, 15 Jan 1927-19 Jan 1927 (fl), *Killip & A. C. Smith 17785* (COL, GH, NY, US); vicinity of Las Vegas, 2600-3000 m, 21 Dec 1926-23 Dec 1926 (fl), *Killip & A. C. Smith 15985* (A, GH, NY, US). **Santander/Boyacá:** Vírolin, Finca La Sierra, 2500-2600 m, 16 May 1976 (fl), *Lozano et al. 2563* (COL). **Tolima:** Roncesvalles, a la orilla de la trocha hacia San José de las Hermosas, 2980 m, 18 Nov 1980 (fl), *Camargo 7633* (COL). **Valle del Cauca:** Los Farallones, Alto del Buey, 3500-3600 m, 11 Oct 1944 (fl, fr), *Cuatrecasas 17889* (F, GH, US); Río Cali, arriba del Silencio, 2800 m, Julio 1938 (fl), *Duque-Jaramillo 4430* (COL); Mun. Río Frío-Daríen, Páramo del Duende, 3000-3850 m, 23-28 Jul 1998 (fl), *W. Vargas 4840* (COL, HUA). **Without department:** 1760-1808 (fl), *Mutis 2034, 2037* (US), 1783-1808 (fl), *Mutis 2087* (F).

VENEZUELA. Apure: distrito Páez, bajada de los Huevos, cerca del sitio La Línea, Páramo de Tamá, 3100 m, 26 Jun 1973 (fl), *Ruiz-Terán & López-Figueiras*

8863 (NY). **Lara:** PN Dinira, Quebrada Las Lajitas, en la vertiente larense de Pico de Cendé, 2600 m, 11 Jan 2001 (fl), *Duno & Riina 1478* (NY). **Mérida:** Sierra Nevada above Mérida, 3400 m, 4 Feb 1939 (fr), *Alston 6866* (BM, L, NY, US); distrito Rangel, PN Sierra Nevada, Quebrada Mitisús, 2750-3100 m, 19 Jun 1988 (fl), *Dorr & Barnett 5612* (CAS, MO, NY); páramo above El Molino, 3000 m, 23 Jan 1987 (fl, fr), *Hahn & Grifo 3346* (NY); trail La Escalera-Puente de La Escalera, 2950-2500 m, 1 Nov 1978 (fl, fr), *Luteyn et al. 6231* (CAS, F, L, MICH, MO, NY, US); Bailadores-La Grita road, La Granzonera region, 3000 m, 26 Jan 1978 (fl, fr), *Luteyn et al. 5263* (CAS, F, GB, MO, NY); Los Aserruchos area, Estanques-Páramo del Molino road, below Páramo de los Colorados, 3 Feb 1978 (fl), *Luteyn et al. 5419* (NY); distrito Miranda, Cerro Caracacho, Páramo de Palmira, 3200-3300 m, 24 May 1975 (fl, fr), *Ruiz-Terán & López-Figueiras 12299* (NY). **Táchira:** camino de La Revancha, entre el Descanso y Puertoñoco, 2900 m, 17 Jan 1973 (fl), *Cuatrecasas et al. 28371* (F, US); Páramo el Zumbador, 14 km S of El Cobre, 2500 m, 31 Mar 1974 (fl), *Gentry et al. 11079* (MO, NY); Páramo de Tamá, 2500-3200 m, 29 Jan 1978 (fl, fr), *Luteyn et al. 5321* (CAS, MO, NY); Mun. Jáuregui, barranco La Mina, 4 km SE El Cobre, 2500 m, 21 May 1992 (fl), *Pietrangeli 1967* (NY); distrito Junín, cabecera de la quebrada El Reposo, al N de Villa Páez, hacia el extremo NW del gran Páramo de Tamá, 2800 m, 28 Jun 1973 (fr), *Ruiz-Terán & López-Figueiras 8931* (NY). **Trujillo:** distrito Boconó, PN Guaramacal, road from Boconó to Guaramacal, 2200-2500 m, 16 Jul 1995 (fl, fr), *Dorr et al. 8150* (NY). **Zulia:** Perijá, 2800-2900 m, 29 Dec 1950 (fr), *Hno. Gines 1986* (US).

ECUADOR. Azuay: N of Paute, 13 Apr 1945 (fl, fr), *Camp E-2594* (MO, NY, P, US); Sevilla de Oro, 2950 m, 18-20 Apr 1968 (fl), *Harling 8464* (GB, NY); Llamacón, 8 km ENE of Tomebamba on Paute-Cola de San Pablo road, 2600 m, 31 Mar 1985 (fl), *Harling & Andersson 23500* (GB, NY); Jima-San Miguel de Cuyes, Páramos de Palcurco, 3140 m, 4 Dec 1990 (fl, fr), *Jørgensen et al. 92837-*

A (MO, NY, TEX); 22-25 km S of Sigsig road towards Gualaquiza, Páramos de Matanga, 3040-3340 m, 21 Jan 1985 (fl, fr), *Luteyn & Cotton 11150* (NY); Gualaceo-Limón road, 16 km E of Gualaceo, 3050 m, 18 Apr 1978 (fl), *Luteyn & Lebrón-Luteyn 5761* (CAS, NY); Huagrarancha, S of El Pan, bordering Río Collay, 2650-3290 m, 6 Jul 1943 (fl, fr), *Steyermark 53340* (F, US). **Bolívar:** Guaranda, Los Arrayanes, Cerro Mashashingo Alto, 3370 m, 16 Feb 2005 (fl, fr), *H. Vargas et al. 4937* (NY). **Cañar:** Cerro Yausay, E of Azogues, 2800 m, 13 Dec 1980 (fr), *Holm-Nielsen et al. 29169* (K, NY). **Carchi:** Tulcán-Maldonado road, 41-45 km W of Tufiño, 2700 m, 13 Apr 1978 (fl, fr), *Luteyn & Lebrón-Luteyn 5740* (CAS, F, GB, MO, NY); carretera Tulcán-Maldonado, depués del caserio El Laurel, antes del Páramo del Angel, 2800 m, 18 Dec 2003 (fl, fr), *P. Pedraza & C. Pedraza 991* (COL, MO, NY, QCA, QCNE)*, 992* (NY), *993* (QCA). **Imbabura:** Shanshipamba, 2900 m, 11 Nov 1949 (fl), *Acosta-Solis 14182* (F); between Toldadas and Naranjito, E of Volcán Cayambe, 3200 m, 8 May 1944 (fl), *Drew E-174* (NY, US). **Loja:** Loma de Oro, above Saraguro, 2987 m, 3 Oct 1944 (fr), *Camp E-558* (DS, NY); Cordillera de Zamora, E of Loja, 3050 m, 2 Jul 1944 (fl), *Camp E-90* (NY, US); Cerro Villanaco, about 7 km W of Loja, 2430-2880 m, 28 Jul 1944 (fl, fr), *Camp E-249* (NY, US); Saraguro, Bosque Nativo Hushapampa, 6 km S of Saraguro, 2910 m, 6 Apr 2005 (fl), *Clark et al. 9073* (NY); Uritusinga, 28 Nov 1996 (fr), *Cueva 868* (QCA); Yangana-Valladolid road, 2500 m, 24 Feb 1988 (fl), *Jaramillo 10261* (MO, NY); road to Cerro Toledo, 8-10 km E of and above Yangana, 2460-3323 m, 14 Nov 1990 (fl, fr), *Luteyn et al. 14145* (AAU, NY); about 10 km E of Loja along road to Zamora, 2525 m, 15 Jan 1981 (fl, fr), *Luteyn & Clemants 7964* (NY); Fierro Urco road, about 3-5 km W of the Loja-Saraguro road, 2950-3100 m, 3 May 1997 (fl), *Luteyn et al. 15074* (NY); entre Oña y Saraguro, 2600-2900 m, 15 Aug 2004 (fl, fr), *P. Pedraza & N. R. Salinas 1191* (COL, MO, NY, QCA, QCNE); PN Podocarpus, 3300 m, 16 Aug 2004 (fl, fr), *P. Pedraza & N. R. Salinas 1200* (NY, QCA, QCNE), 2700-3300 m, 17 Aug 2004 (fr), *P. Pedraza & N. R. Salinas 1220* (NY, QCA). **Morona-Santiago:** Cordillera de Huaracayo, E of Cordillera del Cóndor and Río Congos, Cerro Ijiach Naint, 1950 m, 20 Mar 2001 (fl), *Neill et al. 13091* (NY); Alao-Huamboya trail, around La Magdalena, 3450-3600 m, 8 May 1982 (fl, fr), *Ollgaard et al. 38379* (F, MO, NY); trail between Pailas and El Pan, 2225-3445 m, 10 Sep 1943 (fl), *Steyermark 54322* (F, US). **Napo:** Guagra Urcu, Jaramillo, 2900 m, 29 Sep 1980 (fl), *Holm-Nielsen et al. 27632* (NY): trail to Volcán El Reventador, 1800 m, 10 Oct 1990 (fl), *Jaramillo et al. 13118* (NY); cantón Tena, Cordillera de los Huacamayos, entre Carachupa-Chacana, 7 Aug 1995 (fl), *Jaramillo & Tapia 18441* (QCA). **Pichincha:** antigua carretera a Santo Domingo de los Colorados (pasando por Chiriboga), 2100 m, 23 Dec 2003 (fl, fr), *P. Pedraza & C. Pedraza 1009* (AAU, COL, MO, NY, QCA, QCNE, US). **Sucumbíos:** camino La Bonita-La Sofia, 2440 m, 16 Sep 1995 (fl), *Garmendia & P. Jaramillo 186* (QCA); 8-12 km ESE of Santa Bárbara, 2780-2880 m, 11 Jan 1985 (fl), *Luteyn & Cotton 11009* (NY). **Zamora-Chinchipe:** El Pangui, 1 km S del destacamento militar Cóndor Mirador, 2000 m, 16 Dec 2000 (fl), *Caranqui et al. 220* (NY); Cordillera de Numbalá, El Tiro pass between Loja and Zamora, 2800 m, 17 Oct 1998 (fl), *Dziedzioch & Gottsberger 125-171098* (NY); Cordillera de Nanguipa, Cerro Colorado, about 8 km by air SSE of Nambija, 2700 m, 18 Feb 2002 (fl), *Neill et al. 13765* (NY); Estación Científica San Francisco, road Loja-Zamora, 2300 m, 6 Dec 2000 (fl), *Werner 173* (NY).

PERU. Amazonas: Prov. Luya, distrito Camporredondo, anexo Tullanya, entre Pájaco Tigre y la Palma, 2500-2600 m, 9 Dec 1996 (fl, fr), *Campos et al. 3150* (COL, MO, NY, USM); Prov. Bongara, 4 km N of Pomacochas on road to Rioja, 2150-2200 m, 2 Jun 1986 (fr), *Knapp et al. 7466* (F, MO, NY, USM); Prov. Chachapoyas, Chachapoyas-Molinopampa road, just above Pipos, 2140 m, 4 Jul 2002 (fl, fr), *Luteyn et al. 15488* (NY); Prov. Chachapoyas, Leymebamba-Balsas road, Kms 412-421, 2450-2900 m, 14 Mar 1978 (fl), *Luteyn & Lebrón-Luteyn*

5571 (CAS, MO, NY, USM); Prov. Chachapoyas, near Piñamonte, 77 km NE of Balsas and 15.6 km SW of Leymebamba, 2850 m, 3 Jul 2002 (fl, fr), *Luteyn et al. 15486* (NY); Prov. Chachapoyas, Chachapoyas-Mendoza road, km 546 W of Molinopampa, 2300-2400 m, 11-12 Mar 1978 (fl), *Luteyn & Lebrón-Luteyn 5555*, (NY, USM). **Cajamarca:** Prov. San Ignacio, San José de Lourdes, entre bajo Picorana y el Picorana, 2420-2470 m, 19 Aug 1998 (fl), *Campos et al. 5626* (NY); Jaén, Sallique, localidad de la Cocha, 2960 m, 21 Jun 1998 (fl, fr), *Campos et al. 5044* (NY); PN Cutervo, Chorro Blanco region, about 15 km N of San Andrés de Cutervo, 2650-2750 m, 13 Sep 1991 (fl, fr), *Gentry et al. 74778* (MO, NY, USM); E of Huancabamba, above Tabaconas, 2400-2500 m, Apr 1912 (fl), *Weberbauer 6109* (F, GH). **Cusco:** Prov. Urubamba, Machu Picchu, above Río Mandor, 5 km from km 114 of the Urabamba railroad, 2920 m, 25 Sep 1982 (fl), *Peyton 1353* (CUZ, MO, NY). **Huánuco:** Prov. Huánuco, Carpish, cumbre entre Huánuco y Tingo María, 2800-2900 m, 9 Aug 1947 (fl), *Ferreyra 2311* (US, USM), 2600-2700 m, 26 Feb 1978 (fl), *Luteyn & Lebrón-Luteyn 5463* (CAS, NY, USM). **Junín:** Satipo, N Cordillera Vilcabamba, E slope, upper river Poyeni watershed, 2050 m, 1 Jul 1997 (fl, fr), *Boyle et al. 4865* (USM). **Pasco:** Prov. Oxapampa, PN Yanachaga-Chemillén, 3450 m, 9 Jun 2006 (fl, fr), *P. Pedraza et al. 1601* (AAU, COL, CUZ, MO, NY, USM), 3400 m, 11 Jun 2006 (fl, fr), *P. Pedraza et al. 1606* (COL, CUZ, MO, NY, QCA, USM), 2380 m, 16 Jun 2006 (fl), *P. Pedraza et al. 1616* (COL, CUZ, F, NY, USM). **San Martín:** Mariscal Cáseres, past Las Palmas, 2650-2750 m, 16 Aug 1986 (fr), *Young 4004* (NY). **Without region:** de Vitoc a Palca, 4 Nov 1863 (fl), *Isern 946* (MA); Altos de Palca, camino de Vitoc a Tarma, 3 Nov 1863 (fl), *Isern 546* (MA); Playapampa, 2900 m, 16-24 Jun 1963 (fl), *Macbride 4488* (F), s.d (fl), *Weberbauer 1089* (F).

BOLIVIA. La Paz: Prov. Nor Yungas, entre Chuspipata y San Rafael, en el camino de construcción del tramo del tunel, 2850 m, 8 Mar 1996 (fl), *St. G. Beck 22670* (LPB); Franz Tamayo, PN Madidi, Pinalito, 29 km al E de Apolo por el camino a San José de Uchupiamonas, 1900-2496 m, 16 Jul 2002 (fl), *Fuentes et al. 5016* (NY); Prov. Larecaja, along trail from Mapiri to Sorata (between Tararani and Yani), 3000-3500 m, s.d. (fl), *Krukoff 11489* (F, NY); Nor Yungas, trail 1.2 km E of Cotapata along road to Yolosa, 3200 m, 7 May 1990 (fl), *Luteyn & Dorr 13562* (BOLV, LPB, NY); Prov. Nor Yungas, en el camino viejo a Coroico, 3100 m, 15 Apr 2005 (fl, fr), *P. Pedraza et al. 1510* (LPB, NY), 3250 m, 16 Apr 2005 (fl, fr), *P. Pedraza et al. 1512, 1513* (COL, LPB, NY); Mapiri, 3050 m, May 1886 (fl), *Rusby 2026* (BM, E, GH, K, L, NY, P, US, WIS); Prov. Bautista Saavedra, carretera al pueblo de Yurilaya-Camata (cabecera Majata), 2300 m, 12 Sep 2001 (st), *Zenteno et al. 1098* (LPB).

Without country. s.d. (fl), *Bonpland s.n.* (F); s.d. (fl), *Bonpland s.n.* (L); [in Vice-regno Peruviano et Chilensi lectae], 1778-1788 (fl), *Ruiz & Pavón s.n.* (F).

Disterigma alaternoides has variable leaves from 0.9 to ca. 5 cm long, 0.4 to 3.5 cm wide, apically acute to obtuse, and with the venation well marked or completely obscure. This vegetative variability was described under different names at the species or variety level (see Smith, 1933; Wilbur, 1992), but all of them share the same combination of reproductive characters namely, fascicles with usually numerous flowers; flowers 4-merous; corollas pink or white, tubular or narrowly urceolate, and characteristically puberulous inside (Fig. 10 C); dense indumentum in the filaments; and seed embryos white. The fruits of *D. alaternoides* are typically purple or violet, but white berries have been sometimes observed in southern Ecuador. Nevertheless, it cannot be said for sure that the species is polymorphic for this character because such reports are very few and could correspond to fruits not fully mature.

Material from both Central and South America have been previously identified as *Disterigma alaternoides* (Luteyn, 1996; Wilbur, 1974, 1992) and scantly separated from another morphologically variable species, *D. humboldtii*, which is very abundant across Central America. However, the study of these species over their entire geographic range revealed that although they are polymorphic, *D. alaternoides* is only confined to South America, while *D. humboldtii* spreads from Mexico to Peru. This findings are supported by the molecular and total evidence analyses where *D. alaternoides* and the OTU's of *D. humboldtii* form different clades (Pedraza-Peñalosa, in press; see phylogeny). This species can be differentiated because while *D. alaternoides* has flowers grouped in 3-9-flowered fascicles (sometimes combined with solitary flowers) and with the corolla puberulous within, *D. humboldtii* has solitary flowers (sometimes combined with 2-3-flowered fascicles) with the corolla glabrous within or nearly so; it can also be generalized that the leaves of *D. alaternoides* are broader overall [(0.4-)0.5-1.9 (-3.5) vs. (0.3-)0.4-0.7(-1.3) cm in *D. humboldtii*]. For morphological comparisons of *D. alaternoides* with other species see *D. pallidum*, *D. verruculatum*, and *D. ovatum*.

Hybrids between *Disterigma alaternoides* and *D. noyesiae* may be present in the area of Munchique (Cauca, Colombia) were the two populations grow sympatrically, mixed together [*González et al. 2941* (COL), *P. Pedraza & Galindo 1154* (COL, HUA, NY), *1156* (CAUP, COL, CUVC, HUA, MO, NY), *1163* (CAUP, COL, MO, NY), *1177* (COL, NY), *1179* (COL, HUA, NY)]. There, some plants have long bracteoles (ca. 7 mm long) extending up to 1.8 mm beyond the calyx and with corollas completely glabrous adaxially (like in *D. noyesiae*); otherwise, their leaves, inflorescence type, and flowers look just like any other *Disterigma alaternoides*. In the other hand, specimens annotated as possible hybrids between *D. alaternoides* and *D. cryptocalyx* by Luteyn (1996) for Ecuador, belong to *D. noyesiae*, a not so rare but variable species.

Local names and uses. This species is known as “Mata de Caballo “ (Norte de Santander), “Capulí silvestre “(Nariño), “Mortiño” (Antioquia, Cundinamarca), and “Chite “ (Cundinamarca) in Colombia. As “Perlillo” (Loja), “Motilón” (Bolívar), “Tira” (Azuay, Loja), and “Zchirpe” (Azuay) in Ecuador. As “borrachera” (Lara) and “Albricias” (Mérida) in Venezuela. And, as “Piku-mullaca” (Amazonas) in Peru. Its fruits have been reported to be edible by both humans and birds throughout its entire distribution.

4. **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. 13)

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 thick and reddish, ridged, more or less smooth, villous, the hairs eglandular and golden-brown, the mature branches indumentum similar but glabrate. **Leaves** 2–3 per cm, spirally arranged, diffuse; petiole 2.8–4 mm long, villose, the hairs eglandular; lamina ovate, 1.8–2.8 x 1.1–1.8 cm, basally obtuse or cuneate, marginally entire, apically ciliolate with eglandular hairs, apically acuminate, adaxially glabrate with eglandular hairs, abaxially glabrate with glandular hairs, the venation 5-nerved on both sides, the midvein adaxially impressed and abaxially raised. Axillary **solitary flowers** and rarely in 2-flowered fascicles; bracts 14–15, chartaceous, ovate, elliptic or suborbicular, 0.7–6.3 x 1.4–6 mm, marginally eciliate, apically obtuse and often splitting, abaxially glabrous; pedicel 0.8–2.4 mm long, reduced and hidden by overlapping bracts, glabrate with eglandular and glandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping to upper half of calyx lobes or 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, the surface smooth, abaxially and adaxially glabrous. **Flowers** 5-merous (one 4-merous flower seen). Calyx aestivation imbricate, campanulate, 5.6–6.5 mm long; tube terete, 2–2.5 mm long, abaxially glabrate with eglandular hairs; limb 4–4.7 mm long, abaxially glabrate with eglandular hairs, adaxially glabrous; lobes ovate, 2.8–3.2 x 2–3.1 mm, marginally eciliate, apically acute; sinuses obscured by the overlapping bases of the imbricate lobes. Corolla pink with darker lobes, thick-fleshy, bistratose, urceolate (distally inflated), 7.1–8 mm long, 4.4 mm diam. (3.5 in dry), 3 mm wide at throat (2.2–3.2 in dry), abaxially and adaxially glabrate with eglandular hairs; lobes 1.2 x 1.2–1.6 mm, apically acute, adaxially rugose. Stamens 10 (-12), 5.9–6.3 mm long, included; filaments connate into a tube, straight, 3–3.3 mm long, abaxially glabrate with very few hairs, adaxially pubescent distally; anthers distinct, papillae only on thecae; thecae 1.5–1.7 mm long, 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, dehiscing introrsely by longitudinal slits, 0.8–1 mm long. Ovary 5-locular; style 6.7 mm long, included. **Berry** color unknown, the persistent calyx lobes converging and overlapping; seeds viviparous, embryo color unknown.

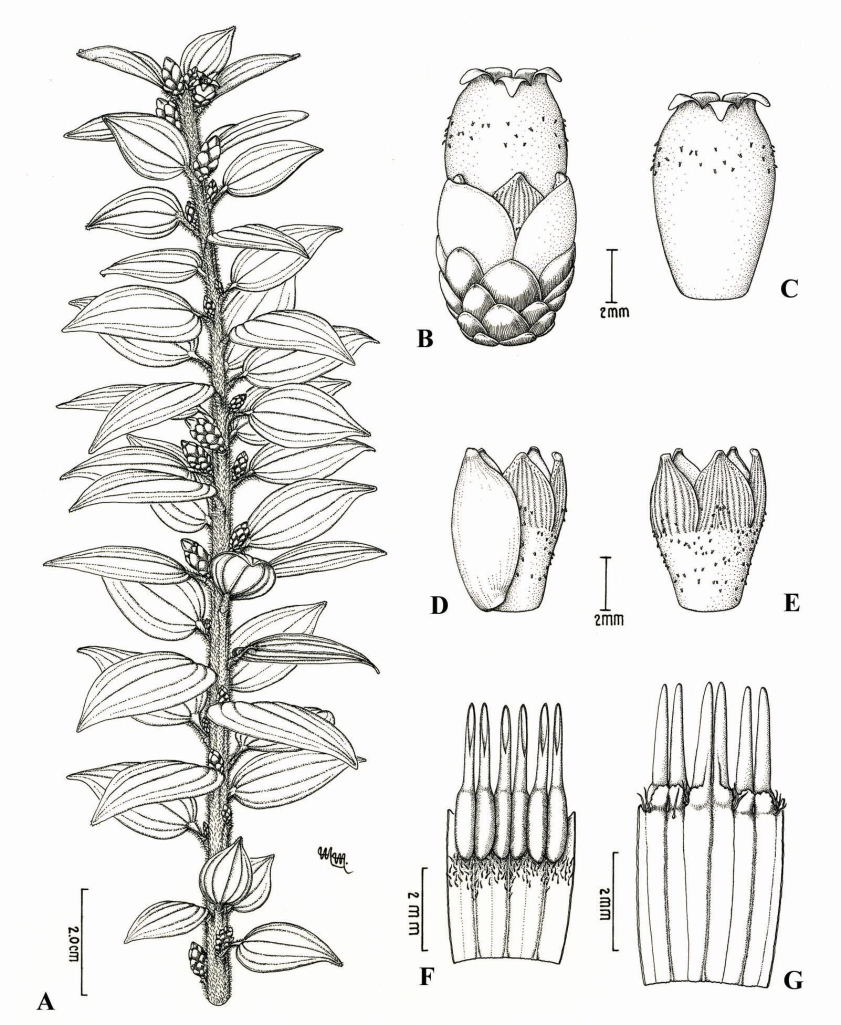


Fig. 13. Illustration of *Disterigma appendiculatum*. **A**. Branch. **B**. Flower with bracts and bracteoles. **C.** Corolla. **D.** Calyx with one bracteole removed. **E.** Calyx with both bracteoles removed. **F.** Adaxial view of connate stamens. **G.** Abaxial view of connate stamens with dorsal flap-like spurs (*P. Pedraza 1113*, COL).

Distribution and ecology. *Disterigma appendiculatum* is endemic to the cloud forests of Serranía de los Paraguas, near Cerro del Inglés (Valle del Cauca, in Colombia), between 1850-2100 m, where it does not seem to be abundant (Map 2). Flowering and fruiting specimens have been collected in April and July.

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

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 (Fig. 6). 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, differentiated 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 a unique combination of characters that separate it from the rest of *Disterigma*, its external morphology recalls that of *D. cryptocalyx* (Colombia and Ecuador). The floral differences between these two species are many and are summarized in Table 8.

Table 8. Morphological comparison between *Disterigma appendiculatum* and *D. cryptocalyx*

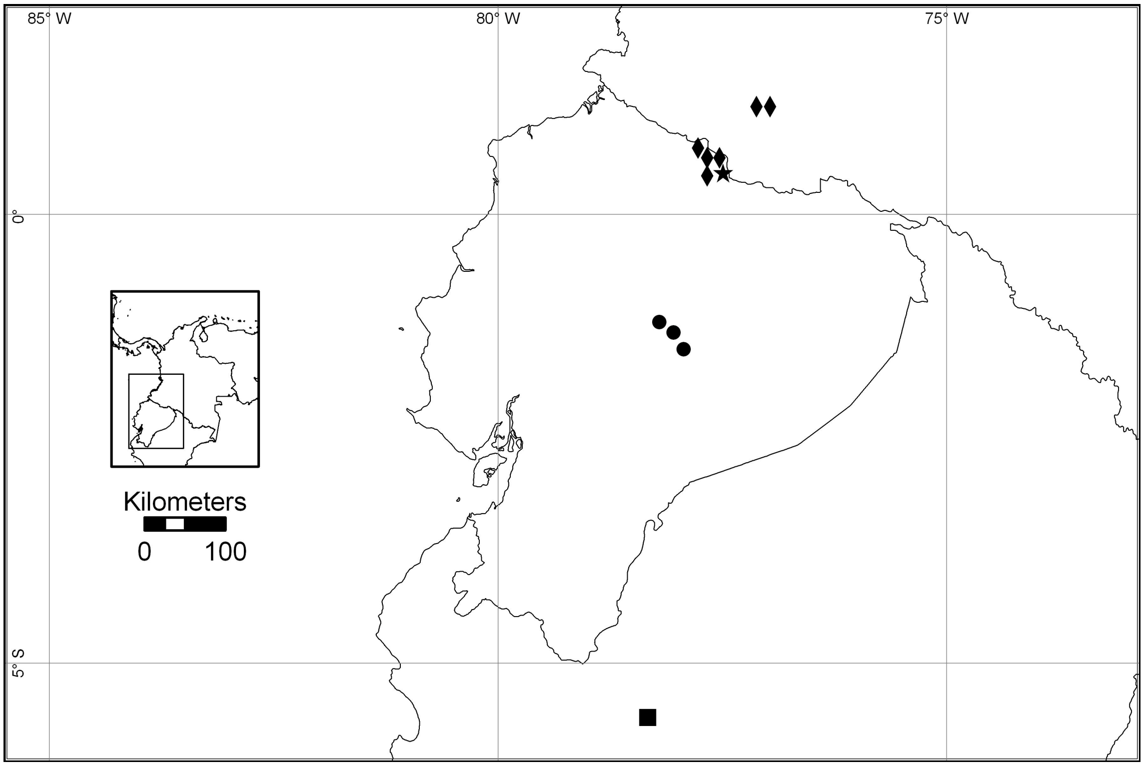
Character	*D. appendiculatum*	*D. cryptocalyx*
Bracteoles extending beyond the calyx	0 mm	2.5–4 mm
Flower merosity	(4-)5-merous	4-merous
Calyx aestivation	Imbricate	Valvate
Overall calyx length; limb length; lobe length	5.6–6.5 mm; 4.0–4.7 mm; 2.8–3.2 mm	2.8–3.6(–4.5) mm; 1–1.7(–2.5) mm; 1-1.7(–2) mm
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

5. **Disterigma baguense** Pedraza **sp. nov.** Type. Peru. Amazonas: Prov. Bagua, Cordillera Colán SE of La Peca, 2350-2450 m, 16 Oct 1978 (fl, fr), *Barbour 4102* (holotype, MO; isotypes, F, NY).

Species nova foliis ovatis, ad margines ciliatis, ciliis deciduis longis crispis eglandulosis, floribus axillaribus solitariis, 4-meris, bracteolis apicalibus tubum calycis omnino obtegentibus, superficie longitudinaliter striata, limbo calycis abaxialiter dense pubescenti, lobis ad margines ciliatis, ciliis longis crispis eglandulosis, sinubus anguste rotundatis, corolla alba tubulari adaxialiter glabra, bacca alba distincta..

Epiphytic **shrubs**. Young branchlets ridged, more or less smooth, villous, the hairs eglandular, brown, the mature branches indumentum similar but glabrate or villous. **Leaves** 4–7 per cm, spirally arranged, ascending; petiole 0.6–0.8 mm long, glabrate, the hairs eglandular or glandular; lamina ovate, (0.6–)0.8–1.1 x (0.3–)0.4–0.5 cm, basally obtuse or cuneate, marginally entire, ciliate with hairs deciduous, long (0.5-1 mm), curly and eglandular, apically blunt acute, adaxially glabrous or glabrate with hairs eglandular, abaxially glabrate with glandular hairs, the venation adaxially and abaxially obscure. Axillary **solitary flowers**; bracts 4, chartaceous, ovate, 1–1.5 x 0.8–1.6 mm, marginally ciliolate with eglandular hairs, apically obtuse or acute, abaxially glabrous; pedicel 0.8–1 mm long, reduced and hidden by overlapping bracts, glabrate with eglandular and glandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping entire calyx tube, covering 50–62% of calyx, ovate, 2.1–3 x 2.5–3 mm, marginally ciliate with hairs curly and eglandular, apically obtuse or very rarely subacute, the surface longitudinally striate, adaxially and abaxially glabrous. **Flowers** 4-merous. Calyx aestivation unknown, campanulate, 3.5–3.6 mm long; tube angled (in dry), 1.5 mm long, abaxially glabrate with eglandular and glandular hairs; limb 2–2.1 mm long, abaxially densely pubescent with eglandular and glandular hairs, adaxially glabrous; lobes triangular, 1.8–2 x 1 mm, marginally ciliate with hairs long (0.5-1 mm long) and eglandular, apically acute; sinuses narrowly rounded (U-shaped). Corolla white (fide collectoris), thin-fleshy, bistratose, tubular, 8–11.5 mm long, 4 mm diam. (in dry), 3 mm wide at throat (in dry), abaxially glabrate or puberulous with eglandular and glandular hairs (especially distally), adaxially glabrous; lobes 1.2–1.4 x 1.1–1.2 mm, apically acute, adaxially rugose. Stamens 8, 7.2–8.3 mm long, included; filaments distinct, straight, more or less linear with parallel sides, 4–5 mm long, abaxially and adaxially glabrate; anthers distinct, papillae on both thecae and tubules; thecae 1.5–1.6 mm long, with or without basal appendages; tubules 2, distinct, 2.2–2.6 mm long, dehiscing introrsely by longitudinal slits, 0.8–1 mm long. Ovary 4-locular; style 7–11.1 mm long, exserted. **Berry** white (fide collectors), the persistent calyx lobes erect or spreading; seed embryo color unknown.

Distribution and ecology. *Disterigma baguense* is only known from the vicinity of La Peca, in the Bagua province from northern Peru (Amazonas) (Map 4). This species grows in cloud forests between 1700-2450 m, and its fruits are eaten by the shiny grassgreen tananger (*Barbour 4102*). Flowering specimens have been collected in June and October, and fruiting specimens in October.



Map 4. Geographic distribution of *Disterigma baguense* ■*, D. balslevii* ◆, *D. campanulatum* ★, and *D. campii* ●.

Etymology. Species named after the province of Bagua, Peru, where the type specimen is from.

Specimens examined. PERU. Amazonas: Prov. Bagua, 12-17 km (by trail) E of La Peca, 1700-2100 m, 28 Jun 1978 (fl), *Barbour 2526* (NY).

Disterigma baguense is likely to be related to *D. balslevii*; they both share their general appearance as well as the curly and long hairs on the leaves and calyx lobes margins. Nevertheless, their distribution is disjoint with *D. baguense* found in the mountains of the Peruvian Amazonas region (two collections from 1978) and *D. balslevii* growing in southern Colombia and in the border with Ecuador.

Disterigma balslevii has never been recorded south of Carchi and Sucumbíos, neither has been observed in many field trips dedicated to document the Ecuadorian Ericaceae. The only exception known is a collection made near Río Tintas, in the border between Morona-Santiago and Zamora-Chinchipe [*Steyermark 53609* (A)], which seem similar to *D. baguense*, but that cannot be identified with confidence because it lacks flowers.

These two species can be differentiated because the calyces of *D. baguense* have both eglandular and glandular hairs (vs. only eglandular in *D. balslevii*); its calyx, calyx limb, and calyx lobes are shorter (3.5-3.6 mm, 2-2.1 mm, 1.8-2 mm respectively vs. 4.3-5.9 mm, 2.8-4.4 mm, 2-3.2 mm); its calyx tube is terete (vs. angled); its corolla is white and tubular (vs. red and narrowly urceolate); its staminal filaments are straight and glabrate (vs. geniculate and puberulous); its thecae is straight in side view (vs. prognathous); and because its papillae are found all over the theca and tubules (vs. only on the thecae).

Furthermore, *Disterigma baguense* is characterized by the following combination of characters, leaves ovate and marginally ciliate with hairs deciduous, long (0.5-1 mm), curly, and eglandular; axillary solitary flowers;

differentiated apical bracteoles enveloping entire calyx tube, marginally ciliate, the surface longitudinally striate; flowers 4-merous; calyx lobes marginally ciliate with hairs deciduous, long (0.5-1 mm), sinuses narrowly rounded (U-shaped); corolla white, tubular, adaxially glabrous; papillae on both thecae and tubules; and white berries.

Local names and uses. Birds have been reported to eat the little berries of this plant.

6. **Disterigma balslevii** Luteyn, Opera Bot. 92: 113, fig. 4. 1987. Type. Ecuador. Sucumbíos: Julio Andrade-El Carmelo road, Km 18, cloud forest, 3200 m, 16 May 1982 (fl, fr), *Luteyn et al. 8405* (holotype, NY; isotypes, AAU, CAS, COL, E n.v., GB, K, L, MO, P, QCA n.v., TEX, U n.v., US). The QCA sheet was not found.

(Fig. 14)

Epiphytic or terrestrial **shrubs**, wiry, pendent. Young branchlets ridged, more or less smooth, villous, the hairs eglandular, curly and brown, the mature branches indumentum similar but glabrate. **Leaves** 5–8 per cm, spirally arranged, ascending; petiole 1.2–1.5 mm long, glabrate, the hairs eglandular; lamina ovate, 0.6–1.3(–1.5) x (0.3–)0.4–0.7 cm, basally obtuse to rounded, marginally entire, slightly revolute towards base, ciliate with hairs long (0.5-1.5 mm), curly and eglandular, or sometimes ciliolate with hairs at least at the apex of young leaves, apically acute or blunt acute, adaxially glabrate with eglandular hairs, abaxially glabrate with eglandular and glandular, both hair types minute and deciduous, the venation obscure or hyphodromous on both sides, the midvein adaxially impressed and abaxially raised. Axillary **solitary flowers**; bracts 6–9,

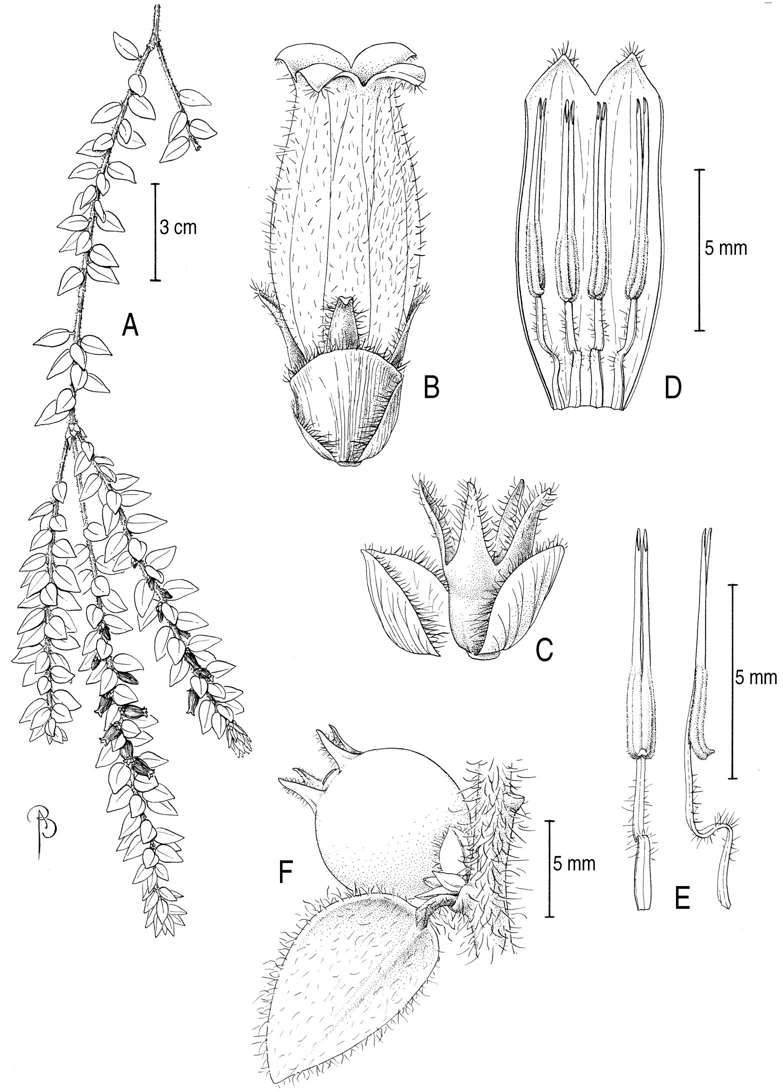


Fig. 14. Illustration of *Disterigma balslevii.* **A.** Branch; **B.** Flower with differentiated apical bracteoles; **C.** Calyx; **D.** Longitudinal section of the corolla; **E.** Adaxial and lateral views of the stamens showing geniculate filaments; **F.** Fruit (*Luteyn et al. 8405*, NY). Modified from Opera Bot. 92, fig. 4 (1987).

chartaceous, ovate, 0.7–3 x 1.1–3 mm, marginally ciliate or ciliolate with long eglandular hairs, apically obtuse or acute, abaxially glabrous; pedicel 0.8 mm long, much reduced and hidden by overlapping bracts, glabrate with minute glandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping entire calyx tube or to part of calyx lobes, covering 38–71% of calyx, ovate or elliptic, 2.6–4.5 x 2.8–4 mm, marginally ciliate with eglandular hairs, apically obtuse or acute, the surface softly longitudinally striate, abaxially and adaxially glabrous. **Flowers** 4-merous. Calyx aestivation valvate, campanulate, 4.3–6 mm long; tube terete, 1.5–2.2 mm long, abaxially glabrate with eglandular hairs; limb 2.8–4.4 mm long, abaxially glabrate or pilulose with eglandular hairs, adaxially glabrous; lobes triangular, 2–3.5 x 1.3–2 mm, marginally ciliate with hairs long (0.5-1.5 mm), curly and eglandular, apically acute; sinuses rounded (U-shaped). Corolla red, thin-fleshy, bistratose, urceolate, 8–12 mm long, 4.5–5.5 mm diam., 2.5–3.2 mm wide at throat, abaxially glabrate or pubescent with eglandular hairs, adaxially glabrous; lobes 1.1–1.5 x 1.1–1.7 mm, apically acute, adaxially smooth. Stamens 8, 6.4–8 mm long, included; filaments distinct, geniculate, broader at base, 3.5–4.5 mm long, abaxially and adaxially puberulous; anthers distinct, papillae on both thecae and tubules; thecae basally prognathous, 1.6–2.1 mm long, without basal appendages; tubules 2, distinct, 2.1–3 mm long, dehiscing introrsely by longitudinal slits, 1.1–1.6 mm long. Ovary 4-locular; style 8.8–10.5 mm long, included. **Berry** white, more or less spherical, 7 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo color unknown.

Distribution and ecology. *Disterigma balslevii* is restricted to southern Colombia in the Cordilleras Central and Occidental (Macizo Colombiano and Nudo de los Pastos), and to northern Ecuador, in the provinces of Carchi and Sucumbíos (Map 4). The species grows scattered in montane cloud forests between 2500-3400(-3700) m and has been collected in both primary and secondary vegetation, including road slopes. Flowering specimens have been collected in January-May and June, and fruiting specimens in February, May, and November-December.

Etymology. This species was named after the Danish botanist Henrik Balslev.

Specimens examined. COLOMBIA. Cauca: Macizo Colombiano, Páramo de Las Papas, alrededor de la Laguna de Cusiyaco, 3490 m, 11 Oct 1958 (fl), *H. G. Barclay & Juajibioy 6036* (COL, US), 3400 m, 13 Oct 1958 (fl), *H. G. Barclay & Juajibioy 6064* (COL, US). **Nariño:** Páramo de Bordoncillo, 3250 m, 5 Mar 1963 (fl), *Espinal 1019* (COL, US); Páramo de El Estero, Río Guames, 2500-2700 m, 5 Nov 1972 (fl), *L. E. Mora 6223* (PSO); Mun. Pasto, Páramo La Pastora, 3200 m, 29 Oct 1980 (fl) *Salazar de Benavides 2620* (PSO). **Putumayo:** alta cuenca del Río Putumayo, entre El Encano y Sibundoy, Páramo de San Antonio del Bordoncillo, 3250 m, 4 Jan 1941 (fl), *Cuatrecasas 11739* (COL, NY, US); Pasto-Sibundoy road, 3000-3130 m, 20 Feb 1979 (fl), *Luteyn & Lebrón-Luteyn 6793* (COL, NY, PSO), 3000-3170 m, 20 Feb 1979 (fl, fr), *Luteyn & Lebrón-Luteyn 6799* (AAU, CAS, F, MO, NY, P).

ECUADOR. **Carchi:** 4.8 km W of Carmelo along Tulcán-Alegría road, 2900 m, 5 Feb 1982 (fl), *Dodson & Gentry 12092* (MO, NY, QCNE, SEL); 13.2 km E of La Estrellita on road to El Carmelo, 3335 m, 15 Nov 1988 (fl, fr), *Dorr & Barnett 6135* (AAU, GB, NY, QCA, QCNE, S, TEX); Tulcán-El Carmelo road, near El Carmelo, 3200 m, 26 Feb 1974 (fl), *Harling & Andersson 12214* (AAU, GB, NY), 3200 m, 18 May 1982 (fl), *Luteyn et al. 8458* (AAU, B, NY, QCA, QCNE, S), 2800-3000 m, 18 Dec 2003 (fl, fr), *P. Pedraza & C. Pedraza 998* (COL, MO, NY, QCA); Julio Andrade-Palestina road, 3300 m, 27 Dec 1980 (fl), *Holm-Nielsen et al. 29723* (AAU, K, NY); 3 km E of Frailejón, between Cruce Cordillera on

Panamericana highway and El Carmelo, 3300 m, 10 Apr 1979 (fl), *Løjtnant et al. 12157* (AAU, GB); Julio Andrade-El Carmelo road, km 18, 3200 m, 16 May 1982, *Luteyn et al. 8406* (QCNE). **Carchi/Sucumbíos:** Julio Andrade-Playón de San Francisco road, 6 Jul 1978, *Jaramillo & Boeke 263* (NY, QCA). **Sucumbíos:** 4 km S of El Playón de San Francisco, 6 Jul 1978 (fl), *Boeke & Jaramillo 2374* (AAU, CAS, MICH, MO, NY, TEX); Cerro El Mirador, SW of Cocha Seca, 3300 m, 27 Feb 1992 (fl), *Gavilanes & Funk 812* (NY, QCA, QCNE); SE of El Playón de San Francisco on slopes of Cerro Mirador, 3700 m, 28 Dec 1980 (fl), *Holm-Nielsen et al. 29910,* (AAU, QCA); Cartagena, km 25 from El Carmelo towards La Bonita, 2800 m, 8 Apr 1979 (fl), *Løjtnant et al. 11972* (AAU, GB); 6-18 km ESE of Santa Bárbara, 2900 m, 10 Jan 1985 (fl), *Luteyn & Cotton 10986* (AAU, NY, QCA, US).

Disterigma balslevii is characterized by its relatively long calyx lobes (2-3.2 mm); its red, narrowly urceolate, adaxially glabrous, and long corollas (8-12 mm); its stamens with geniculate filaments and prognathous anthers (Fig. 7); and by its white berries. Although long (0.5-1.5 mm) and curly hairs on the margins of the leaves and calyx lobes are more frequent in the Ecuadorian specimens, the indumentum of those from Colombia is scarcer and often deciduous on the leaves, being many times only found at the apex of young leaves. For details about morphological similarities between this and other species, look at the discussion under *D. baguense*.

Hybrids between *Disterigma balslevii* and *D. acuminatum* [i.e., *Billiet & Jadin 6928* (MO), *Dryander 1723* (US), *1725* (US); *Guarín-M. 576* (PSO), *583* (COL, PSO); *Idrobo et al. 2972* (COL, L), *3269* (COL), *3305* (COL, L); *Idrobo & Barclay 4083* (COL), *4077* (COL), *4079* (COL); *Jaramillo-M. & Hammen 5225* (COL); *Schultes & Villarreal* 7828 (AMES), *7840* (GH, NY, US); *Ramírez 11879* (PSO); *Salazar de Benavides 1882* (COL, PSO), *Sneidern 1874* (A, F, NY, S, US)] are suspected in the regions of Putumayo, Nariño, and Cauca, where the two species co-occur in the same type of vegetation. These specimens have features and dimensions intermediate between the two putative parents, and their major differences are summarized in Table 9.

Table 9. Summary of differences between *Disterigma acuminatum*, *D. balslevii,* and their putative hybrid.

Characters	***D. acuminatum* (large corolla populations)**	***D. balslevii* x *D. acuminatum***	***D. balslevii***
Leaves shape & dimensions	Ovate, 0.4–0.9 x 0.3–0.5 cm	Ovate, intermediate	Ovate, 0.6–1.3(–1.5) x (0.3–)0.4–0.7 cm
Leaf apex	Long-acuminate	Blunt acute	Acute or blunt acute
Bracteoles and calyx lobes margins	Ciliolate	Ciliate or ciliolate	Ciliate
Calyx lobes length	1.2-1.5 mm	1.5-2 mm	2-3.5 mm
Corolla length	4.2-6 mm	5.7-8(-9) mm	8-12 mm
Corolla color	White	Bright red	Red
Staminal filaments	Straight	Straight or geniculate	Geniculate
Fruits	Purple (fide collectoris for long corolla collections)	White	White

Field observations as well as morphological and molecular studies are necessary to test for hybridization and explain the observed variation; unfortunately, the exploration of the areas where these populations grow was not feasible.

Local names and uses. This species is known as “Pipisiki” in Sucumbíos (Ecuador), and in the same province its berries are reported as edible by humans.

7. **Disterigma campanulatum** Pedraza, **sp. nov.** Type. Ecuador. Sucumbíos: Santa Bárbara-La Bonita road, trail towards La Bonita, 25-28 km S of Santa Bárbara, along Río Chingual, 0˚34’N, 77˚30’W, 2100-2350

m, 17 May 1982 (fl, fr), *Luteyn et al. 8454* (holotype, QCA; isotypes, CAS, GB, K, MO, NY, QCNE, TEX).

(Fig. 15)

Species nova foliis crassis, in sicco leviter rugosis, oblongis vel interdum ellipticis, ad basem truncatis, floribus axillaribus solitariis, bracteolis apicalibus usque ad basim loborum calycis obtegentibus, longitudinaliter striatis, floribus 4-meris, aestivatione calycis valvata, sinubus acutis, corolla alba campanulata, lobis ad margines apicesque abaxialiter puberulis, adaxialiter glabris, staminibus brevibus, bacca alba distincta.

Epiphytic or terrestrial **shrubs**, wiry. Young branchlets not ridged, more or less smooth, villosulous, the hairs eglandular and brown, the mature branches indumentum similar but glabrate. **Leaves** 7–8 per cm, spirally arranged, diffuse; petiole 0.8–1(–1.4) mm long, glabrous; lamina succulent and drying slightly wrinkled, oblong or sometimes elliptic, 0.7–0.9 x 0.3–0.5 cm, basally truncate, marginally entire, slightly revolute at base, apically ciliolate with inconspicuous eglandular and glandular hairs (especially in young leaves), apically obtuse, adaxially glabrous or glabrate (in young leaves) with eglandular hairs towards base, abaxially glabrous or glabrate with inconspicuous glandular hairs, the venation adaxially obscure, abaxially 3-nerved with the midvein raised. Axillary **solitary flowers**; bracts 3–4, chartaceous, ovate, 0.4–1.5 x 0.5–1.8 mm, marginally eciliate, apically obtuse, abaxially glabrous; pedicel 0.3–0.6 mm long, much reduced and hidden by overlapping bracts, glabrous; differentiated apical bracteoles 2, distinct, chartaceous, enveloping to the base of calyx lobes, covering 48–54% of calyx, transverse-elliptic, 1.6–2 x 2–2.5 mm, marginally ciliolate with minute eglandular hairs, apically obtuse, the surface longitudinally striate, abaxially and adaxially glabrous. **Flowers** 4-merous. Calyx aestivation

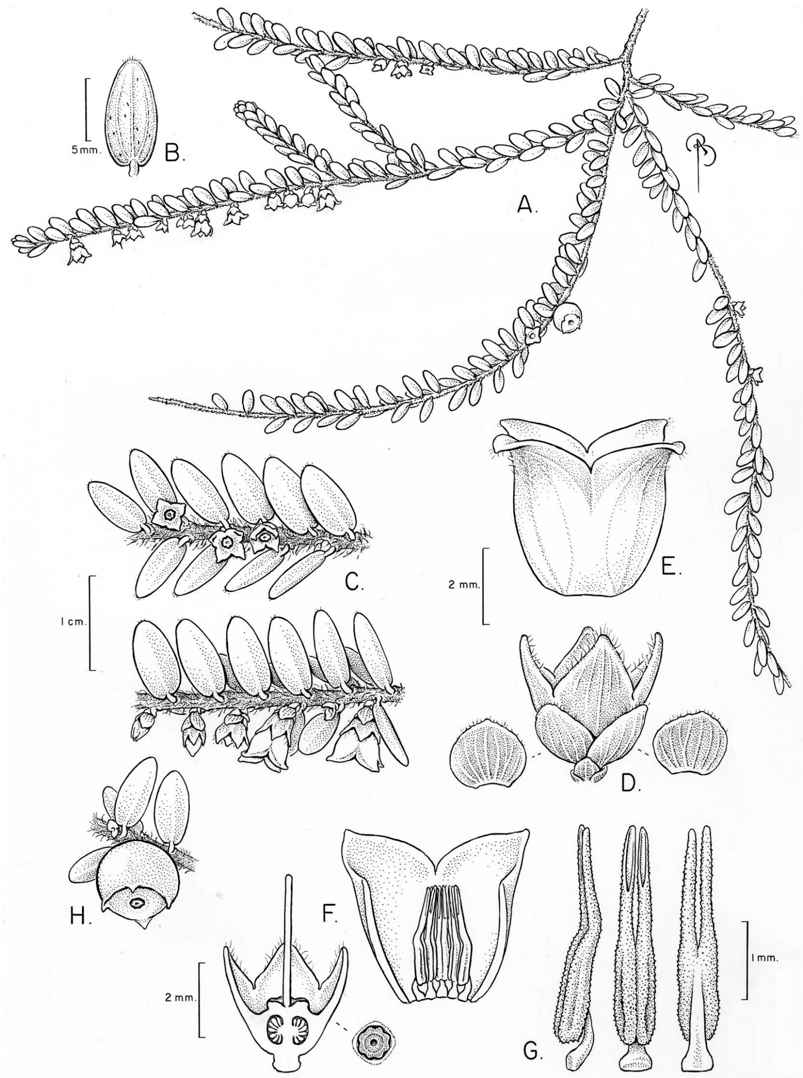


Fig. 15. Illustration of *Disterigma campanulatum*. **A.** Branch; **B.** Leaf; **C.** Detail of a branch with solitary flowers; **D.** Calyx clasped by a pair of longitudinally striate apical bracteoles; **E.** Corolla with puberulous lobes abaxially; **F.** Longitudinal sections of the corolla and of the calyx and inferior ovary, with a detail of the nectariferous disk; **G.** Lateral, adaxial, and abaxial views of the stamens. **H.** Fruit (*Luteyn 8454,* NY).

valvate, campanulate, 3–3.3 mm long; tube angled, 1–1.3 mm long, abaxially glabrous; limb 1.9–2 mm long, abaxially glabrate with eglandular hairs (apically), adaxially glabrous; lobes triangular, 1.5–1.9 x 1.3–1.8 mm, marginally ciliate with eglandular hairs, apically acute; sinuses acute (V-shaped). Corolla white, thin-fleshy, bistratose, campanulate, 4.5–4.7 mm long, 4.5–5 mm diam., 4.5–5 mm wide at throat, abaxially glabrate with scattered glandular hairs on the tube and puberulous towards lobes margins and apex with eglandular hairs, adaxially glabrous; lobes 1.4–1.7 x 2.2–2.5 mm, apically acute, adaxially smooth. Stamens 8, 3.2–3.3 mm long, included; filaments distinct, straight, broader at base, 0.9–1 mm long, abaxially and adaxially glabrous; anthers distinct, small papillae on both thecae and tubules; thecae 1.3 mm long, without basal appendages; tubules 2, distinct, 1.4–1.6 mm long, dehiscing introrsely by longitudinal slits, 0.7 mm long. Ovary 4-locular; style 3.5 mm long, included. **Berry** white, hemispherical, 6–9 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo color unknown.

Distribution and ecology. *Disterigma campanulatum* is only known from two collections made in the vicinity of La Bonita, in the Ecuadorian province of Sucumbíos (Map 4). This species is found in primary montane cloud forests between 2100-2350 m. Flowering and fruiting specimens have been collected in April and May.

Etymology. Species named after its distinctively campanulate corollas.

Specimens examined. ECUADOR. Sucumbíos: km 40-46 from El Carmelo to La Bonita, 0˚34'N, 77˚30'W, 2200-2350 m, 11 Apr 1979 (fl), *Løjtnant, B. et al. 12250* (GB).

Disterigma campanulatum is characterized by a wiry habit; leaves oblong or sometimes elliptic, basally truncate, and apically obtuse; differentiated apical bracteoles enveloping to the base of calyx lobes and longitudinally striate; corollas white, campanulate, abaxially puberulous on the lobes and adaxially glabrous; stamens 3.2–3.3 mm long with filaments 1 mm long or less; and white berries. The wiry habit, small entire leaves, and campanulate corollas of *D. campanulatum* recall, in different degrees, those of *D. campii* and *D. dumontii*. However, the differences among them are many and are given in Table 10.

Table 10. Summary of differences between *Disterigma campanulatum*, *D. campii,* and *D. dumontii*

Character	*D. campanulatum*	*D. campii*	*D. dumontii*
Leaf shape	Oblong or sometimes elliptic	Ovate, elliptic or rarely obovate	Ovate or sometimes elliptic or obovate
Differentiated apical bracteoles	Longitudinally striate	Smooth	Smooth
Calyx tube	Angled	Angled	Shortly winged
Corolla color	White	Green	Dark red
Corolla length	4.5-4.7 mm	4.4-6.3 mm	6.4-8.8 mm
Corolla lobes	Less than half the corolla length & spreading	More than half the corolla length & strongly reflexed	Less than half the corolla length & spreading
Corolla abaxially	Puberulous on lobes	Glabrous	Glabrous
Stamen length	3.2-3.3 mm	4.4-5.5 mm	(3.6-)4.8-5.6 mm
Filament length	0.9-1 mm	1.2-2.4 mm	(1.6-)2.0 mm
Tubule aperture	Longitudinal slits	Pores	Pores

8. **Disterigma campii** A. C. Sm., Mem. New York Bot. Gard. 8(1): 51. 1952. Type. Ecuador. Pastaza: valley of Río Pastaza, near junction of the El Tigre

and Pastaza rivers, below Topo, 1700 m, 9 May 1944 (fl), *Camp E-1692* (holotype, US; isotype, NY). Photo NY neg. 9886 ex NY.

Epiphytic or terrestrial **shrubs**, wiry, scandent, or prostrate and decumbent. Young branchlets ridged, more or less smooth, puberulous, the hairs eglandular, brown, the mature branches indumentum similar but glabrate. **Leaves** 4–8 per cm, apparently distichous, patent or sometimes diffuse; petiole 0.8–1.2 mm long, puberulous, the hairs eglandular; lamina ovate, elliptic, or rarely obovate, 0.5–1.3 x (0.2–)0.3–0.7 cm, basally obtuse or truncate, marginally entire, often slightly revolute, apically ciliolate with eglandular hairs, apically obtuse, adaxially glabrous or glabrate with eglandular hairs, abaxially glabrate with glandular hairs, the venation adaxially hyphodromous with the midvein impressed, abaxially hyphodromous or 3-nerved with the midvein raised. Axillary **solitary flowers**; bracts 4–5, chartaceous, ovate or transverse-elliptic, (0.5–)1–1.6 x 1–1.6 mm, sometimes marginally ciliolate with eglandular hairs, apically obtuse, abaxially glabrous; pedicel (0.4–)0.5 mm long, much reduced and hidden by overlapping bracts, glabrate with eglandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping entire calyx tube, covering 37–60% of calyx, ovate or suborbicular, 1.6–3 x 1.6–3 mm, sometimes marginally ciliolate with eglandular hairs, rarely with glandular hairs, apically obtuse, the surface smooth, abaxially and adaxially glabrous. **Flowers** 4-merous (rarely 5-merous calyces or 3-merous corollas seen). Calyx aestivation valvate, campanulate, 3.2–4.8 mm long; tube slightly angled, 1.2–2.4 mm long, abaxially glabrous or glabrate with eglandular or glandular hairs; limb 2–3.3 mm long, abaxially glabrate or puberulous (apically) with eglandular or glandular hairs, adaxially glabrous; lobes triangular, 1.6–2.8 x 0.8–1.2 mm, marginally ciliolate with eglandular hairs, apically acute; sinuses rounded (U-shaped). Corolla light green (occasionally suffused with brick-red), thin-fleshy, bistratose, campanulate, 4.4–6.3 mm long, 3–4 mm diam., 3–4 mm wide at throat, abaxially and adaxially glabrous; lobes 2.8–3.6 x 2.8–4 mm, apically acute or obtuse, adaxially smooth. Stamens 8, 4.4–5.5 mm long, exserted about half of their length; filaments distinct, straight, more or less linear with parallel sides or broader at base, 1.2–2.4 mm long, abaxially glabrate, adaxially puberulous; anthers distinct, papillae on both thecae and tubules; thecae 1.6–2.5 mm long, without basal appendages; tubules 2, distinct, 0.8–1.3 mm long, dehiscing apically by terminal pores, 0.2 mm long, marginally irregular. Ovary 4-locular; style 4.8 mm long, exserted about half of its length. **Berry** white, more or less spherical, 6 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo color unknown.

Distribution and ecology. *Disterigma campii* is only found in the Ecudorian province of Pastaza, in a relatively small area near Puyo, Mera, and Shell, and the vicinity of the rivers El Tigre, Anzú, Alpayacu, and Pastaza (Map 4). This species grows in premontane forests between 800-1700 m. Flowering specimens have been collected in May and August-January, and fruiting specimens in May and November.

Etymology. Species named after the type collector and student of Ericaceae, W. H. Camp.

Specimens examined. ECUADOR. Pastaza: Río Pastaza gorge, W of Mera, 1000 m, 6 Aug 1976 (fl), *Argent & Burbridge 428,* (MO, QCA); low hills E of Puyo, valley of the Río Pastaza, 914 m, 12 May 1944 (st), *Camp E-1700* (NY), *Camp E-1699* (NY); Shell, 1200 m, 30 Jan 1994 (fl), *Cornejo & Bonifaz 1405* (NY); Mera-Río Anzú road, near Mera, 1400-1450 m, 6 Oct 1992 (fl), *Luteyn & Sylva 14672,* 1070-1340 m, 14 Nov 1996 (fl, fr), *Luteyn et al. 15052* (QCA), *15056*

(AAU, NY, QCA); carretera de tierra entre Mera y el Río Anzú, después del puente sobre el Río Alpayacu, 1100-1300 m, 21 Aug 2004 (fl), *P. Pedraza & N. R. Salinas 1237* (AAU, COL, E, HUA, K, LPB, MO, NY, PMA, QCA, QCNE, US); cantón Puyo, Los Vencedores, Estación Experimental E.S.P.O.C.H., S of Puyo, 800-1040 m, 13 Dec 1995 (fl), *Soejarto et al. 9380* (F, HUA). **Without province:** 29 Sep 2003 (fl), *Cubey 1* (E) cultivated at The Royal Botanic Garden Edinburgh.

Disterigma campii can be easily distinguished because of its wiry habit; its apparently distichous and small leaves; its smooth differentiated apical bracteoles; its corollas light green, adaxially glabrous, and campanulate with the lobes more than half the corolla length and strongly reflexed as to expose the upper half of the stamens; its anthers dehiscing apically by terminal pores with irregular margins; and because of its white berries. The flowers from cultivated plants (*Cubey 1*) have smaller proportions when compared to the wild specimens above described, that is corolla 3.6 mm long, corolla lobes 2-2.4 x 1.2 mm, stamens 3.2 mm long, and filaments 0.8-1 mm long. Given that the total available specimens of this species are few, it is hard to know if the variation seen in cultivation is representative of the taxon or not. This species is compared with morphologically similar taxa in Table 10.

Conservation status. *Disterigma campii* has a very restricted geographical distribution and the areas where it has been collected are currently occupied by secondary vegetation; it has been reported in remnants of forests or roadsides. Historically *Disterigma campii* has been rarely collected and during repeated expeditions to Ecuador it was evident the impoverishment of its habitat due to the accelerated colonization and increasing extraction of wood (Pedraza-Peñalosa, pers. observ.). Living specimens were confirmed to be at the Royal Botanic Garden of Edinburgh in 2003, coming from a collection made by G. C. G. Argent in 1976. In the IUCN red list of plants endemic to Ecuador it is categorized as VU D2 (Pedraza-Peñalosa et al., in press).

9. **Disterigma chocoanum** Pedraza, **sp. nov.** Type. Colombia. Valle del Cauca: corregimiento El Boquerón, vereda El Brillante, Cerro del Inglés, en la Serranía de los Paraguas, 4° 44' 22.6"N, 76° 18' 23.5"W, 2100 m, 23 Jul 2004 (fl, fr), *P. Pedraza & C. Pedraza, 1121* (holotype, COL; isotypes, AAU, CAUP, CUVC, FMB, HUA, MO, NY).

(Fig. 16)

Species nova foliis ut videtur distichis obovatis vel interdum ellipticis, ad basem attenuatis vel interdum cuneatis, bracteolis apicalibus tubum calycis omnino vel ex parte lobos calycis obtegentibus, floribus 4-meris, aestivatione calycis valvata, sinubus acutis, corolla rubrescenti vivide vel pallide roseola tubulari, adaxialiter puberula; filamentis obtriantularibus pilulosis, bacca alba, embryone seminis alba distincta.

Epiphytic or terrestrial **shrubs**, scandent, or prostrate and decumbent. Young branchlets ridged, more or less smooth, puberulous, the hairs eglandular, light brown, the mature branches indumentum similar but glabrate or puberulous. **Leaves** 4–9 per cm, apparently distichous, ascending or patent; petiole 1–1.8 mm long, puberulous, the hairs eglandular; lamina obovate or less often elliptic, (0.5–)0.6–1(–1.2) x (0.3–)0.4–0.6 cm, basally attenuate or sometimes cuneate, marginally entire, apically ciliolate with eglandular hairs, apically obtuse, adaxially glabrous, abaxially glabrate with glandular hairs, the venation obscure or hyphodromous on both sides, the midvein adaxially impressed and abaxially raised. Axillary **solitary flowers** and rarely 2-flowered fascicles; bracts 5–7,

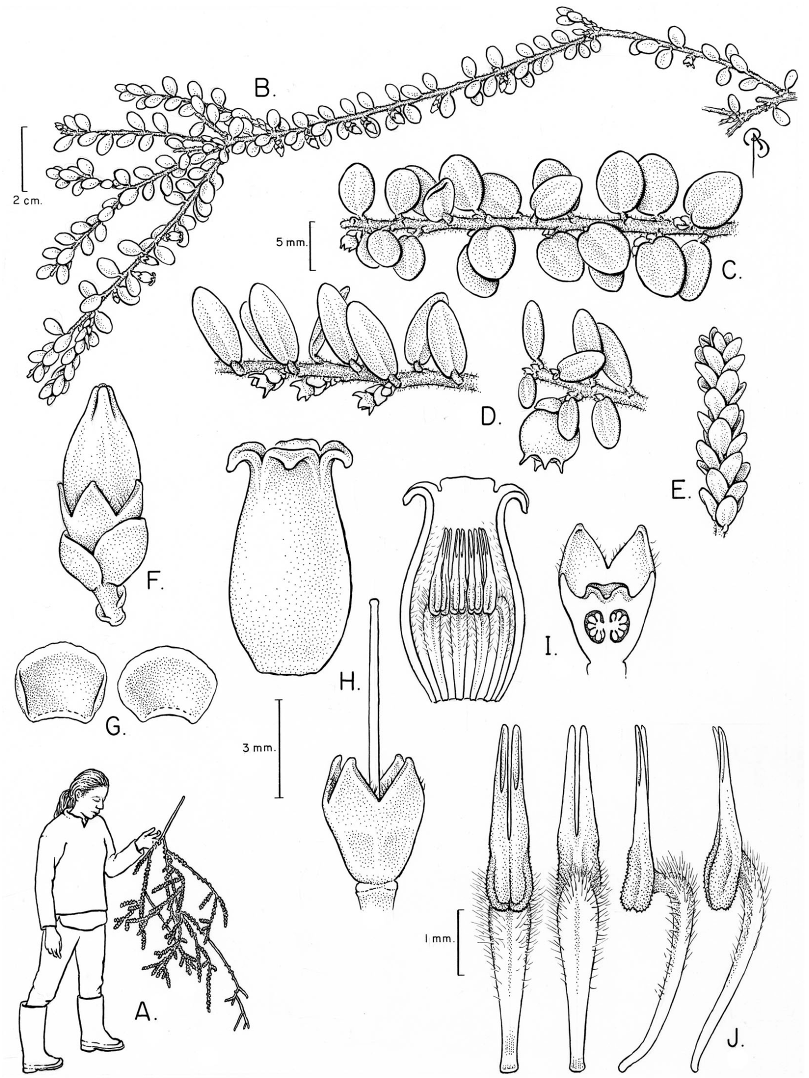
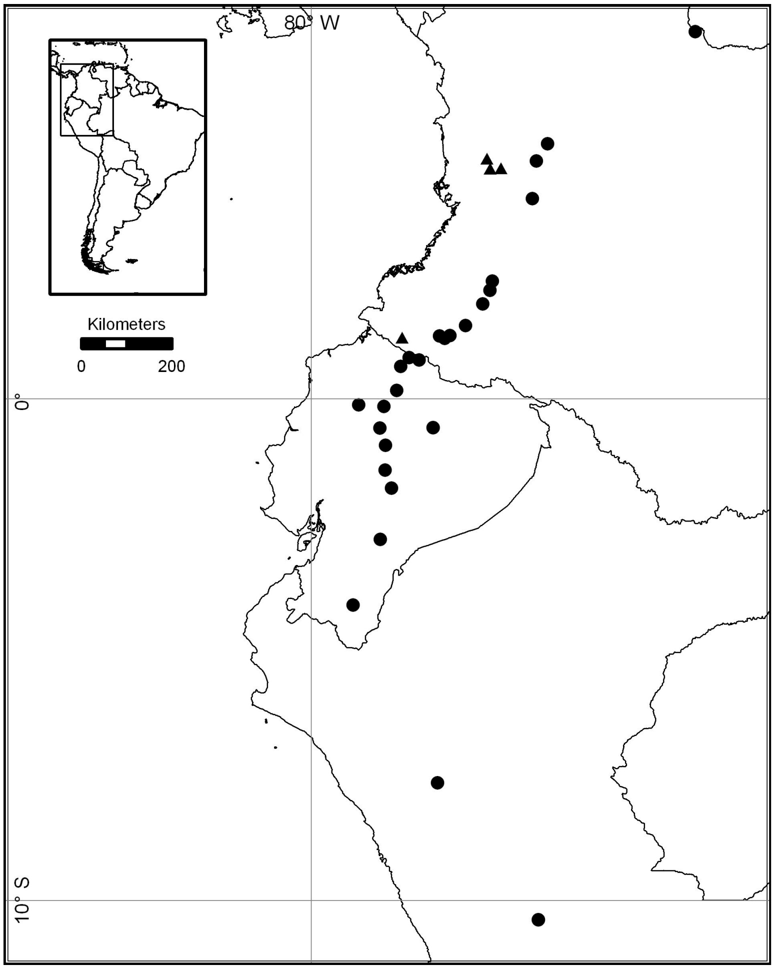


Fig. 16. Illustration of *Disterigma chocoanum*. **A.** General view; **B.** Branch showing apparently distichous leaves, the lamina mostly obovate; **C-E.** Examples of leaf variation, C and D are mature branches bearing floral buds and fruits, while E illustrates a young shoot; **F.** Floral bud; **G.** Detail of the differentiated apical bracteoles; **H.** Calyx (bracteoles removed) and corolla; **I.** Longitudinal section of the corolla and of the calyx and inferior ovary; **J.** Adaxial, abaxial, and lateral view of the stamens (A-C, E-J: *P. Pedraza & C. Pedraza 1121*, NY; D: *P. Pedraza & C. Pedraza 1139*, NY).

chartaceous, ovate or elliptic, 0.4–0.8 x 0.8–1.2 mm, marginally eciliate, apically obtuse, abaxially glabrous; pedicel 0.5–1.6 mm long, reduced and hidden by overlapping bracts or occasionally with a portion not completely obscured, glabrate with glandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping entire calyx tube or to part of calyx lobes, covering 36–75% of calyx, transverse-elliptic or ovate, 1.5–2.6 x 2.6–3.2 mm, marginally eciliate, apically obtuse, the surface smooth, abaxially and adaxially glabrous. **Flowers** 4-merous. Calyx aestivation valvate, campanulate, (2.8–)3–3.8 mm long; tube angled, 1.2–1.5 mm long, abaxially glabrous; limb 1.7–2.3 mm long, abaxially and adaxially glabrous; lobes triangular, (1.1–)1.3–2 x 1–1.7 mm, marginally ciliate with eglandular hairs, apically acute; sinuses acute (V-shaped). Corolla reddish, bright pink, or the tube pale pink with darker lobes, thin-fleshy, bistratose, tubular, (5–)5.5–7(–7.5) mm long, 1.5–2.8 mm diam., 1.5–2.8 mm wide at throat, abaxially glabrous, adaxially puberulous with minute hairs; lobes (0.9–)1–1.4 x (0.9–)1.1–1.2 mm, apically acute, adaxially rugose. Stamens 8 (-10), (4.3–)4.8–5.8 mm long, exserted; filaments distinct, straight, obtriangular, (2.5–)3–3.8 mm long, abaxially and adaxially pilulose distally; anthers distinct, papillae only on thecae; thecae 0.8–1.2 mm long, without basal appendages; tubules 2, distinct, (1–)1.2–1.6 mm long, dehiscing introrsely by longitudinal slits, 0.9–1.1 mm long. Ovary 4-locular; style 5.3–7.5 mm long, exserted. **Berry** white, more or less spherical, 7 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo white.

Distribution and ecology. *Disterigma chocoanum* is known from the Colombian Cordillera Occidental (Map 5). It grows in the humid premontane and montane cloud forests around Barbacoas (Nariño), Serranía de los Paraguas (Valle del Cauca/Chocó), and on the nearby road to San José del Palmar



Map 5. Geographic distribution of *Disterigma chocoanum* ▲ and *D. codonanthum* ●.

(Chocó), between 1185-2800 m . Flowering specimens have been collected throughout the year, except for the months of February and September, and fruiting specimens in April and July. Bumblebees have been seen visiting this species (*P. Pedraza & C. Pedraza 1121*).

Etymology. This species is named after the Chocó biogeographic region, where it occurs.

Specimens examined. COLOMBIA. Cauca: 2000 m, 1851-1857 (fl), *Triana 2658 p.p.* (NY). **Chocó:** km 55 de la carretera Ansermonuevo-San José del

Palmar, 1700-1950 m, 19 Mar 1980 (fl), *Lozano & Díaz 3189* (COL); 10 km towards San José del Palmar from the Valle-Chocó border, 1524-2050 m, 15 May 1984 (fl), *Luteyn et al. 10517* (COL, NY); Mun. San José del Palmar, vereda Río Negro, Cerro del Torrá, 1900 m, 18 Aug 1988 (st), *Ramos & Silverstone-Sopkin 1354* (NY), 1870 m, 6 Jan 1984 (fl), *Silverstone-Sopkin et al. 1551* (NY), 2500 m, 12 Jan 1984 (fl), *Silverstone-Sopkin et al. 1777* (COL), 2730 m, 13 Jan 1984 (fl), *Silverstone-Sopkin et al. 1799* (NY), 1920-1950 m, 8 Aug 1988 (fl), *Silverstone-Sopkin et al. 4221* (NY), 2730 m, 15 Aug 1988 (fl), *Silverstone-Sopkin et al. 4423* (NY), 2500-2550 m, 17 Aug 1988 (fl), *Silverstone-Sopkin et al. 4461* (NY), 2700-2800 m, 21 Aug 1988 (fl), *Silverstone-Sopkin et al. 4644* (NY). **Nariño:** Mun. Barbacoas, corregimiento Junín, 1300 m, 8 Nov 1991 (fl), *Guerrero 204* (HUA, PSO), 1300 m, 16 Jun 1988 (fl), *Salazar de Benavides 9963* (NY, PSO); Mun. Barbacoas, about 0-3 km NW of Barbacoas, 1185 m, 7 Oct 1997 (fl), *Luteyn et al. 15197* (COL, NY). **Valle del Cauca:** Mun. El Cairo, corregimiento El Boquerón, vereda Las Amarillas, Serrania de los Paraguas, along road to Cerro Inglés, 1750-2050 m, 13 May 1988 (fl), *Luteyn et al. 12297* (NY); Mun. El Cairo, km 60-62 road Ansermonuevo-San José del Palmar, 1870-1950 m, 19 Apr 1979 (fl, fr), *Luteyn et al. 7275* (CAS, NY, QCA), 1870-1950 m, 19 Apr 1979 (fl), *Luteyn et al. 7283* (NY), *Luteyn et al. 7294* (AAU, COL, CUVC, NY); 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-Gensini 12643* (AAU, COL, CUVC, MO, NY); Mun. El Cairo, Serranía de los Paraguas, Cerro Inglés, 2300-2400 m, 28 Dec 1986 (fl), *Silverstone-Sopkin et al. 2720* (NY). **Valle del Cauca/Chocó:** Alto de Galápagos, carretera Ansermonuevo-San José del Palmar, 2100 m, 27 Aug 1976 (fl), *Forero et al. 2191* (COL, MO), 2000 m, 27 Apr 1989 (fl), *Luteyn et al. 12693* (NY), 2070 m, 24 Jul 2004 (fl, fr), *P. Pedraza & C. Pedraza 1139* (COL, CUVC, HUA, MO, NY). **Without department:** s.d. (fl), *Lehmann k177* (K).

Disterigma chocoanum is easily distinguished because its leaves are apparently distichous and often patent; the lamina is obovate with attenuate base and obtuse apex; the corollas are tubular, pink, and puberulous inside; the filaments are much broader distally (obtriangular) where they have the same width of the anther; and the berries are white. Although the obovate leaves make this species unmistakable, it may look similar to sterile material of *D. dumontii,* from Nariño, bearing obovate leaves instead of the most characteristic ovate shape. *Disterigma dumontii* differs from *D. chocoanum* by usually having narrower leaves [(0.1-)0.2-0.4(-0.6) mm vs. (0.3-)0.4-0.6 mm respectively], by corollas campanulate and dark red, and by having filaments elliptic.

Local names and uses. This species is known as “Los reales” in Carchi (Ecuador), and as “Chaquilulo” in Nariño (Colombia).

10. Disterigma codonanthum S. F. Blake, J. Washington Acad. Sci. 16: 363. 1926. Type. Ecuador. Tungurahua: [Chimborazo: Mount Mulmúl], s.d. (fl), *Spruce 5138* (holotype, GH; isotypes, BM, CGE, E, fragment F, G, K n.v., fragment L, NY, fragment NY ex G, OXF, P, fragment US ex GH). Photo F neg. 8623 ex G, photo NY neg. 9887 ex NY. The K sheet was not found.

Terrestrial **shrubs**, prostrate and decumbent, often forming dense cushions, or erect, 0.1–1 m tall. Young branchlets ridged, more or less smooth, pubescent or puberulous, the hairs eglandular, light brown, the mature branches indumentum similar but glabrate or puberulous. **Leaves** 9–12 per cm, spirally arranged, ascending; petiole 0.6–2 mm long, glabrate, the hairs eglandular; lamina elliptic or lanceolate, 0.4–1.4 x (0.1–)0.2–0.6 cm, basally attenuate or less often cuneate, marginally crenulate, apically ciliolate with eglandular hairs, apically acute or blunt acute, adaxially glabrous or glabrate with eglandular hairs over midvein (especially in young leaves), abaxially glabrate with minute and deciduous glandular hairs, the venation obscure or hyphodromous on both sides, the midvein adaxially impressed and abaxially raised. Axillary **solitary flowers** and very rarely 2–3-flowered cymes; bracts 6–11, chartaceous, ovate or transverse-elliptic, 0.4–2.2 x 0.6–3.2 mm, marginally eciliate, apically obtuse, abaxially glabrous; pedicel 1.2–2.5 mm long, reduced and hidden by overlapping bracts or rarely with a portion not completely obscured, glabrous or glabrate with eglandular or glandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping entire calyx tube or to part of calyx lobes, covering 36–80% of calyx, ovate or elliptic or transverse-elliptic, 2–4.3 x 3–5.2 mm, rarely marginally ciliolate with eglandular hairs, apically obtuse, the surface softly longitudinally striate (rarely smooth in few herbarium specimens), abaxially and adaxially glabrous. **Flowers** 4-merous (one flower seen with a 5-merous corolla). Calyx aestivation valvate, campanulate, (4–)4.5–5.5 mm long; tube angled, (1–)1.5–2.5 mm long, abaxially glabrate with glandular hairs; limb (2.8–)3–3.5 mm long, abaxially glabrate, with eglandular or glandular hairs, adaxially glabrous; lobes triangular, (2–)2.3–3 x (1.5–)1.9–2.7 mm, rarely marginally ciliolate with eglandular hairs, apically acute; sinuses acute (V-shaped). Corolla light green, often suffused with brick-red distally or rarely completely brick-red, thick-fleshy, bistratose, campanulate, (5.2–)6.7–10(–10.5) mm long, 6.5–9.5 mm diam., 6.5–9.5 mm wide at throat, abaxially glabrate with glandular hairs, adaxially glabrous; lobes (1.4–)2–3 x 2–4 mm, apically acute, adaxially rugose. Stamens 8 (10 in the 5-merous corolla), (4.7–)5.3–7.5 mm long, included (the tips exerted in few herbarium specimens); filaments distinct, straight or rarely geniculate, broader at base, (2.8–)3.5–5 mm long, abaxially and adaxially glabrate or puberulous; anthers distinct, papillae on both thecae and tubules; thecae, (1.4–)1.6–2.1 mm long, without basal appendages; tubules 2, distinct, 1.3–2.1 mm long, dehiscing apically by oblique pores, 0.4–0.7 mm long. Ovary 4-locular; style (5.5–)6–7.7 mm long, included (exserted in few herbarium specimens). **Berry** white, more or less spherical, 7.5–10 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo white.

Distribution and ecology. *Disterigma codonanthum* is known from scattered localities throughout all the three cordilleras in Colombia and from north to south in the Ecuadorian Andes (Map 5). In Peru this species is very rare and it is only known from few collections from the north and center of the country. The species is mainly found at high altitudes between 2700-3800 m, both in humid, dry, grassy, or shrubby páramos and subpáramos, and less often in montane cloud forests. Flowering specimens have been collected throughout the year; fruiting specimens have been collected year-round except for the months of January, June, and October.

Etymology. The name of this species makes reference to its campanulate corollas (*kodono* is a Greek word for bell).

Representative specimens examined. COLOMBIA. Caldas: PNN Los Nevados, en borde del Río Barbo, 3480 m, May 2004 (fl, fr), *C. Pedraza & Lizcano 17* (COL, HUA, CUVC, NY); Páramo de las Letras, en la carretera entre Manizales y Mariquita, antes del PNN los Nevados, 3370 m, 2 Jul 2004 (fl, fr), *P. Pedraza & C. Pedraza 1041* (COL, CUVC, FMB, HUA, NY). **Cauca:** Páramo de las Papas, entre Letreros y Santo Domingo, 3350 m, 15 Sep 1958 (fl), *Idrobo et al. 3340* (COL); Páramo de las Papas, filo de las colinas entre el Boquerón y el Cerro de los Remedios, 3330-3460 m, Sep 13 1958 (fl), *Idrobo et al. 3304* (COL); Páramo de Las Papas, entre El Boqueron y La Hoyola, camino San

Agustin-Valencia, 3200-3510 m, 7-27 Sep 1958 (fl), *Idrobo et al. 3079* (COL); Mun. Coconuco, PNN Puracé, 2050 m, 30 Jul 1980 (fl), *Lozano 3029* (COL)**,** 2987 m, 4 Mar 1979 (fl, fr), *Luteyn & Lebrón-Luteyn 6928* (CAS, COL, NY); Mun. Puracé, Valle del Paleterá, km 55 vía Itsnos, cerca del Valle de los Frailejones, 9 Aug 2004 (fl), *P. Pedraza & Gómez 1249* (COL, NY). **Nariño:** Mun. Pasto, SFF Volcán Galeras, 3500 m, 13 Nov 1982 (fr), *Albert de Escobar & Salazar de Benavides 2961* (HUA), 18 Sep 1957 (fl), *H. G. Barclay 4619* (COL), 31 Oct 1999 (fl), *P. Pedraza & Alvear 656* (COL), 3000-3600 m, 30 Aug 1999 (fl), *B. R. Ramírez 12357* (PSO), 3300 m, 20 Sep 1983 (fl, fr), *Salazar de Benavides 4250* (PSO), 3800 m, 12 Mar 1984 (fl), *Salazar de Benavides 4608* (COL, MO, PSO), 2800-3300 m, 17-18 Jul 2003 (fl), *N. R. Salinas 244* (COL, NY); Mun. La Cruz, Alto de Ledezmas, Volcan doña Juana, 3400 m, Sep 1997 (fl, fr), *Bravo 36* (COL); Sumaco, Jun 1865 (fl), *Isern 548* (MA); Mun. Pasto, Serranía de Morasurco, NE de la ciudad de Pasto, 3400-3450 m, 19 Feb 1998 (fl, fr), *B. R. Ramírez 11144* (PSO); Mun. Pasto, Volcán Galeras, vereda San Felipe, Quebrada Mijitayo, 3000-3300 m, 1 Mar 1992 (fl), *B. R. Ramírez & Guayal 4601* (HUA); Mun. Pasto, Serranía de Morasurco, Páramo de Tacines, 3200 m, 17 Oct 1986 (fl), *Salazar de Benavides 6957* (PSO). **Norte de Santander:** Mun. Toledo, Páramo de Santa Isabel, Finca Santa Isabel, 2900 m, 3 Nov 1994 (fl), *Orozco et al. 2982* (COL). **Quindio:** Mun. Pijao, Páramo de Chili, above finca Maizopolis, 3550 m, 18 May 1989 (fl, fr), *Luteyn et al. 12959* (COL, CAS, MO, NY).

ECUADOR. Azuay: Sevilla de Oro, 2730-3030 m, 14 Aug 1945 (fl, fr), *Camp E-4717A* (CAS, F, GH, MO, NY, US), 2720-3030 m, 14 Aug 1945 (fl), *Camp E-4717B* (F, GH, MO, NY, US), 3700 m, 29 Jun 1947 (fl), *Harling 1282, 1283* (S), 3000-3200 m, 13 Sep 1976 (fl), *Ollgaard & Balslev 9446* (MO, NY, S); Páramo del Castillo, trail between Sevilla de Oro and Méndez, 3353 m, 21 Aug 1945 (fl), *Camp E-4869* (NY), 3460 m, 17 Dec 1944 (fl), *Camp E-1632* (NY, US); slopes of Huagrarancha, S of El Pan, 3140-3350 m, 8 Jul 1943 (fl), *Steyermark 53436* (A, F, NY). **Carchi:** Tulcán-Maldonado road, 21-26 km W of Tufiño, 3630 m, 14 Apr 1978 (fl), *Luteyn & Lebrón-Luteyn 5757B* (NY); Tulcán-Maldonado road, 50-53 km from Tulcán, 3200-3350 m, 1 Aug 1976 (fl, fr), *Ollgaard & Balslev 8314* (MO, NY); Espejo, camino Libertad-Morán, nacimiento del Río Morán al NW de la Reserva Ecológica El Angel, 3400 m, 2 Nov 1993 (fl), *W. Palacios 11789* MO, NY); Páramo del Angel, carretera Tulcán-Maldonado, 3400 m, 18 Dec 2003 (fl, fr), *P. Pedraza & C. Pedraza 997* (COL, QCA, NY); Maldonado-Tulcán road, 3500 m, 30 Sep 1981 (fl), *Werling & Leth-Nissen 12* (GH, NY, QCA, QCNE). **Chimborazo:** betwen Pungo de Castillo and Pungo de Timarán-Yacu, 3650 m, 8 Mar 1944 (fl), *Acosta-Solis 7642* (F, NY). **Cotopaxi:** 52 km E of San Miguel de Salcedo, 3300 m, 23 Jul 1982 (fl), *Clemants et al. 2122* (NY, QCA), *2116* (NY, QCA, QCNE). **Imbabura:** trail between Toldadas and Río Arturo, E of Volcán Cayambe, 3030 m, 15 May 1944 (fl, fr), *Drew E-223* (MICH, NY, US); Mojanda, about 10 km SSW of Otavalo, 2900-3150 m, 12 Dec 1966 (fl), *Sparre* 13500 (S); trail between Río Clavadero and Las Toldadas, E of Cayambé, 3500 m, 27 Jul 1944 (fl), *Wiggins 10503* (DS). **Loja:** PN Podocarpus, trail to El Mirador, 3020-3160 m, 2 Nov 2000 (fl), *Jørgensen et al. 2177* (NY); PN Podocarpus, Cerro Toledo around radio station, 3400-3450 m, 26 Feb 1985 (fl), *Ollgaard et al. 58153* (NY, MO). **Morona-Santiago:** Alao-Huamboya trail, vicinity of La Magdalena, 3550-3700 m, 7 May 1982 (fr), *Ollgaard et al. 38336* (MO, NY, QCA). **Napo:** near Salcedo (San Miguel), Salcedo-Napo road, 3200 m, 4 Feb 1977 (fl, fr), *Boeke 882* (NY, US), 3380 m, 12 May 1997 (fl), *Luteyn & Fuller 15117* (COL, NY, TEX); Cordillera de los Llanganates, NE side of Laguna Encantada, 3430 m, 16 Mar 1983 (fl), *Holm-Nielsen et al. 41864* (MO); Cordillera de los Llanganates, Cerro Negro, 3440 m, 15 Mar 1983 (fl), *Holm-Nielsen et al. 41736* (MO, NY); near Cerro Sumaco, 3700 m, 24 Apr 1979 (fl, fr), *Holm-Nielsen et al. 17130* (NY, QCA), 3750 m, 25 Apr 1979 (fl), *Holm-Nielsen et al. 17228,* (NY, QCA), 3750 m, 5 May 1979 (fl), *Madison 6937* (NY, SEL), 3350 m, 5 May 1979 (fr), *Holm-Nielsen et al. 17970*

(NY, QCA); alrededores de la Laguna de Papallacta, 3300 m, 12 Dec 2003 (fl, fr), *P. Pedraza & C. Pedraza 966* (COL, MO, NY, QCA, QCNE); Quijos Cantón, Reserva Ecológica Antisana, road Pifo-Papallacta, Laguna Miguacocha-Río Tumiguina, 3420 m, 25 Jul 1998 (fl), *H. Vargas et al. 1971* (MO, QCNE). **Napo/ Pastaza:** ENE of Volcán Cayambe, 3240 m, 12 Aug 1961 (fl), *Cazalet & Pennington 5547* (B, CAS, NY, US). **Pichincha:** W slopes of Pichincha and Tablahuasi, 12 Jul 1931 (fl), *Benoist 4590* (L, NY); Corredor La Cocha, near San Juan (via Chiriboga), 3360 m, 17 Aug 1976 (fl), *Dávalos et al. 8* (NY, QCA); Volcán Atacazo, W slope, 5-17 km from San Juan, 2750-2850 m, 25 Aug 1980 (fl), *Holm-Nielsen & Azanza 25094* (NY, QCA), *25113* (MO, NY, QCA); Yanacocha, Volcán Pichincha, 8 Apr 1978 (fl), *Jaramillo 219* (NY, QCA), 3500 m, 8 Apr 1978 (fl), *Luteyn et al. 5689* (CAS, F, GB, NY, QCA, TEX, US); Quito-Chiriboga road, entre La Cocha y San Juan, 3360 m, 17 Aug 1976 (fl), *Temple 393* (L). **Tungurahua:** Páramo de Minza, 3800 m, 10 Apr 1939 (fl, fr), *Penland & Summers 390* (F, GH, NY). **Without province:** s.d. (fl), *Isern 15, 16* (MA).

PERU. Pasco: Prov. Oxapampa, distrito Huancabamba, PN Yanachaga-Chemillén, Abra Yanachaga, 18 Feb 2005 (fl), *E. Ortiz et al. 322* (HOXA, HUSA, MO, NY), 2900 m, 3 Aug 2005 (fl, fr), *E. Ortiz & Francis 723* (HOXA, MO, NY, USM). **San Martín:** Prov. Mariscal Cáceres, Pampa de Cuyes, 25 Jul 2000 (fl, fr), *B. León & Young 4552* (USM).

Disterigma codonanthum is characterized by its leaves marginally crenulate, softly longitudinally striate differentiated apical bracteoles, its light green campanulate corollas often heavily suffused with brick-red, adaxially glabrous, and by its tubules dehiscing by oblique terminal pores. The filaments of *D. codonanthum* are straight throughout its entire range, except for *Luteyn 5757B*, *Dávalos 8*, *León 4552*, and *Jørgensen 2177*, which have flowers either with some filaments straight and others softly geniculate, or flowers with all the filaments

Table 11. Summary of differences between *Disterigma codonanthum*, *D. pernettyoides,* and *D. empetrifolium*

Character	*D. codonanthum*	*D. pernettyoides*	*D. empetrifolium*
Distribution	Colombia through central Peru (Pasco)	Central Peru (Junín) through Bolivia	Colombia through Bolivia
Leaf base	Mostly attenuate or some cuneate	Obtuse	Attenuate
Differentiated apical bracteoles	Softly longitudinally striate (rarely smooth in pickled)	Smooth	Smooth
Corolla shape & color	Campanulate & light green	Campanulate & white	Urceolate & pink
Corolla length	(5.2-)6.7-10(-10.5) mm	(10-)11.5-17 mm	6-10.7(-12) mm
Corolla diam. at throat	6.5-9.5 mm	5.8-8.7 mm	2.5-3 mm (1.7 mm in dry)
Corolla lobes length	(1.4-)2-3 mm	2.8-4 mm	0.7-15 mm
Stamen filaments	Straight & rarely softly geniculate	Softly geniculate	Strongly geniculate & rarely straight
Anther dehiscence	Oblique pores 0.4-0.7 mm long	Longitudinal slits 0.9-1.5 mm long	Longitudinal slits 0.4-1 mm long

geniculate. Although rare, this polymorphism is also present in the type collection; however, it is possible that the soft curvature of the filaments could have been lessen during the preparation of the herbarium specimens, and therefore so infrequently unobserved. This polymorphic character is of especial interest because it also occurs in *D. empetrifolium*, a species that is thought to be closely related to *D. codonanthum*. These two taxa share many reproductive characters with another geniculate taxon, *D. pernettyoides* (e.g., solitary flowers, very rarely few cymes or fascicles, similar stamens, white berries, white seed embryos, etc.), and the narrow-leaved collections of all of them are practically indistinguishable from each other when sterile. Nevertheless, they can be easily distinguishable when flowering and the major differences between them are summarized in Table 11.

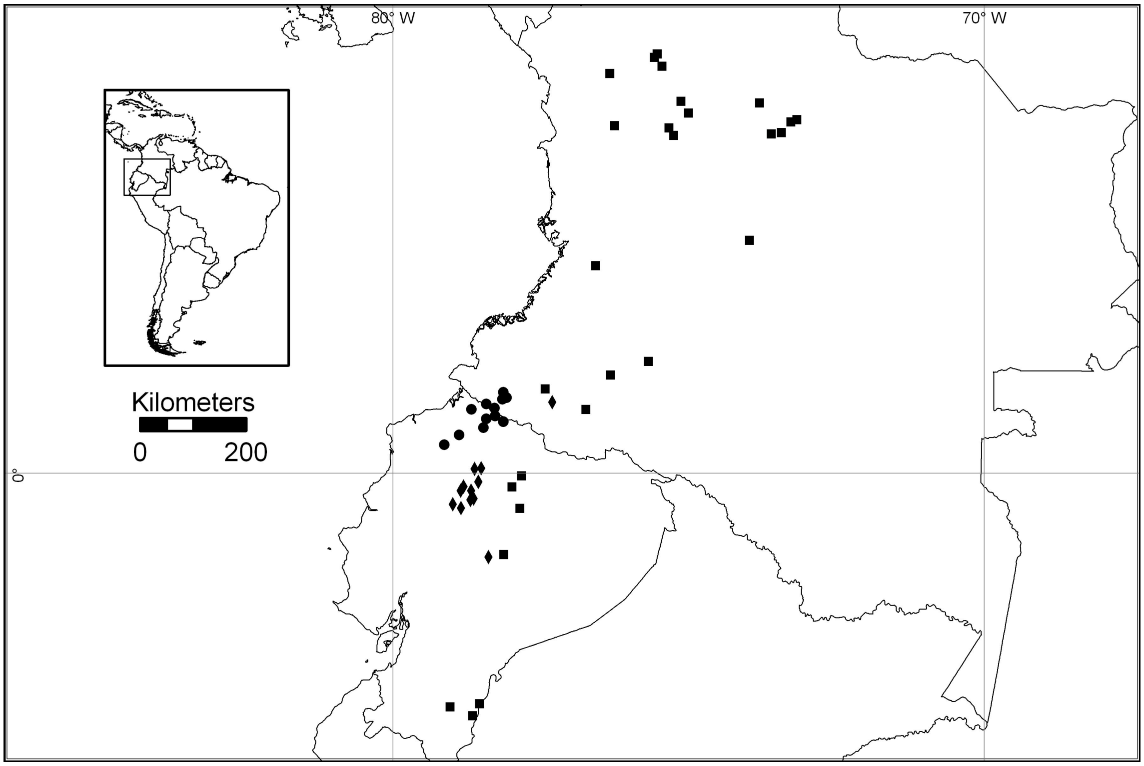
11. Disterigma cryptocalyx A. C. Sm., Contr. U.S. Natl. Herb. 29(8): 355. 1950. Type. Colombia. Huila: W slope of the Cordillera Oriental, between Gabinete and Andalucia, 2200-2300 m, 24-25 Mar 1940 (fl), *Cuatrecasas 8675* (holotype, US; isotype, COL). Photo NY neg. 13025 ex US.

(Fig. 10 D)

Epiphytic or terrestrial **shrubs**, scandent or erect, 0.5–2 m tall. Young branchlets ridged or not ridged, more or less smooth, villous, the hairs eglandular and brown, the mature branches indumentum similar but glabrate. **Leaves** 1–4 per cm, apparently distichous, diffuse or patent; petiole 1–2.8 mm long, puberulous, the hairs eglandular; lamina ovate or narrowly elliptic, 1.2–3.4 x (0.3–)0.7–1.7 cm, basally obtuse or cuneate, marginally entire, apically ciliolate with eglandular hairs (especially in young leaves), apically acute or acuminate, adaxially and abaxially glabrate with eglandular hairs, the venation adaxially hyphodromous with the midvein impressed, abaxially 3-nerved with the midvein raised. Axillary **solitary flower**s and rarely 2 -flowered fascicles; bracts 8–11, chartaceous, elliptic, suborbicular or transverse-elliptic, 1.2–4.4 x 2–6 mm, marginally eciliate, apically obtuse, abaxially glabrous or glabrate with glandular hairs; pedicel 0.8 mm long, reduced and hidden by overlapping bracts, glabrous or glabrate with glandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, extending beyond calyx 2.5–4.0 mm (covering 100% of calyx), obovate or broadly elliptic, (5.2–)6–9 x 5.2–6.3 mm, marginally eciliate, apically obtuse (and usually splitting), the surface smooth, abaxially glabrous or sometimes glabrate with glandular hairs, adaxially glabrous. **Flowers** 4-merous. Calyx aestivation valvate, campanulate or cylindric, 2.8–3.6(-4.5) mm long; tube weakly angled, 1.5–1.8 mm long, abaxially glabrate with glandular hairs; limb 1–1.7(–2.5) mm long, abaxially glabrate or apically puberulous, the hairs minute, eglandular, and deciduous, adaxially glabrous; lobes triangular, 1–1.7(–2) x 1.4–2 mm, marginally eciliate, apically acute; sinuses acute (V-shaped). Corolla pink and white or sometimes light green and white, thin-fleshy, bistratose, urceolate (inflated at the middle or more distally), (6.8–)7.5–10.7 mm long, 4.8–6.5 mm diam. (4.0 mm in dry), 3–3.5 mm wide at throat (2.4 mm in dry), abaxially glabrate with glandular hairs, adaxially glabrous; lobes 1.2–2.8 x 1.2–2.5 mm, apically acute, adaxially rugose. Stamens (7-)8, 6–8(–10) mm long, included; filaments distinct, straight, broader at base, 3.6–4(–7) mm long, abaxially pilulose, adaxially glabrate; anthers distinct, papillae only on thecae; thecae 1.6–2.1 mm long, without or sometimes with basal appendages; tubules 2, (2–)2.4–2.8 mm long, dehiscing introrsely by longitudinal slits, (0.8–)1–1.7 mm long. Ovary 4-locular; style 7.2–9 mm long, exserted (the style many times remain enclosed by the enveloping bracteoles after the corolla is shed; when the fruit is maturing it falls off and the bracteoles spread out). **Berry** white, more or less spherical, 7–9 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo white.

Distribution and ecology. Although not very abundant, *Disterigma cryptocalyx* is known from localities throughout the three cordilleras in Colombia and from scattered localities in the Ecuadorian Andes (Map 6). The species is mainly found between 1000-2750 m, in both primary and secondary vegetation within the premonate and montane cloud forest. Flowering specimens have been collected throughout the year; fruiting specimens have been April, August, and November.

Etymology. The name of this species makes reference to the long bracteoles that hide the calyx.



Map 6. Geographic distribution of *Disterigma cryptocalyx* ■*, D. dendrophilum* ◆, and *D. dumontii* ●.

Representative specimens examined. COLOMBIA. Antioquia: Mun. San Luis, vereda Manizales, vía a San Carlos, Río Dormilón, 1440 m, 26 Jun 1987 (fl), *Callejas et al. 4311* (HUA, MO); Mun. Yarumal-Briceño vía Santa Ana-Briceño, 1710-1980 m, 18 Sep 1992 (fl), *Gómez et al. 785* (HUA, NY), 27 Mar 1993 (fl), *Gómez et al. 890* (HUA, NY), 13 Aug 1992 (fl, fr), *Gómez & Callejas 780* (NY); 4 Jun 1993 (fl), *Gómez & Callejas 920* (HUA, NY); Páramo de Sonsón, 3000 m, 26 Jan 1945, *Hno. Daniel 3435* (COL, MEDEL, NY); Mun. Yarumal, Yarumal-Ventanas road junction with Santa Ana-Briceño turn-off, 1800-2000 m, 31 Oct 1996 (fl), *Luteyn et al. 14993* (NY); Mun. Frontino, corregimiento Nutibara, Nutibara-La Blanquita road, region Murrrí, alto de Río Cuevas, 1700-1800 m, 19 Apr 1988 (fl), *Luteyn et al. 12085* (NY), 1900-2000 m, 21 Apr 1988 (fl), *Luteyn et al. 12167* (COL, GB, NY, S, US), 7 Jun 1989 (fl), *Luteyn & Sylva 13280* (COL, NY); Mun. La Unión, vereda Santa Cruz, La Unión-Sonsón road, S of La Unión, 2360 m, 6 Apr 1988 (fl), *Luteyn et al. 11910* (K, NY); Medellín-Sonsón road, NE of Sonsón towards Argelia, 2440-2530 m, 27 Mar 1979, *Luteyn & Lebrón-Luteyn 7156* (CAS, COL, MO, NY); Mun. Yarumal, verada El Cedro, sector Alto de Ventanas, 1-3 km de la carretera al Cedro, desde la troncal del Caribe, 2000 m, 9 Jul 2004, *P. Pedraza et al. 1071, 1073* (COL, NY); Mun. Guatapé, ca. 8 km. NNE of Guatapé, vereda Santa Rita, finca Montepinar, 1840 m, 20 Nov 1986 (fl), *Zarucchi 4186* (HUA, K, MO, NY). **Boyacá:** Parte abierta del Cañon de Arcabuco, 2830 m, 28 Aug 1967, *Jaramillo-M. et al. 2970* (COL); region of Mt. Chapon, 2200 m, 23 May 1932, *Lawrence 103* (A, F, NY, US); Arcabuco, La Cumbre, Bosque de Robles, 2300 m, 8 Oct 1980 (fl), *Lozano & Díaz 3713* (COL); Mun. Duitama, Finca la Pradera, vía Duitama-Charalá a 11 Km. de la escuela El Carmen, 2700 m, 22 Mar 1994 (fl), *Rangel et al. 11920* (NY); Los Naranjos, carretera Arcabuco-Villa de Leiva y en la cascada Gachantiva, 2400-2700 m, 13 May 1993 (fl), *Rangel et al. 13209* (COL); Arcabuco, Vereda Piedras Blancas, finca Las Delicias, 2600-2750 m, 12 May 1996, *Rangel et al. 13185* (COL); Vereda El Carare, 3 Aug 1978 (fl), *Snow 23* (COL); Arcabuco, 2650 m, 11 Nov 1965 (fl), *Uribe-Uribe 5466* (COL, L). **Chocó:** alto de La Clara, NW of El Carmen, 2680 m, 29 Feb 1944 (fl), *Core 315* (COL, NY, US); km 125-134 Medellín-Quibdó road, 1158-1463 m, 3 Apr 1979 (fl), *Luteyn & Lebrón-Luteyn 7203* (COL, NY); towards Caicedo, NNE of Carmen del Atrato, 2440 m, 25 May 1988 (fl), *Luteyn & Roldán 12423* (CAS, MO, NY). Huila: comisaría de Caquetá, en Gabinete, 2300-2450 m, 21 Mar 1940 (fl), *Cuatrecasas 8419* (COL, F, US); km 28-32 along road Pitalito-Mocoa, 2100-2240 m, 29 Apr 1979 (fl), *Luteyn et al. 7545* (CAS, COL, F, MO, NY, US). **Meta:** Mun. Acacías, colonia penal y agricola de Oriente, arriba del campamento de La Argentina, 2100 m, 1 Aug 1981, *Jaramillo-M. et al. 7544* (COL). **Nariño:** Sumaco, Jun 1865, *Isern 576* (MA). **Putumayo:** Mun. Mocoa, carretera Sibundoy-Mocoa, localidad el Mirador, 2000 m, 7 Sep 1998, *Mendoza et al. 6456* (FMB, MEDEL); Mun. Mocoa, vereda Medio Afán, arriba del Río Afán, a 2 hrs de Mocoa, 1200-1600 m, s.d. (fl, fr), *J. Ramos et al. 2467* (CUVC, NY). **Santander:** Mun. Charalá, carretera El Carmen-Virolín, 2200 m, 3 Jun 1995 (fl), *J. C. Betancur et al. 6147* (COL, NY); Region about Landazuri, 70 km N of Vélez, Cerro del Páramo, Cerro de Armas, 1900 m, 30 Jun 1944 (fl), *Fassett 25416* (NY, US); Gámbita, El Volcán, 2100 m, 11 Nov 1981 (fl, fr), *Villamil et al. 49* (COL). **Valle del Cauca:** Mun. Cali, Finca Zingara, carretera Cali-Buenaventura, vía a Dapa, corregimiento de la Elvira, 1900 m, 16 Oct 1994 (fl), *Giraldo-Gensini & Olver 490* (NY).

ECUADOR. Napo: Sendero Precooperativa, 2000-2200 m, 9 Sep 1990 (fl, fr), *Jaramillo et al. 12482* (NY); Baeza-Puyo road, near Cosanga, 1890-2073 m, 13 Nov 1996 (fl), *Luteyn et al. 15048* (AAU, COL, E, HUA, MO, NY, QCA), 1830-1920 m, 13 Nov 1998 (fl, fr), *Luteyn & Mogollón 15355* (NY, QCA), 1830-2130 m, 15 Oct 1992 (fl), *Luteyn & Sylva 14692* (CAS, NY, QCNE, US); Oyacachi valley, between Pueblo Viejo and Río Chalpi, 2500 m, s.d. (fl), *Ståhl et al. 3090* (QCA). **Pastaza:** Río Pastaza: 1300 m, Augl 1976 (fl), *Argent 2342* (E); Mera-Río Anzú road, 1400-1450 m, 1 May 1992 (fl), *Luteyn & A. Freire 14582* (NY, US), 1070-1340 m, 14 Nov 1996 (fl), *Luteyn et al. 15055* (NY). **Zamora-Chinchipe:** 10 km E of Paquisha, 1500 m, 13 Apr 1985 (fl, fr), *Harling & Andersson 24101* (GB, NY); Cantón Nangaritza, sector Pachicutza, camino hacia el Hito, 950-1800 m, 4 Dec 1990 (fl), *Jaramillo & Grijalva 13361* (MO, NY, QCA); Loja-Zamora road, km 16, near the pass to Loja, 2700 m, 20 May 1967 (fl), *Sparre 16515* (S).

Disterigma cryptocalyx is characterized by having leaves large (up to 3 cm long and 1.7 broad) and thick-coriaceous; subsessile flowers, with the pedicel reduced (0.8 mm long,) and hidden by numerous and conspicuous overlapping bracts; differentiated apical bracteoles large (up to 9 mm long) and extending well beyond the calyx (> 2.5 mm); urceolate light green or white corollas, very constricted in the throat, and usually with the lobes pink; and by having papillae only on the thecae (Fig. 10 D). The general morphology of *D. cryptocalyx* reminds that of the large-leaved forms of the variable *D. noyesiae*. The size gap between *D. cryptocalyx* and the small-leaved forms of *D. noyesiae* (like the specimens from Munchique and the Tulcán-Maldonado road) may seem significant, but a closer look reveal that they are just miniaturized versions of the same suit of characters. Both species have differentiated apical bracteoles proportionally extending beyond the calyx and even enclosing the basal half of the corolla. However *D. cryptocalyx* can be differentiated from *D. noyesiae* because its bracteoles are numerous (8-11 vs. 5-6, respectively), usually larger [(5.2-)6-9 mm vs. 2.4-6(-7) mm], and extend well beyond the calyx (2.5-4 mm vs. just as long as the calyx or extending up to 2 mm). The differences with *D. appendiculatum* are in Table 8.

12. **Disterigma dendrophilum** (Benth.) Nied., Bot. Jahrb. Syst. 11: 210. 1889. *Vaccinium dendrophilum* Benth., Pl. Hartweg. 219. 1846. Type. Ecuador. Pichincha: Volcán Pichincha, W slopes, woods of Guayán, 1845 (fl), *Hartweg 1204* (holotype, K; isotypes, B†, BM, CGE (x2), fragment F, FI-W n.v., G (x2), NY, fragment NY ex K, OXF, P (x2), W n.v.). Photo NY neg. 13030 ex K, photo F neg. 31962 ex W, photo F neg. 4639 ex B†, photo NY s.n. ex P.

Epiphytic or terrestrial **shrubs**, scandent or erect, 0.5–3 m tall. Young branchlets ridged, more or less smooth, villosulous, the hairs eglandular and brown, the mature branches indumentum similar but glabrate. **Leaves** 4–7 per cm, apparently distichous, diffuse or patent; petiole 0.8–1 mm long, puberulous, the hairs eglandular; lamina elliptic, or sometimes ovate, (0.5–)0.7–1.2 x (0.2–) 0.4–0.6 cm, basally obtuse or cuneate, marginally entire, apically ciliolate with eglandular hairs, apically acute, acuminate, or long-acuminate, adaxially glabrate with minute eglandular and glandular hairs, abaxially glabrate with glandular hairs, the venation adaxially obscure or hyphodromous with the midvein impressed, abaxially obscure. **Inflorescence** axillary, of 2(-3)-flowered fascicles or flowers solitary; bracts 5–8, chartaceous, broadly ovate, suborbicular, or transverse-elliptic, 0.5–1.3 x 0.9–1.6 mm, marginally eciliate, apically obtuse, abaxially glabrous; pedicel 1–2 mm long, evident or at least with a portion of it not completely obscured by overlapping bracts, glabrous or glabrate with glandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping entire calyx tube or to lower half of calyx lobes, covering 50–62(–100)% of calyx, suborbicular or reniform, 2–3 x 2.8–3.2 mm, marginally eciliate or rarely ciliolate with minute eglandular hairs, apically obtuse, the surface smooth, abaxially and adaxially glabrous. **Flowers** 4-merous. Calyx aestivation valvate, campanulate, 2.4–3.6 mm long; tube angled, 1.2–1.7 mm long, abaxially glabrous or glabrate with glandular hairs; limb 1–2 mm long, abaxially and adaxially glabrous; lobes triangular, 0.8–1.6 x 0.9–1.2 mm, marginally eciliate, apically acute, sinuses acute (V-shaped). Corolla pink or white, chartaceous, bistratose, tubular (sometimes a little constricted at the throat but not inflated; in dry), 4.4–5.6 mm long, 2.4–3 mm diam. (in dry), (1.8–)2–3 mm wide at throat (in dry), abaxially glabrate with glandular hairs, adaxially glabrous; lobes 1–1.6 x 1–1.4 mm, apically acute, adaxially smooth. Stamens 8, (4–)4.4–5 mm long, the tips exserted; filaments distinct, straight, more or less linear with parallel sides, 2.2–2.4 mm long, abaxially pilulose, adaxially glabrate; anthers distinct, papillae only on thecae; thecae (1–)1.2–1.5 mm long, basally appendaged; tubules 2, distinct, (1.3–)1.5–2 mm long, dehiscing introrsely by longitudinal slits, 0.8–1 mm long. Ovary 4-locular; style 4.8–6 mm long, exserted. **Berry** white, more or less spherical, 6–7.5 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo white.

Distribution and ecology. *Disterigma dendrophilum* is mostly found in Ecuador, more specifically in Pichincha (where the type specimen is from), with very few collections made in the provinces of Bolívar, Cotopaxi, and Tungurahua, and only one specimen from southern Colombia (Nariño) (Map 6). This species grows in montane cloud forests between 2000-3200 m. Flowering specimens have been collected in January, April, June-September, November-December, and fruiting specimens in April, August, and November.

Etymology. From the Greek *dendro* (tree) and *philia* (love). The type collection of this species is terrestrial (as many others), therefore it is thought that the name makes reference to the woods of Guayán, where the type was collected.

Representative specimens examined. COLOMBIA. Nariño: Pasto, 17 Jun 1976 (fl), *André 2975 p.p.* (F, NY).

ECUADOR. Bolívar: San Jacinto de la Unión, 2500 m, 14 Aug 1939 (fl), *Asplund 8239* (NY, S). Cotopaxi: Cantón Sigchos, Triunfo Grande, finca del Sr. Galo Roballo, 2427 m, 2 Aug 2003 (fl), *J. Ramos et al. 6816* (NY). **Cotopaxi:** Cantón Sigchos, camino al Río Escaleras, cerca de parcelas del Alisal, 3098 m, 20 Jul 2003 (fl), *J. Ramos et al. 6324* (NY). **Pichincha;** Bosque de Saloya, 1800 m, 5 Sep 1943 (fl), *Acosta-Solis 5658* (F, NY); Quito-Santo Domingo new road, 2700 m, 12 Aug 1976 (fl, fr), *Argent & Burbridge 528* (E, GH, L, MO, NY), 2750-2900 m, 2 Apr 1978 (fl, fr), *Luteyn & Lebrón-Luteyn 5627* (CAS, NY); Santo Domingo-Quito road, 3000 m, 21 Jun 1982 (fl), *Balslev 2758* (B, F, GH, NY), 2591 m, 15 Jan 1945 (fl), *Camp E-1729* (NY); Reserva Floristica-Ecologica Rio

Guajalito, km 59, Quito-Santo Domingo old road, 2200 m, 7 Jun 1991 (fl), *Grijalva 528* (MO, NY), 1800-2200 m, 16 Aug 1985 (fl), *Jaramillo & Zak 8095* (DUKE, F, GB, K, MO, NY, S, TEX, US); old road to Santo Domingo de los Colorados, 2000 m, *Holm-Nielsen et al. 24800* (F, MO, NY), 2438 m, 8 Aug 1978 (fl), *Palser 1* (NY), 2650 m, 24 Dec 2003 (fl), *P. Pedraza & C. Pedraza 1012* (NY, QCA, QCNE), 3200 m, 4 Aug 1980 (fr), *Wunderlin et al. 8712* (L, NY, SEL), 2500 m, 22 Aug 1978 (fl), *Zarucchi et al. 2406* (COL, GH, NY, S, US); below San Juan towards Chiriboga, 2600 m, 2 Aug 1955 (fl), *Asplund 17165* (B, K, L, LL, NY, P, S); Cerro Pugsi, NW slope of Volcán Pichincha, 3020 m, 27 Sep 1980 (fl), *Bleiweiss 1141* (NY); Parroquia Calacali, Reserva Geobotánica Pululahua, 2000-2500 m, 16 Nov 1987 (fl, fr), *Cerón-M. & Cerón 2754* (GB, MO, NY); Parroquia Nanegal, Bosque Protector Maquipucuna, Cerro Sosa, 2375 m, 16 Jul 1992 (fl), *Webster et al. 29458* (NY). **Tungurahua:** Baños, Río Ulba, 2000 m, 14 Jan 1933 (fl), *Heinrichs 210* (NY). **Without province:** Andes of Quito, s.d. (fl), *Jameson 291* (CGE, BM, K, NY, OXF); Andes Ecuatoriales, 2400 m, s.d. (fl, fr), *Jameson 34* (NY); Flora Andium Quitensium, s.d. (fl), *Sodiro 92/26* (F, NY).

Without country. Americae aequinoctialis, s.d (fl), *André 885* (K, NY); Niebli, 17 Jun 1876 (fl), *André 2975* (K); s.d., *Jameson s.n.* (K).

As with other species that share similar leaves and small flowers, the confusion with *Disterigma dendrophilum* has been caused by the introduction of nomenclatural changes based on a restricted number of collections and without the consultation of key type specimens, some of which are of difficult access. *Disterigma dendrophilum* has been associated with species with very different overall morphology, like *D. alaternoides* [*Vacciniopsis tetramera*; see Blake], or more recently with *D. acuminatum* (see Luteyn, 1996; Smith, 1933), with which it shares its small, ovate, and acuminate leaves. The differences between these two species are many, as it has already been discussed in *D. acuminatum*, thus *D.*

dendrophilum is here resurrected. All the possible hybrids between *D.* acuminatum and *D.* cryptocalyx mentioned by Luteyn (1996) are now under *D. noyesiae*. More comparisons with other species with similar leaves are provided in the discussion of *D. staphelioides* and in Table 12 under *D. micranthum*.

Disterigma dendrophilum is characterized by having solitary flowers with the pedicel evident or at least with a portion of it not completely obscured by overlapping bracts; differentiated apical bracteoles often only covering the calyx tube and with the surface smooth; corolla white or light pink, tubular, 4.4-5.6 mm long, and adaxially glabrous; and by having stamens almost as long as the corolla with papillae only on thecae.

Local names and uses. This species has been reported as edible.

13. Disterigma dumontii Luteyn, Brittonia 29(2): 178, fig. 2. 1977. Type. Colombia. Nariño: between Altaquer and Junín, km 129-130, 1130 m, 30 Jan 1976 (fl), *Luteyn* et al. *5093* (holotype, COL; isotypes, DUKE, F, GH, L, NY, fragment NY, US). Photo NY neg. 9888 ex NY.

(Fig. 17)

Epiphytic or terrestrial **shrubs**, scandent. Young branchlets not ridged, more or less smooth, villosulous, the hairs eglandular, brown, the mature branches indumentum similar but glabrate. **Leaves** 5–9 per cm, apparently distichous, mostly diffuse or patent; petiole 0.5 mm long, puberulous, the hairs eglandular; lamina elliptic, less often ovate or obovate, (0.4–)0.5–1.3 x (0.1–)0.2–0.4(–0.6) cm, basally cuneate, marginally entire, apically ciliolate with eglandular hairs (especially in young leaves), apically obtuse or sometimes acute, adaxially glabrous or glabrate with eglandular hairs, abaxially glabrate with glandular hairs,

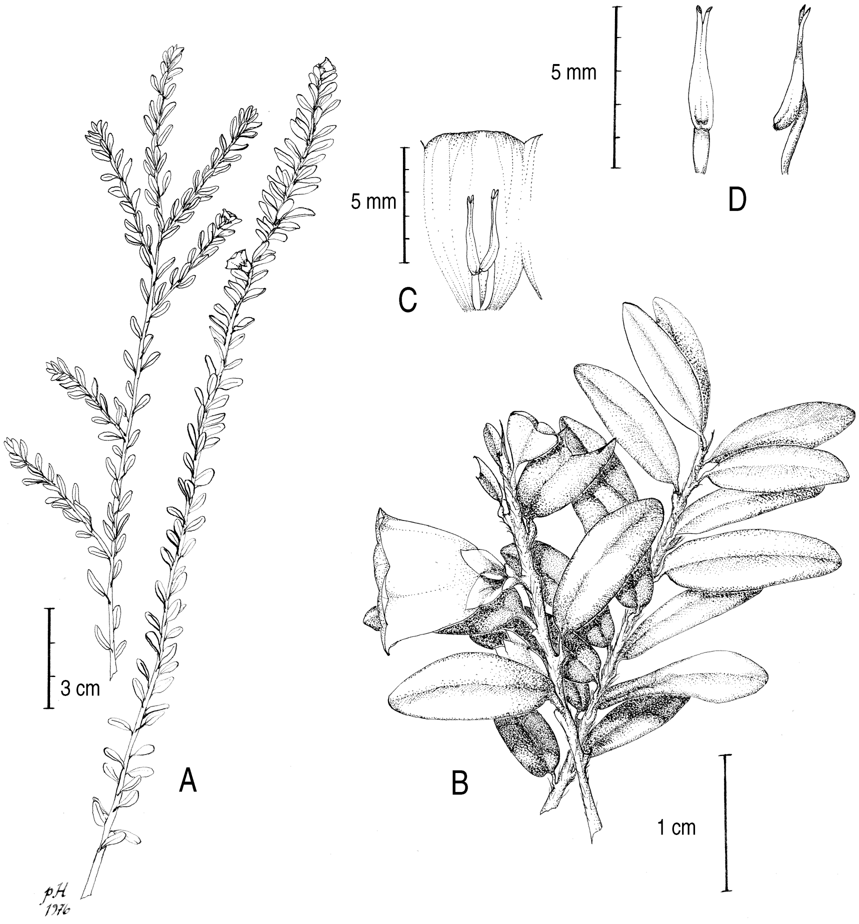


Fig. 17. Illustration of *Disterigma dumontii.* **A.** Branches; **B.** Close up of the branch with a flower, note the short wings on the calyx; **C.** Longitudinal section of the corolla; **D.** Stamens (*Luteyn* et al. *8405*, NY). Modified from Brittonia 29:179, Fig. 2 (1977).

the venation adaxially obscure or hyphodromous with the midvein impressed, abaxially 3-nerved with the midvein raised. Axillary **solitary flowers**; bracts 2–5, chartaceous, ovate, 0.4–0.5 x 0.8–1.2 mm, marginally eciliate, apically obtuse, abaxially glabrous; pedicel 0.8–1.6(–2) mm long, reduced and hidden by overlapping bracts or with a portion not completely obscured, glabrate with minute glandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping the base of calyx tube, covering 12–18(–29)% of calyx, orbicular, transverse-elliptic, or reniform, 1.2–2 x 1.6–2 mm, occasionally marginally ciliolate with minute eglandular or glandular hairs, apically obtuse or truncate, the surface smooth, abaxially and adaxially glabrous. **Flowers** 4-merous. Calyx aestivation valvate, campanulate, 2.8–4 mm long; tube shortly winged, 1.2–1.6 mm long, abaxially glabrate with glandular or eglandular hairs (especially over the wings); limb 1.6–2.4 mm long, abaxially glabrate with glandular hairs, adaxially glabrous; lobes triangular, 1.2–1.6 x 1.6–2.8 mm, marginally ciliate with eglandular hairs, apically acute; sinuses acute (V-shaped). Corolla red, chartaceous, not bistratose, campanulate, 6.4–8.8 mm long, (4.8–)6.4 mm diam., 3.2–4 mm wide at throat, abaxially glabrate with glandular hairs, adaxially glabrous; lobes 1.2–2.4 x 2.8–3.6 mm, apically obtuse and apiculate, adaxially smooth. Stamens (7-)8, (3.6–)4.8–5.6 mm long, included; filaments distinct, straight, elliptic, (1.6–)2 mm long, abaxially puberulous, adaxially pubescent (especially apically); anthers distinct, papillae only on thecae; thecae basally prognathous, 1.6–2 mm long, without basal appendages; tubules 2, distinct, (1.2–)1.6–2.4 mm long, dehiscing apically by oblique pores, 0.3 mm long. Ovary 4-locular; style 5.2–5.6 mm long, included. **Berry** white, hemispherical, 6.8–7.1 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo white?.

Distribution and ecology. *Disterigma dumontii* is found in the Chocó biogeographic region. It is only found on the western slopes of the southernmost department of Colombia, Nariño, and the nearby Ecuadorian provinces of Carchi, Esmeraldas, and Imbabura (Map 6). This species grows between 250-1500 (-1890) m, in very humid tropical rainforests and premontane forests, both in primary and secondary vegetation. Flowering specimens have been collected throughout the year except for October, and fruiting specimens in February, April, May, September, and November.

On one occasion, ants from the subfamily Myrmicinae (*P. Pedraza* & *C. Pedraza 1006*, kindly identified by Roberto Keller) were found nesting in the twigs and leaves of *Disterigma dumontii*.

Etymology. This species was named for the mycologist Kent P. Dumont.

Specimens examined. COLOMBIA. Nariño: Mun. Barbacoas, vereda El Barro, Reserva Natural Río Ñambí, 1300 m, 9 Aug 1992 (fl), *Arias 113* (PSO), 1300-1500 m, 1 Dec 1993 (fl), *Gómez et al. 941* (COL, NY), 1440-1500 m, 5-6 Aug 1997 (fl), *Luteyn et al. 15177* (COL, NY, PSO), 1350-1400 m, 1 Sep 1997 (fl), *Pipoly et al. 21063* (PSO), 1350-1400 m, 5 Sep 1997 (fl), *Pipoly et al. 21316* (PSO), 1380 m, s.d (fl), *N. R. Salinas et al. 368* (NY), 1200-1400 m, 17 Apr 2004 (fl), *N. R. Salinas et al. 495* (COL, NY); Mun. Barbacoas, corregimiento Junín, sitio La Guarapería, a 3 km de Junín, vía Junín-Tumaco, 1100 m, Mar 1995 (fl), *J. L. Fernández et al. 12540* (COL, PSO); vía Tumaco-Túquerres, 2-8 km E de Junín, 1100 m, 26 Jul 1986 (fl), *Gentry et al. 55245* (COL, MO, PSO); Altaquer-Junín road, 7-10 km W of Altaquer, 1250 m, 25 Feb 1979 (fl, fr), *Luteyn & Lebrón-Luteyn 6841, 6850* (COL, NY).

ECUADOR. Carchi: N of San Marcos, 660 m, 17 Jan 1983 (fl), *Barfod 41451* (AAU, NY); San Marcos, along trail leading to Río San Juan, 660 m, 3 Mar 1983 (fl), *Barfod 41627* (AAU, MO, NY, QCA); San Marcos valley, 600 m, 20 Nov 1983 (fl), *Barfod et al. 48820* (AAU, NY); Reserva Indígena Awá, community of Baboso, 1080 m, 10 April 1995 (fl, fr), *H. T. Beck et al. 3069* (NY); embankments along Río Verde, 1890 m, 29 Nov 1987, *Hoover 1962, 1929* (MO); Reserva Indígena Awá, Gualpi Chico, Awá encampment, 1330 m, 17 Jan 1988 (fl), *Hoover et al. 2674* (NY, QCA); Río Gualpi Chico area, 1161-1258 m, 18 Jan 1988 (fl), *Hoover et al. 2596* (QCA), 1161 m, 22 Jan 1988 (fl), *Hoover et al. 3529* (MO, NY, QCA); Reserva Indígena Awá, Trail San Marcos-Gualpi bajo, 800-1000 m, 12 Mar 1988, *Jørgensen et al. 65226* (AAU), 1000 m, 7 Feb 1985 (fl, fr), *Ollgaard et al. 57442* (AAU, NY); Reserva Indígena Awá, Gualpi Medio, 900 m, 21 May 1992 (fl), *Quelal et al. 641* (MO, NY, QCNE). **Esmeraldas:** Reserva Indígena Awá, community of La Unión, 310 m, 10 Jul 1994 (fl), *H. T. Beck et al. 2274* (MO, NY); cantón San Lorenzo, parroquia Alto Tambo, Reserva Indígena Awá, Río Bogotá community, 350-600 m, 11 Feb 2003 (fl), *Clark et al. 7106* (NY); Reserva Cotacachi-Cayapas, La Cascada (Charco Vicente), 250 m, 8 May 1998 (fl), *Cornejo & Bonifaz 6271* (NY); Lita-San Lorenzo road, 10-34 km NW of Lita, 500 m, 12 May 1991 (fl), *Gentry et al. 70010, 70138* (MO, NY, QCNE), 28 Sep 1991 (fl, fr), *Ollgaard 99161* (AAU, NY, QCA, QCNE); Lita-El Cristal road, finca of Dr. Lalama, 13.5 km S of Lita, 1350 m, 2 Nov 1992 (fl, fr), *Luteyn et al. 14728* (CAS, GB, K, MO, MSC, NY, QCA, QCNE), 1350 m, 13 May 1992 (fl, fr), *Luteyn & Quelal 14610* (COL, NY, QCA, S, TEX); Quininde, parroquia Malimpia, Cristóbal Colón, Cooperativa, Tesoro Escondido, camino al Río Gualpi, 500 m, 13 Mar 2004 (fl), *Narváez et al. 1124* (NY); San Lorenzo, Reserva Indígena Awá, 2 km S of Lita-San Lorenzo road, 350 m, 6 Apr 2002 (fl), *Neill e al. 13924* (NY). **Imbabura:** vicinity Río Verde, 5 km SW from Mani, Río Cachaco, 1740 m, 6 Jun 1980 (fl), *Sperling & Bleiweiss 5069* (NY, QCA, QCNE). **Imbabura/Esmeraldas:** carretera Lita-Alto Tambo-San Lorenzo, 800-900 m, 20 Dec 2003 (fl), *P. Pedraza & C. Pedraza 1005* (AAU, COL, MO, NY, QCA, QCNE, US).

Disterigma dumontii is distinguished by leaves apparently distichous and small; calyx tube shortly winged; corolla dark red, campanulate, and adaxially glabrous; anthers basally prognathous; tubules dehiscing by oblique terminal pores; berries white; and by seed embryos white. The similarities of *D. dumontii* with other taxa are discussed in *D. campanulatum* in Table 10.

Local names and uses. In Nariño, Colombia, this plant is known as "Chaquilulo" and its fruits are eaten by local people. In Ecuador it is called "Los Reales" in Carchi.

14. Disterigma empetrifolium (Kunth in Humb., Bonpl. & Kunth) Drude, Nat. Pflanzenfam. 4(1): 52. Aug 1889. *Vaccinium empetrifolium* Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. Pl. 3: 263, pl. 248. 1818. *Metagonia empetrifolia* (Kunth in Humb., Bonpl. & Kunth) Nutt., Trans. Amer. Phil. Soc. N.S. 8: 265. 1843. *Vaccinium penaeoides* Kunth in Humb., Bonpl. & Kunth forma *empetrifolia* (Kunth in Humb., Bonpl. & Kunth) Wedd., Chlor. And. 2: 179. 1857. Type. Ecuador. Pichincha: Volcán Antisana, between Pintag and Pinantura, May (fl), *Humboldt & Bonpland s.n.* (holotype, P-Bonpl.; isotype, B-W 7352-1). Photo NY s.n. ex P-Bonpl. The isotype at B-W is marked with the number 2279, but besides this, it is identical to the holotype.

Vaccinium penaeoides Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. Pl. 3: 264. 1818. *Metagonia penaeoides* (Kunth in Humb., Bonpl. & Kunth) Nutt., Trans. Amer. Phil. Soc. N. S. 8: 265. 1843. *Disterigma penaeoides* (Kunth in Humb., Bonpl. & Kunth) Nied., Bot. Jahrb. Syst. 11: 210. Sep

1889. Type. Ecuador. Tungurahua: Volcán Tungurahua, near Cuchilla de Guandisava, 3100 m, Jun (fl), *Humboldt & Bonpland s.n.* (holotype, P-Bonpl.; isotypes, B†, B-W 7351-1, fragment F ex P, P). Photo F 4641 ex B†, photo NY s.n. ex P. The isotypes at B† and P are marked with the number 3212, but besides this, they are identical to the other type collections.

Vaccinium penaeoides Kunth in Humb., Bonpl. & Kunth var. *penaeoides* forma *densa* Wedd., Chlor. And. 2: 179. 1857, pro syn., invalid name, no type specimen given.

Vaccinium epacridifolium Benth., Pl. Hartweg. 221. 1846. *Vaccinium penaeoides* Kunth in Humb., Bonpl. & Kunth var. *epacridifolium* (Benth.) Wedd., Chlor. And. 2: 179. 1857. *Disterigma epacridifolium* (Benth.) Nied., Bot. Jahrb. Syst. 11: 210. Sep 1889. Type. Colombia. Cauca: in the Andes near Pitayo and the slopes of Volcán Sotará, Oct 1843 (fl), *Hartweg 1212* (holotype, K n.v.; isotypes, B†, BM, C n.v., CGE (x2), G (x2), NY, fragment NY ex K, OXF, P). Photo F neg. 4640 ex B. The K sheet was not found.

Disterigma weberbaueri Hoer., Bot. Jahrb. Syst. 42: 334. 1909, **syn. nov.** Type. Peru. Junín: Prov. Tarma, Huacapistana, 3000-3100 m, Jan 1903 (fl), *Weberbauer 2079* (holotype, B†. Lectotype, here designated, MOL holotype; isolectotype, fragment F ex B, fragment NY ex B). Photo F neg. 4643 ex B, photo NY neg. s.n. ex B.

Disterigma margaricoccum S. F. Blake, Proc. Biol. Soc. Washington 35: 119. 1922. Type. Ecuador. Tungurahua: slopes of Volcán Tungurahua, 3050-3965 m, 8 Mar 1921 (fl, fr), *Popenoe 1287* (holotype, US). Photo NY s.n. ex US.

Disterigma leiopodandrum S. F. Blake, J. Washington Acad. Sci. 16: 363. 1926. Type. Colombia. Cauca: Llano de Paleterá, 2950-3100 m, 15-17 Jun 1922 (fl, fr), *Pennell 6928* (holotype, US; isotypes GH, NY.) Photo NY neg. 9890 ex NY.

(Fig. 18)

Terrestrial **shrubs**, prostrate and decumbent, sometimes forming dense cushions, or erect, up to 0.5 m tall. Young branchlets ridged, more or less smooth, puberulous, the hairs eglandular, light brown or white, the mature branches indumentum similar but glabrate. **Leaves** 4–11 per cm, spirally arranged, ascending or diffuse; petiole 0.5–1.5 mm long, glabrate, the hairs eglandular; lamina often succulent, lanceolate or narrowly elliptic, sometimes ovate or obovate, 0.4–1(–1.2) x 0.1–0.4(–0.6) cm, basally attenuate, marginally crenulate or occasionally entire, sometimes apically ciliolate with eglandular hairs, apically acute, blunt acute, acuminate or rarely subacute, adaxially glabrous or glabrate with eglandular hairs over the midvein of the young leaves, abaxially glabrate with glandular hairs, the venation adaxially and abaxially obscure, sometimes hyphodromous abaxially with the midvein raised. Axillary **solitary flowers** and very rarely 2-flowered cymes; bracts 3–7, chartaceous, ovate or elliptic, 0.5–2.2 x 0.7–2.2 mm, occasionally marginally ciliolate with eglandular hairs, apically obtuse or acute, abaxially glabrous; pedicel 1–5.7(–11) mm long (usually elongating when fruiting), at least with a portion of it not completely obscured by overlapping bracts or sometimes reduced and hidden, glabrate with eglandular hairs or rarely also with glandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping entire calyx tube or to lower half of calyx lobes, covering

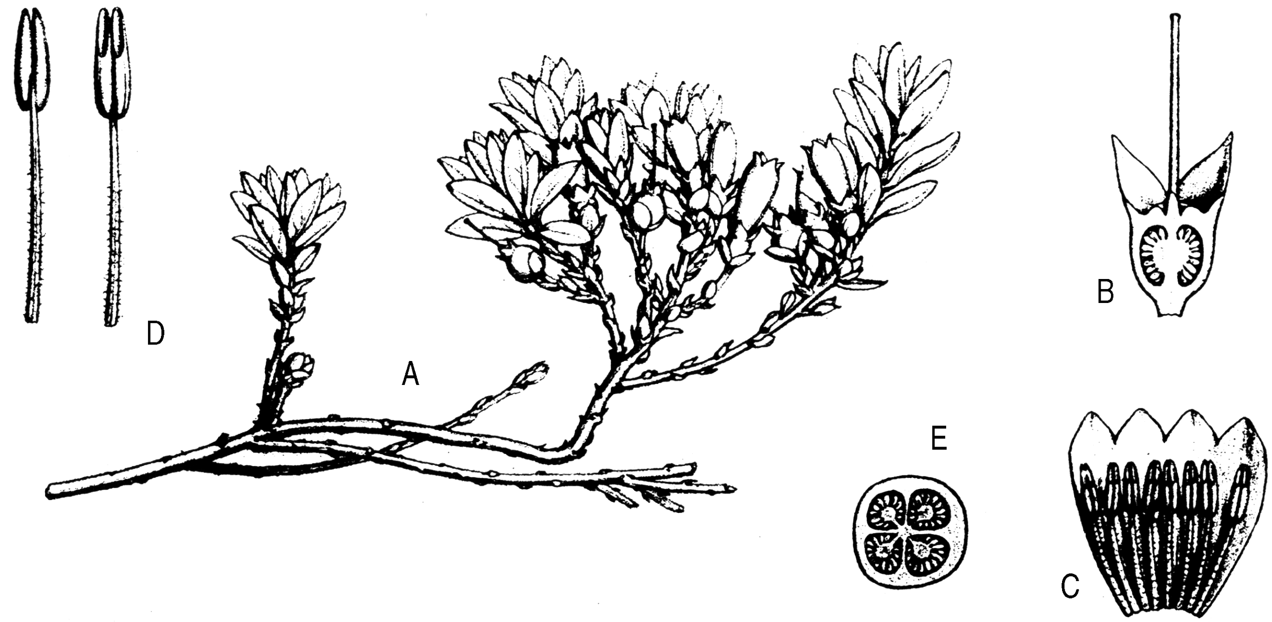
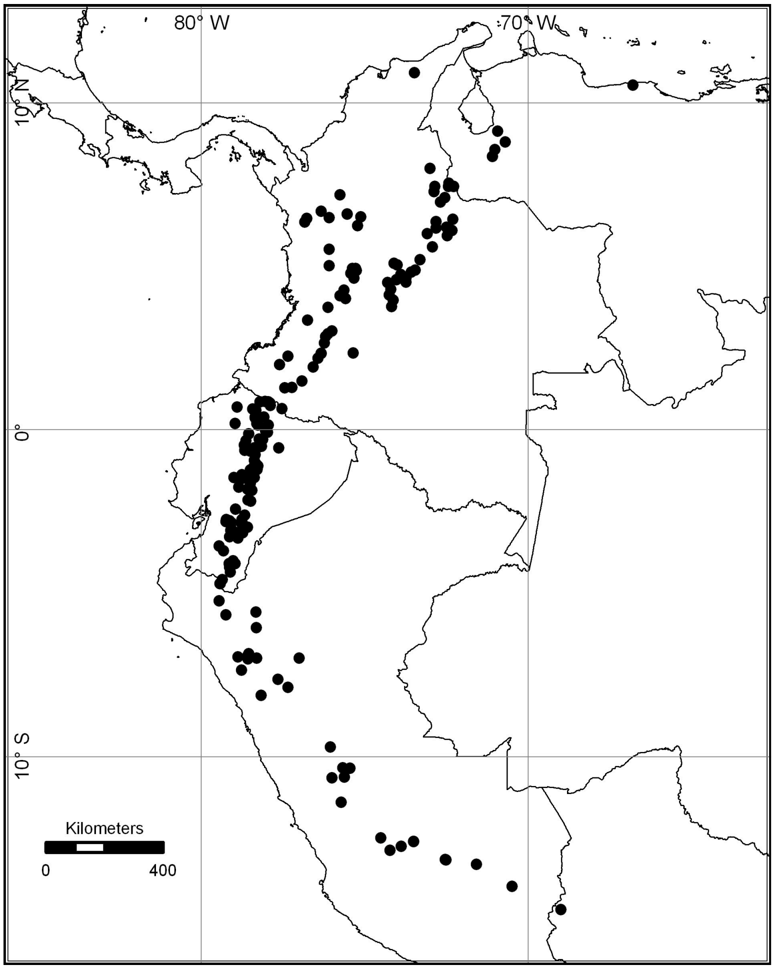


Fig. 18. Illustration of *Disterigma empetrifolium.* **A.** Habit; **B.** Longitudinal section of the calyx and inferior ovary; **C.** Open corolla exposing the stamens; **D.** Adaxial and abaxial views of the stamens; **E.** Transversal section of the ovary. Originally published as *Vaccinium penaeoides.* Modified from Chloris Andina 2, pl. 73 (1857).

32–65% of calyx, ovate or transverse-elliptic, 2–3.5 x 1.5–4 mm, sometimes marginally ciliolate with eglandular hairs, apically obtuse, the surface smooth, abaxially and adaxially glabrous. **Flowers** 4-merous. Calyx aestivation valvate, campanulate, 3.4–5.5 mm long; tube terete or slightly angled, 1.2–2.6 mm long, abaxially glabrate with eglandular hairs; limb 1.9–3 mm long, abaxially glabrous or apically puberulous with eglandular and glandular hairs, adaxially glabrous; lobes triangular, 1.2–2.2 x 1.2–2 mm, sometimes marginally ciliolate with eglandular hairs, apically acute; sinuses acute (V-shaped). Corolla red or pink , thick-fleshy, bistratose, urceolate (occasionally some corollas split after pressing and then looks campanulate in dry specimens), 6–10.7(–12) mm long, 5–5.5(–6.5) mm diam. (3.5–4.5 mm in dry), 2.5–3 mm wide at throat (1.7 in mm dry), abaxially glabrate with eglandular hairs, adaxially glabrous; lobes 0.7–1.5 x 0.8–1.8 mm, apically acute, adaxially rugose. Stamens 8, 5–7(–8.2) mm long, included; filaments distinct, mostly geniculate from S-shaped to strongly folded, or less often straight, at times geniculate and straight filaments happening in the same plant or even in the same flower, more or less linear with parallel sides or broader at base, 3.2–5.2(–5.8) mm long, abaxially and adaxially glabrate or pubescent; anthers distinct, papillae on both thecae and tubules; thecae 1–1.6(–2) mm long, with or without basal appendage; tubules 2, distinct, 0.6–1.7(–2.1) mm long, dehiscing introrsely by longitudinal slits, 0.4–1 mm long; style 5.7–7.5(–10.3) mm long, exserted. **Berry** white, more or less spherical, 7–10 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo white.

Distribution and ecology. *Disterigma empetrifolium* is a widespread species that is very abundant in the high elevations of the northern Andes. It is found in Colombia, Ecuador, Peru, and northern Bolivia (only one collection), reaching western Venezuela (Map 7). This species occurs between (2000?)2500-4500 m, where it is restricted to humid, dry, grassy, or shrubby páramos (jalcas in northern Peru), subpáramos, and humid punas (Bolivia); occasionally, it can be found in the gaps or edges of the dwarf and high cloud forests. *Disterigma empetrifolium* grows in both primary and secondary vegetation, growing on dark soil, exposed on bare soil among rocks, or in *Sphagnum* bogs where it often forms compact cushions like those of *Distichia* (Cyperaceae). Flowering and fruiting specimens have been collected all year-round.



Map 7. Geographic distribution of *Disterigma empetrifolium*.

Etymology. *Empetrum* is the Greek word for rock and although this species does not resemble rocks in the way that some Crassulaceae do, the name probably makes reference to the fact that *Disterigma empetrifolium* is commonly found growing over gravel and rocky outcrops in the páramos.

Representative specimens examined. COLOMBIA. Antioquia: Mun. Urrao, Inspección Jaiperá, vereda El Chuscal, localidad Llanogrande, Páramo de Frontino, 3400 m, 5 Apr 1989 (fl), *Callejas et al. 7592* (CAS, MO, NY); Mun. Ituango, camino entre el Retiro y Cerro Paramillo, 2900-3200 m, 25 Feb 1993 (fl), *Cuadros 5027* (NY); Mun. Belmira, Páramo El Morro, 3100 m, 22 Apr 1993 (fl, fr), *Fonnegra & Tuberquia 4630* (HUA); Mun. Andes, alrededores de la Laguna de Santa Rita, 3450-3750 m, 13 Mar 1996, *D. Sánchez & Parra 2538* (MEDEL). **Arauca:** Sierra Nevada del Cocuy, quebrada El Playón, Hoya San Luis, 3530 m, 13 Mar 1973 (fl), *Cleef 9109* (COL, L). **Bolivar/Antioquia:** Páramo de Chaquiro, 3000-3200 m, 23 Feb 1918 (fl), *Pennell 4267* (NY). **Boyacá:** Páramo de Pisba, Morros de San Gabriel, 2 km al SSW de la Laguna Batanera, 3740 m, 18 Jun 1972 (fl), *Cleef 4713* (COL, L); Páramos de la Rusia, NWN de Duitama, a 1 km de la estación de television, 3605 m, 13 Dec 1972 (fl), *Cleef 7154* (L); Páramo de la Rusia, km 7-20 along road from Duitama to San Gil, 2900-3375 m, 8 May 1979 (fl), *Luteyn et al. 7595* (COL, NY); Sierra Nevada del Cocuy; 3100 m, 15 Aug 1957 (fl), *Grubb et al. 504* (MICH, US); W de Santa Rosa, 3200 m, 11 Feb 1965 (fl), *Uribe-Uribe 5096* (COL, NY). **Caldas:** Páramo del Nevado del Ruíz; 3900-4200 m, 5 May 1940 (fl), *Cuatrecasas 9284* (COL, NY, US); PNN Los Nevados, alrededores del centro de visitantes Las Brisas; 4100 m, 2 Jul 2004 (fl, fr), *P. Pedraza & C. Pedraza 1043* (COL, HUA, NY); Páramo del Quindio, 4100-4300 m, 15-20 Aug 1922 (fl), *Pennell & Hazen 9861* (GH, NY, S, US). **Casanare:** Las Salinas, Quebrada Contadero, 3100 m, 19 Nov 1996 (fl, fr), *Dueñas & Robles 49* (COL). **Cauca:** Páramo de las Papas, alrededores de la

Laguna de Cusiyaco, 3360 m, 7-13 Oct 1958 (fl), *H. G. Barclay & Juajibioy 5943* (COL); Volcán Puracé, Laguna de San Rafael y alrededores, 3300 m, 6 Jan 1972 (fl), *Cleef & Fernández-P. 582* (COL); PNN Puracé, termales de San Juan, 3080 m, 12 Dec 1985 (fr), *Duque 118* (NY), 3080 m, 16 Jul 1976 (fl), *Jaramillo-M. & Hammen 5150* (COL); Puracé, PNN Puracé, cercanias de la laguna de San Rafael, 3300 m, 6 Oct 1984 (fl), *Lozano et al. 4641* (COL, WIS), 3200 m, 18 Apr 1982 (fl), *Torres et al. 923* (COL); Páramo de Buena Vista, 3000-3600 m, Jan 1906 (fl), *Pittier 1163* (US); Mun. Paleterá, Coconuco, llano de la Quebrada El Depósito, 2900 m, 17 Oct 1986 (fl, fr), *Restrepo & Duque 237* (NY). **Cundinamarca:** Bogotá, Cerro de Guadalupe, 3500 m, 17 Jul 1949 (fl), *Haught 6491* (COL, MICH, US); La Cruz, near Bogotá, Nov 1911 (fl), *Hno. Apollinaire & Hno. Arthur 29* (US); Mun. Junin, Reserva Biológica Carpanta, 3050 m, 22 Aug 1989 (fl), *Jaimes et al. 29* (COL); Páramo de Chisacá [PNN Sumapaz], 3375-3450 m, 17 May 1979 (fl), *Luteyn et al. 7759* (NY); PNN Chingaza, camino Suacie, Mirador Chuza, 3163 m, May 2004 (fl, fr), *C. Pedraza & Umaña 13* (NY, COL, CUVC); PNN Chingaza, vía La Calera-Piedras Gordas, 3500 m, May 2004 (fl), *C. Pedraza & Umaña 7* (COL, HUA, NY); Bogotá D.C., PNN Sumapaz, Laguna Los Tunjos, 3650 m, 16 Mar 1998 (fl), *P. Pedraza & Alvear 55* (COL); Páramo de Siberia, 3400-3500 m, 24 Feb 1952 (fl), *Schneider 1172* (COL, S); Páramo de Zipaquirá, 3200-3250 m, 6 Aug 1949 (fl), *Schneider 861* (COL, S). **Guajira:** Sierra Nevada de Santa Marta, vertiente Río San Miguel, 3100-3700 m, 16 Aug 1986 (fl), *Cuadros & Gentry 2756* (MO). **Huila:** Mun. Gigante, subida desde Vereda Ventanas al Páramo de Miraflores, 2700-2970 m, 12-16 Aug 1997 (fl), *J. L. Fernández et al. 14923* (COL). **Meta:** PNN Sumapaz, entre el plano del Nevado y la Laguna del Sorbedero, 3400-3500 m, 13 Jul 1981 (fl), *Díaz-P. et al. 2798* (COL); Cubarral, orilla de la Laguna de La Guitarra, 3420 m, 10 Jul 1981 (fl), *Franco & Rangel 307* (COL). **Nariño:** Azufral, 18 May 1976 (fl), *André 3230* (F, GH, NY); Mun. Pasto, Volcán Galeras, 3900 m, 15 Feb 1971 (fl), *Marks 9*

(MO); Mun. La Cruz, Alto de Ledezmas, Volcán Doña Juana, 3400 m, Sep 1997 (fl), *Narváez-Bravo 37* (COL); Mun. Pasto, Volcán Galeras, 3950 m, 6 Aug 1977 (fl), *Pinto-E. et al. 1835, 1838* (COL), 4000 m, 22 Oct 1968 (fl, fr), *Plowman 1961* (GH); Mun. Cumbal, Volcán Chiles, 3900-4100 m, 23 Oct 1978 (fr), *Sturm & Abouchaer 101* (COL). **Norte de Santander:** Páramo de Tamá, alrededores de la Cueva, 3000-3200 m, 28 Oct 1941 (fl), *Cuatrecasas et al. 12655* (COL, F, GH); Páramo de Romeral, 3800-4200 m, 30 Jan 1927 (fl), *Killip & A. C. Smith 18636* (GH, NY, US), *18685* (US); Mun. Cucutilla, vereda El Carrizal, camino entre Sisavita y el Páramo El Romeral, 2300-3000 m, s.d (fl), *R. Sánchez et al. 5146* (COL); Ocaña, Páramos, 2400-3050 m, 1846-1852, *Schlim 353* (NY, P). **Quindio:** Mun. Pijao, Páramo de Chili, above finca Maizopolis, 3550 m, 18 May 1989 (fl, fr), *Luteyn et al. 12944* (NY); Salento. **Risaralda:** Mun. Pereira, alrededores de la Laguna del Otún, 4000-4300 m, 3 Feb 1980 (fl), *Díaz-P. et al. 1749* (COL); Mun. Santuario, al SW del Cerro Ventanas, Macizo de Tatamá, 3820 m, 2 Feb 1983 (fl), *Torres et al. 1834* (COL). **Santander:** Onzaga, Chaguacá, alto de la Laguna de Los Bobos, 3890 m, 7 Aug 1958 (fl), *Jaramillo-M. et al. 937* (COL); Páramo de Santurbán, near Vetas, 3700 m, 17 Jan 1927 (fl), *Killip & A. C. Smith 17949* (GH, NY, US); Santander; Páramo de las Coloradas, above La Baja, 3900-4100 m, 27 Jan 1927 (fl), *Killip & A. C. Smith 18414* (US); Páramo del Almorzadero, 32-34 kms S of Chitagá, 3400 m, 12 May 1979 (fl, fr), *Luteyn et al. 7659* (COL, NY). **Tolima:** Nevado del Tolima, 2800-3500 m, 26 Jan 1948 (fl), *Archibald 4049* (E); Páramo del Ruíz, 4000 m, 30 Oct 1957, *H. G. Barclay 5260* (COL); Mun. Murillo, PNN Los Nevados, 3945-3990 m, 9 May 1991 (fl, fr), *J. C. Betancur & S. Churchill 2434* (COL, HUA, NY). **Valle del Cauca:** Los Farallones, extremo N, Cerro Alto del Buey, 3500-3600 m, 11 Oct 1944 (fl), *Cuatrecasas 17913* (COL, F, GH, US); Mun. El Cerrito, Páramo Pan de Azúcar, arriba de Tenerife, 3600 m, 21 Feb 1992 (fl, fr), *Silverstone-Sopkin et al. 6503* (NY); Rio Frío-Darien, Páramo del Duende, 3300-3850 m, 23-28 Jul 1998 (fl, fr), *W. Vargas*

4748 (COL); Mun. Bugalagrande, cuenca Río Bugalagrande, 3800 m, Mar 1996 (fl), *W. Vargas. 2996* (HUA). **Without department:** 1760-1808 (fl), *Mutis 2019, 2020, 2043, 3833* (US).

VENEZUELA. Apure: distrito Páez, Bajada de los Huevos, cerca al sitio La Línea, Páramo Tamá, 3100 m, 26 Jun 1973 (fl), *Ruiz-Terán & López-Figueiras 8830* (NY); Río Talco (Oirá) entre Alto de Cruces y Tierra Negra, Páramo Pata de Judio, SE del Páramo Tamá, 3000-3200 m, 19 Jan 1968 (fl), *Steyermark et al. 101102* (F, L, NY, US). **Mérida:** distrito Libertador, PN Sierra Nevada de Mérida, entre La Aguada y Laguna La Fría, 3400 m, 16 Jan 1998 (fl), *Berg 98-8-21* (NY); Mérida, 1844-1845 (fl), *Moritz 1343* (GH, L); distrito Campo Elías, Los Adobes, Páramo de los Conejos, Sierra de la Culata, 3500-3650 m, 25 Mar 1972 (fl), *Ruiz-Terán 7021* (NY), 3350-3400 m, 19 Oct 1972 (fl), *Ruiz-Terán 7673* (NY); distrito Miranda, Cerro Caracacho, Páramo de Palmira, 3200-3300 m, 24 May 1975 (fl), *Ruiz-Terán & Dugarte 12272* (NY); distrito Miranda, Cerro Caracacho, Páramo de Palmira, 3200-3300 m, 24 May 1975 (fl), *Ruiz-Terán & Dugarte 12276, 12310* (NY). **Táchira:** Páramo de Tamá, 2500-3000 m, 12 Nov 1976 (fl), *Charpin & Jacquemound 13200* (NY), 2500-3200 m, 29 Jan 1978 (fl), *Luteyn 5311* (CAS, F, GB, MO, NY, TEX); Pata de Judio, 3100-3500 m, 19 Oct 1978 (fl), *Luteyn et al. 5915* (CAS, MO, NY).

ECUADOR. Azuay: PN Cajas, Laguna Toreadora, 3800 m, 10 Oct 1995 (fl), *Alexander 38* (MO); between Loja and Paramos de Silván, 37 km S of Cuenca, 3200 m, 30 Jul 1959 (fl), *H. G. Barclay & Juajibioy 8363* (MO); along Río Matadero, W of Cuenca, 3030-3200 m, 3 Mar 1945 (fl, fr), *Camp E-2021* (NY, UC, US); Cuenca, Páramo Quinoas, 3600 m, 7 Jul 1947 (fl), *Harling 1473* (L, S); Gualaceo-Limón road, 12-21 km E of Gualaceo, 2960-3600 m, 1-2 Dec 1989 (fl), *Luteyn 13403* (NY); 22-25 km S of Sigsig along road to Gualaquiza, Páramo de Matanga, 3040-3340 m, 21 Jan 1985 (fl), *Luteyn & Cotton 11155* (NY, QCNE). **Cañar:** Huairacaja, 10-20 km NE of Azogues, 3330 m, 2 Feb 1945 (fl), *Camp*

E-1777 (NY, US); El Tambo-Zhud road, side road to Culebrillas, 3200 m, 13 Aug 1987 (fl), *Valencia 133* (MO, NY). **Carchi:** Páramo del Angel, 3850 m, 26-28 Sep 1959 (fl, fr), *H. G. Barclay & Juajibioy 9317* (NY, US); Cerro Golondrinas, 2850-2860 m, 24 Jul 1993 (fl), *Boyle & Hibbs 2309* (MO); Tulcán-Maldonado road, 21-26 km W of Tufiño, 3400-3630 m, 14 Apr 1978 (fl), *Luteyn & Lebrón-Luteyn 5757A* (NY); SW side of Volcán Chiles, 4300 m, 20 Jun 1995 (fl), *Sklenar & Kosteckova 38-8* (QCA). **Chimborazo:** carretera Riobamba-Baños, carretera vieja a Puela, 2650 m, 19 Feb 1987 (fl), *Jaramillo 9448* (F, NY); vicinity of Nevado El Altar, near Río Blanco, 3400 m, 31 Mar 1983 (fl, fr), *Juncosa 870* (MO, NY); 4 km from Alao, 3350-3500 m, 5 May 1982 (fl), *Ollgaard et al. 38024* (MO NY); Carihuairazo, 4200 m, Apr 1927 (fl), *Rorud s.n.* (F). **Cotopaxi:** PN Cotopaxi, 3800 m, 15 Dec 1989 (fl), *Cerón-M. 8002* (MO, NY, QCNE); carretera Latacunga-Iluchi-Yanatacu, 3500-3700 m, 1 Mar 1987 (fl), *Romoleroux et al. 319* (COL). **Imbabura:** Volcán Cotacachi, SW slopes, 4100-4320 m, 9 Nov 1983 (fl), *Larsen et al. 45653* (NY, QCNE); Reserva Ecológica Cayambe-Coca, 3700 m, 11 Apr 1991 (fl), *Macias et al. 143* (NY, QCNE). **Loja:** PN Podocarpus, above Cajanuma, 3400 m, 6 Jun 1992 (fl), *Keating 117* (NY, QCNE); Cerro Villonaco, 10 km W of Loja, 2590 m, 7 Mar 1965 (fl), *Knight 564* (US, WIS). **Morona-Santiago:** Sígsig-Gualaquiza road, Cordillera Matanga, 3200 m, 10 May 1968 (fl), *Harling 8152* (A, GB, UC); Gualaceo-Limón (General Plaza) road, 2800-3300 m, 2 Apr 1974 (fl), *Harling & Andersson 13108* (GB, MO, NY). **Napo:** Archidona Cantón, PN Napo-Galeras, Volcán Sumaco, 3732 m, 16 Mar 1996 (fl, fr), *Clark 2187* (MO QCNE); Laguna de Papallacta, 3900 m, 19 Aug 1976 (fl), *Dávalos et al. 25* (NY); cantón Tena, PN Llanganates, near Laguna de Yanacocha, San Martín area, 3600 m, 9 Oct 1998 (fl), *Narváez et al. 170* (NY); Reserva Cayambe-Coca, abajo del sitio La Virgen, 4300 m, 14 Dec 2003 (fl, fr), *P. Pedraza & C. Pedraza 971* (NY, QCA); cantón Quijos, Reserva Ecológica Antisana, carretera Pifo-Papallacta, Páramo de Guamaní, 3900 m, 27 Julio 1998 (fl), *H. Vargas et al. 2016* (MO, QCNE).

Pichincha: Quito, Parroquia Tumbaco, Reserva Ecológica Antisana, cooperativa Inga Alto Monserrat, 2700-2750 m, 9 Mar 1996 (fl), *Alvarez & Columba 1391* (MO, QCNE); Cerro Corazón, 4400 m, 1 Nov 1955 (fl), *Asplund 17533* (L, NY, S); Atacazo, 4200 m, 1 Sep 1928 (fl), *Firmin 537* (F, US); Mojanda to Otavalo, 3500 m, s.d (fl), *Lehmann 676* (BM, US); Volcán Pichincha, Yanacocha trail, 3500 m, 8 Apr 1978 (fl), *Luteyn et al. 5688* (CAS, GB, MO, NY); 11-16 km E of Olmedo along road to Laguna San Marcos, 3720 m, 13 Jan 1985 (fl, fr), *Luteyn & Cotton 11057* (NY, QCNE); cantón Machachi, Reseva Ecológica Los Illinizas, detrás de Cerro Corazón, lugar Laureles del Pongo, 3340 m, 20 Aug 2003 (fl, fr), *Ramos et al. 7494* (NY). **Sucumbíos:** Playón de San Francisco, El Mirador, 16 Aug 1978 (fl), *Boeke & Jaramillo 2700* (NY). **Tungurahua:** Alto de Pasa, 3500 m, 28 Oct 1944 (fl), *Acosta-Solis 8755* (F); Cordillera de Llanganates, near Las Torres, 3800 m, 23 Nov 1939 (fl), *Asplund 9943* (S); Volcán Tungurahua, 2560 m, 28 Apr 1951 (fl), *Bell 786* (A, BM, NY); Hacienda Sabanag, 3500 m, 28 Sep 1955 (fl), *Boecher et al. 115* (S); Mocha, parroquia Pinguili, Reserva Faunística del Chimborazo, base del Cerro Carihuairazo, 3860 m, 2 Jul 1992 (fl, fr), *Cerón-M. 19243* (NY); Parroquia San José de Paoló, Loma Potrerillos, 3200 m, 4 Apr 1987 (fl), *Cerón-M. & Cerón 1132* (MO, NY, QCNE); Mount Mulmúl, 1857-1859 (fl), *Spruce 5204* (S); cantón Baños, PN Llanganates, Páramo de Soguillas-Valle de los Frailejones, 3660 m, 12 Oct 1998 (fl), *H. Vargas et al. 2780* (MO, NY). **Without locality:** s.d. (fl), *Bonpland 3212* (F).

PERU. Amazonas: Prov. Bagua, Cordillera Colán, NE of La Peca, 3260 m, 9 Sep 1978 (fl), *Barbour 3458* (MO, NY); Prov. Luya, distrito Camporedondo, Tullanya, cerro Huicsonga, 3320 m, 8 Dec 1996 (fl), *Vásquez & Rojas 21997* (USM). **Ayacucho:** Prov. La Mar, between Tambo, San Miguel, Ayna, and Hacienda Luisiana, 3400-3600 m, 24 May 1968 (st), *Dudley 12020B* (NA); Prov. Huanta, Cueva de Puytac, Montañas de Huanta, Sep 1866 (fl), *Raimondi 9420* (USM). **Cajamarca:** Prov. Cajamarca, camino a Chaquisisñegas, 3500 m, 26 Feb

1987 (fl, fr), *Becker & Terrones 1730* (NY); Paramillo de Pomacahua, antes del pajonal, 3200 m, 8 Nov 1999 (fl), *Díaz et al. 10899* (USM); Prov. San Miguel, Llapa-Uchuquinua, 2700 m, 14 May 1977 (fl), *Sagástegui et al. 8910* (F, MO, NY); Prov. Cajamarca, Cerro Maqui Maqui, ruta Shanta Alta, 4070 m, 15 May 1994 (fl), *I. Sánchez-V. et al. 7164* (F); Prov. Celendín, Sorochuco, carretera Michiquillay-El Punre, 3570 m, 8 Sep 2001 (fl, fr), *I. Sánchez-V. et al. 10917* (F, NY). **Cusco:** Urubamba, Machu Picchu, in Urcoscancha, a pampa above the village of Palcay, 3810 m, 3 Jul 1982 (fl), *B. Peyton & S. T. Peyton 737* (MO, NY); Paucartambo, 4000 m, s.d. (fl), *Soukup 390* (F). **Huánuco:** Prov. Huánuco, Zapatococha, above Acomayo, 3300-3400 m, 16 Jun 1973 (fl), *O'Neill s.n.* (USM). **Junín:** Prov. Tarma, carretara hacia Illic (Palca), 2750 m, 13 Jan 1987 (fl), *Díaz-S. & Baldeón 2226* (MO, NY, USM). La Libertad: Prov. Santiago de Chuco, Schulcahuanga, 4100-4200 m, 30 Oct 2002 (fl), *Cano E. et al. 12726* (USM). **Pasco:** Prov. Oxapampa, distrito Huancabamba, PN Yanachaga-Chemillén, alrededores de la escuela Santa Bárbara, 3400 m, 10 Jun 2006 (fl, fr), *P. Pedraza et al. 1605* (COL, CUZ, NY, USM); Prov. Oxapampa, distrito Huancabamba, PN Yanachaga-Chemillén, alrededores de la escuela Santa Bárbara, 3400 m, 10 Jun 2006 (fl), *P. Pedraza et al. 1603* (COL, CUZ, MO, NY, USM). **Piura:** Prov. Huancabamba, La Cruz, 4 Jun 1961 (fl), *Acleto 359, 395* (USM); Prov. Huancabamba, Tambo-La Huaca, 28 Nov 1961 (fl), *Friedberg 823* (USM). **Puno:** Tambo de Quiton-quitón, camino de Ayapata a San Gabán, Sep 1864 (fl), *Raimondi 9674* (USM). **San Martín:** Prov. Mariscal Cáceres, Paredones, PN Río Abiseo, 3650 m, 16 Mar 1988 (fl), *B. León 1590* (NY), 3450 m, 21 Nov 1985 (fl), *Young 1968* (NY), 3450 m, 20 Nov 1985 (fl, fr), *Young 1776* (NY), 3425 m, 31 May 1986 (fl), *Young & Watson 3480* (NY, USM); Prov. Mariscal Cáseres, Pampa de Cuyes, 25 Jul 2000 (fl), *B. León & Young 4542* (USM).

BOLIVIA. La Paz: Prov. Franz Tamayo, senda Pelechuco-Mojo, sector Tambo Quemado, 3490 m, 30 Apr 2003 (fl), *Maldonado et al. 3248* (NY).

Without country. Quito-Popayán-Bogotá, Oct 1843, *Hartweg 1201* (BM, CGE, NY, OXF); 1846, *Hooker s.n.* (NY); 1849, *Hooker s.n.* (NY); s.d. *Triana 4332* (F).

Disterigma empetrifolium is characterized by its small leaves, usually less than 5 mm wide and marginally crenulate; its often long and evident pedicels; its smooth bracteoles; its pink, urceolate, and adaxially glabrous corollas; its long and usually geniculate staminal filaments (although only plants with straight filaments have have been illustrated, see Fig. 18); and its white berries and seed embryos. As mentioned before in the discussion of *D. codonanthum,* sterile specimens of *D. empetrifolium* could be mistaken with *D. codonanthum* (Colombia, Ecuador, through central Peru) and *D. pernettyoides* (southern Peru through central Bolivia). Moreover, when the thick urceolate corollas of *D. empetrifolium* split after being pressed, the separation of this material from the campanulate *D. codonanthum*, although not impossible, requires of careful observation. The differences of this species with other closely related taxa are in Table 11.

Disterigma weberbaueri is here added to the many synonyms of this species. As Smith (1933) pointed out, the vegetative variation of the synonymized species, varieties, and forms, represent individual or population traits and not different species. Their flowers are indistinguishable and their differences are found in characters (leaves and habit) that are likely to be shaped by micro-environmental factors, especially under the extreme and changing conditions of the páramos.

Local names and uses. This species is known as “Anisillo de Monte”, “Uvilla de monte” (Chimborazo), “Chirimote” (Tungurahua), “Orcu Mote” (Tungurahua), and “Joyapa” (Loja) in Ecuador, and as “Pushgay blanco” in Peru (Cajamarca). Its fruits have been reported to be edible throuhtout its entire range, and the infusion of the plant is used for treating nerves.

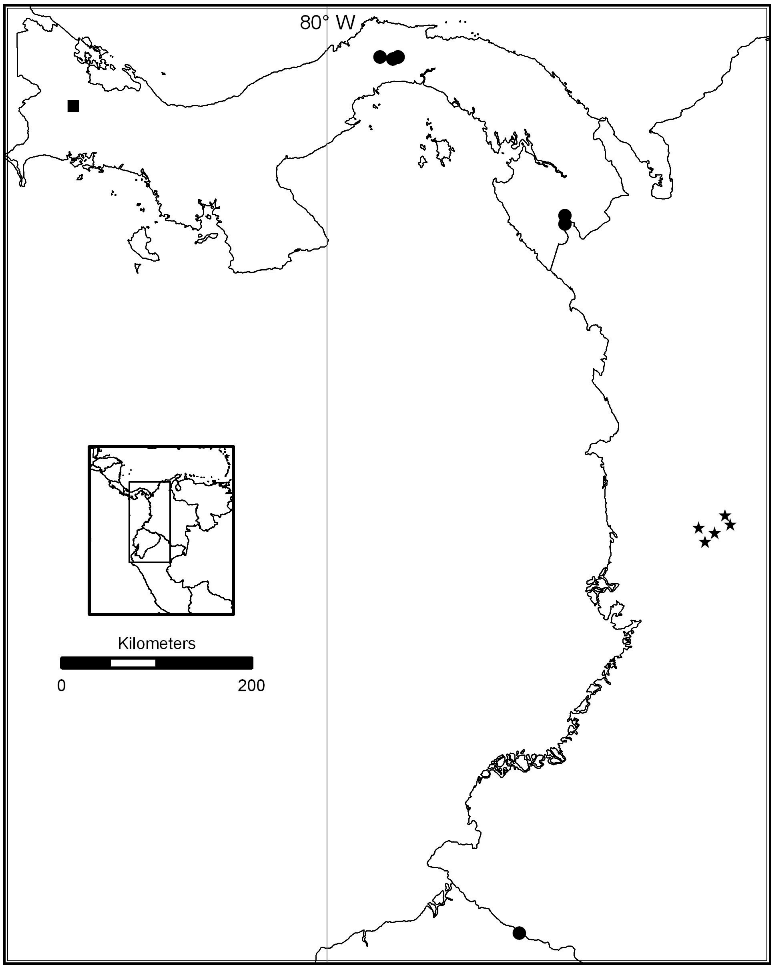
15. **Disterigma hammelii** Wilbur & Luteyn, Ann. Missouri Bot. Gard. 68: 160-162. 1981. Type. Panama. Chiriquí: Chiriquí-Bocas del Toro border, trail along continental divide, about 5 mi NE of Boquete near Cerro Pate Macho above Palo Alto, 2160 m, 23 May 1979, *Hammel 7390* (holotype, DUKE; isotype, NY).

Epiphytic **shrubs**, wiry, pendent. Young branchlets ridged, more or less smooth, pubescent, the hairs eglandular, brown-reddish, the mature branches indumentum similar but glabrate. **Leaves** 8–9 per cm, apparently distichous, patent; petiole 0.5–1 mm long, glabrous; lamina lanceolate or sometimes elliptic, (0.4–)0.5–0.8 x (0.1–)0.2(–0.3) cm, basally cuneate, marginally entire, apically ciliolate with deciduous eglandular or glandular hairs, apically blunt acute, adaxially glabrous, abaxially glabrate with minute glandular hairs, the venation adaxially obscure, abaxially hyphodromous with the midvein raised. Axillary **solitary flowers**; bracts 5–8, chartaceous, ovate, 0.6–2 x 0.6–2 mm, sometimes marginally ciliolate with few minute eglandular hairs, apically obtuse or rarely obtuse and cuspidate, abaxially glabrous; pedicel 0.8–1 mm long, much reduced and hidden by overlapping bracts, glabrous; differentiated apical bracteoles 2, distinct, chartaceous, enveloping to the base of calyx lobes, covering 33–50% of calyx, ovate, 1.6–2.2(–2.7) x 2.2–2.3 mm, marginally ciliolate with minute eglandular hairs, apically obtuse or obtuse and cuspidate, the surface smooth, abaxially and adaxially glabrous. **Flowers** 4-merous. Calyx aestivation valvate, campanulate, 4–4.8 mm long; tube slightly angled, 1.2–1.4(–1.8) mm long, abaxially glabrous; limb 2.7–3.4 mm long, abaxially puberulous with eglandular hairs (apically), adaxially glabrous; lobes triangular, 2.5–3.1 x 0.7–0.9 mm, marginally ciliolate with eglandular hairs (especially apically), apically acute; sinuses acute (V-shaped). Corolla pink or white (fide collectoris), chartaceous, bistratose, tubular (in herbarium specimens), 11–14.3 mm long (in dry), 2.4–3 mm diam. (in dry), 2.4–3 mm wide at throat (in dry), abaxially glabrate with eglandular hairs, adaxially glabrous; lobes 1.5–2(–2.3) x 0.8–0.9 mm, apically acute, adaxially rugose. Stamens 8, 12–13 mm long, exserted; filaments distinct, straight, more or less linear with parallel sides, 8.5–9 mm long, abaxially and adaxially pilulose; anthers distinct, papillae on both thecae and tubules; thecae 1.4–1.6 mm long, without basal appendages; tubules 2, distinct, 2.4–2.7 mm long, dehiscing introrsely by longitudinal slits, 0.8–1.3 mm long. Ovary 4-locular; style 13–14.3 mm long, exserted. **Berry** unknown.

Distribution and ecology. *Disterigma hammelii* is endemic to the province of Chiriquí, Panama, around Cerro Pate Macho and Palo Alto (close to the border with Bocas del Toro) (Map 8). This species grows in cloud forests between 1800-2200 m, and has not been collected since 1988. Flowering specimens have been found in February, March, May, and December.

Etymology. Species dedicated to the collector, Barry Hammel.

Specimens examined. Panama. Chiriquí: Cerro Pate Macho at continental divide, 1800-2100 m, 13 Mar 1988 (fl), *Almeda 6122* (CAS), 2150 m, 31 Dec 1985 (fl), *de Nevers & Charnley 6686* (DUKE, MO); 1 km E of Cerro Pate Macho, along continental divide, 2100-2200 m, 7 Feb 1986 (fl), *Grayum 6430* (DUKE, MO).



Map 8. Geographic distribution of *Disterigma hammelii* ■, *D. hiatum* ★, and *D. panamense* ●.

Disterigma hammelii is characterized by having a wiry habit; leaves apparently distichous, patent, small, and narrow; corollas pink or white, tubular, more than 1 cm long; stamens and style more than 1 cm long; and papillae on both thecae and tubules. Vegetatively, *D. hammelii* recalls *D. agathosmoides*; details about their overall similarities are provided in the discussion of *D. agathosmoides*.

16. 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.19)

Folia obovata vel elliptica, apice obtuso et apiculato. Inflorescentiae e fasciculis 2-11-floris compositae. Flores 5-meri. Calyx aestivatione valvata; lobis deltatis; sinubus 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 ridged, more or less smooth, generally glabrous or glabrate, the hairs inconspicuous, eglandular, and white, the mature branches indumentum similar. **Leaves** 1–2(–3) per cm, spirally arranged, sometimes appearing secund, diffuse; petiole 3–5 mm long, glabrous or glabrate, the hairs eglandular; lamina obovate or elliptic, (1.6–)2.2–4.5 x (0.9–)1.3–2.7 cm, basally attenuate, marginally entire, sometimes revolute, apically ciliolate with eglandular hairs, apically obtuse and apiculate, adaxially and abaxially glabrate with minute and deciduous eglandular and glandular hairs, the venation 3- or 5-nerved on both sides, the midvein adaxially impressed and abaxially raised. **Inflorescence** axillary, of 2–11-flowered fascicles, sometimes flowers appearing solitary due to asynchrony of floral bud development; bracts 2–3, chartaceous, ovate, 0.5–1.7 x 0.5–2.5 mm, marginally eciliate, apically obtuse, abaxially glabrous; pedicel 0.5–1.5 mm long, reduced and hidden by overlapping bracts, glabrous; differentiated apical bracteoles 2, distinct, enveloping the base of calyx tube or entire calyx

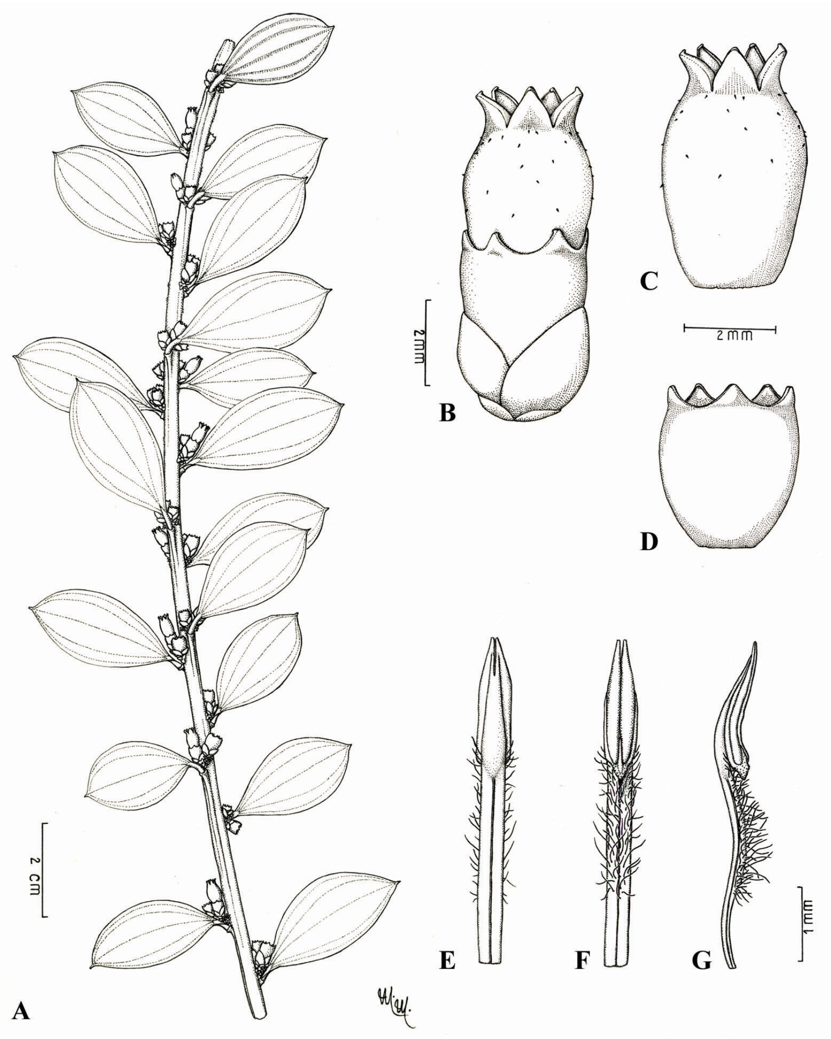


Fig. 19. Illustration of *Disterigma hiatum*. **A.** Branch. **B.** Flower with bracts and bracteoles. **C.** Corolla. **D.** Calyx with bracteoles removed. **E.** Stamen, abaxial view. **F.** Stamen, adaxial view. **G.** Stamen, lateral view (*P. Pedraza 1112*, COL).

tube, covering 39–50(–85)% of calyx, suborbicular or transverse-elliptic or reniform, 2.2–3.2 x 3.7–4 mm, occasionally ciliolate with minute eglandular hairs, apically obtuse, the surface smooth, abaxially glabrous, adaxially glabrous. **Flowers** 5-merous (rarely calyces 4- and 6-lobed). Calyx aestivation valvate, cylindric, 3.3–4 mm long; tube terete, 2–2.1 mm long, abaxially glabrous; limb 1.4–2.1 mm long, abaxially and adaxially glabrous; lobes triangular, 0.3–0.5 x 0.5–1 mm, marginally eciliate, apically acute; sinuses rounded (U-shaped). Corolla pale pink or white, very thick-fleshy, bistratose, urceolate (distally inflated), 5.2–6.4 mm long, 2.6–3.5 mm diam. (2.0–2.6 mm in dry), 1.8–2.2 mm wide at throat (1.5–1.8 mm in dry), abaxially glabrate with minute glandular hairs, adaxially puberulous even in the lobes; lobes 0.8–1 x 0.7–1 mm, apically acute, adaxially rugose. Stamens 10, 4–4.7 mm long, included; filaments distinct, straight, more or less linear with parallel sides, 3.4–4 mm long, abaxially glabrous, adaxially pubescent distally; anthers distinct, papillae on both thecae and tubules, the ones on tubules minute; thecae 1.5–1.7 mm long, basally appendaged; tubules 2, distinct, 0.2–0.5 mm long, very reduced and hard to differentiate from thecae, dehiscing introrsely by a cleft that runs from tubule tip to theca base, 1.4–1.5 mm long. Ovary 5-locular; style 4.5–5 mm long, included, micropapillose. **Berry** immature, white, more or less spherical, the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as berry; seeds with a mucilaginous coat, the embryo color unknown.

Distribution and ecology. *Disterigma hiatum* is known from a small area at Serranía de los Paraguas (Valle del Cauca/Chocó), around Cerro del Inglés and on the road to San José del Palmar (Chocó) (Map 8). This species grows in cloud forests between 1500-2100 m. Flowering specimens have been found in April, May, and July, and fruiting specimens in April, May, July, and August.

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

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. 19). This particular anther dehiscence, in which the aperture goes along the theca and is not confined to the tubules, is similar to that of *Lateropora* (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 species of *Disterigma* in the region (*D. chocoanum, D. appendiculatum, D. sterophyllum, D. verruculatum*) by obovate or elliptic leaves that are apically obtuse and apiculate, 5-merous flowers, very reduced calyx lobes with the sinuses rounded, adaxially puberulous corolla, micropapillose style, and seeds with a mucilaginous coat. For comparison with other species see *D. utleyorum.*

17. Disterigma humboldtii (Klotzsch) Nied., Bot. Jahrb. Syst. 11: 224. 1889. *Vaccinium humboldtii* Klotzsch, Linnaea 24: 57. 1851. *Vaccinium myrtifolium* Willd. in Klotzsch, Linnaea 24: 58. 1851, pro syn., nom. illeg. Type. "South America" [Colombia], s.d. (fl), *Humboldt & Bonpland 2065 p.p.* (holotype, B-W 7350-1; isotypes, fragment F ex P, fragment L ex P, fragment NY ex P, P). Photo F neg. 4765 ex B-Willd, photo NY neg. 13026 ex P, photo NY neg. 38270 ex P. The isotypes have no collection number but otherwise they are identical to *Humboldt & Bonpland 2065 p.p.* at B-W. *Humboldt & Bonpland 2065 p.p.* is a mixed collection and the sheet at P-Bonpl. is the holotype of *D. acuminatum*; in fact few loose leaves of *D. humboldtii* can be found inside the packet of this sheet. The photos from P are from two different sheets, but the one corresponding to NY neg. 38270 was not found.

Vaccinium pachyphyllum Hemsl., Biol. centr.-amer. bot. 2: 275. 1881. *Disterigma pachyphyllum* (Hemsl.) S. F. Blake, J. Washington Acad. Sci. 16: 365. 1926. Type. Costa Rica, Aug 1875 (fl), *Endres 154* (holotype, K n.v.; isotype, fragment NY ex K). Photo neg. s.n. and drawing from K type at NY. The K sheet was not found.

Disterigma mayanum Lundell, Wrightia 5(4): 85. 1975. Type. Guatemala. Baja Verapaz: Unión Barrios, Salama-Cobán road, 6 Feb 1975 (fl), *Lundell & Contreras 18936* (holotype, LL).

Disterigma pilosum Wilbur, Bull. Torrey Bot. Club 119(3): 285-286. 1992, **syn. nov.** Type. Costa Rica. Limón: Cordillera de Talamanca, Atlantic slope, S side of a cordillera between the Río Terbi and Río Siní, 2-4 airline km W of the Costa-Rican border, 2300-2500 m, 11 Sep 1984 (fl), *Davidse et al. 28937* (holotype, DUKE).

Disterigma ecuadorense Luteyn, Fl. Ecuador 54: 280. 1996, **syn. nov.** Type. Ecuador. Pichincha: Quito-Santo Domingo de los Colorados old road, disturbed roadside slopes through premontane forest, ca. 2-4 km from the road in area called Bella Vista at Km 69 of old road, 2400 m, 13 Nov 1992 (fl, fr), *Luteyn et al. 14770* (holotype, NY; isotypes, AAU, CAS, E n.v., GB, K, MEXU n.v., MO, MSC n.v., QCA n.v., QCNE n.v., TEX n.v., US). The sheets at QCA and QCNE were not found.

(Fig. 20)

Epiphytic (more common in Central America) or terrestrial **shrubs**, scandent, pendent, or erect, 1–3 m tall. Young branchlets ridged, more or less smooth, pubescent, puberulous, villosulous, or occasionally pilose, the hairs eglandular and light brown, the mature branches indumentum similar but glabrate or pilulose. **Leaves** 1–7 per cm, apparently distichous or spirally arranged, diffuse; petiole 1–2.5(–3.5) mm long, glabrate or puberulous, the hairs eglandular; lamina

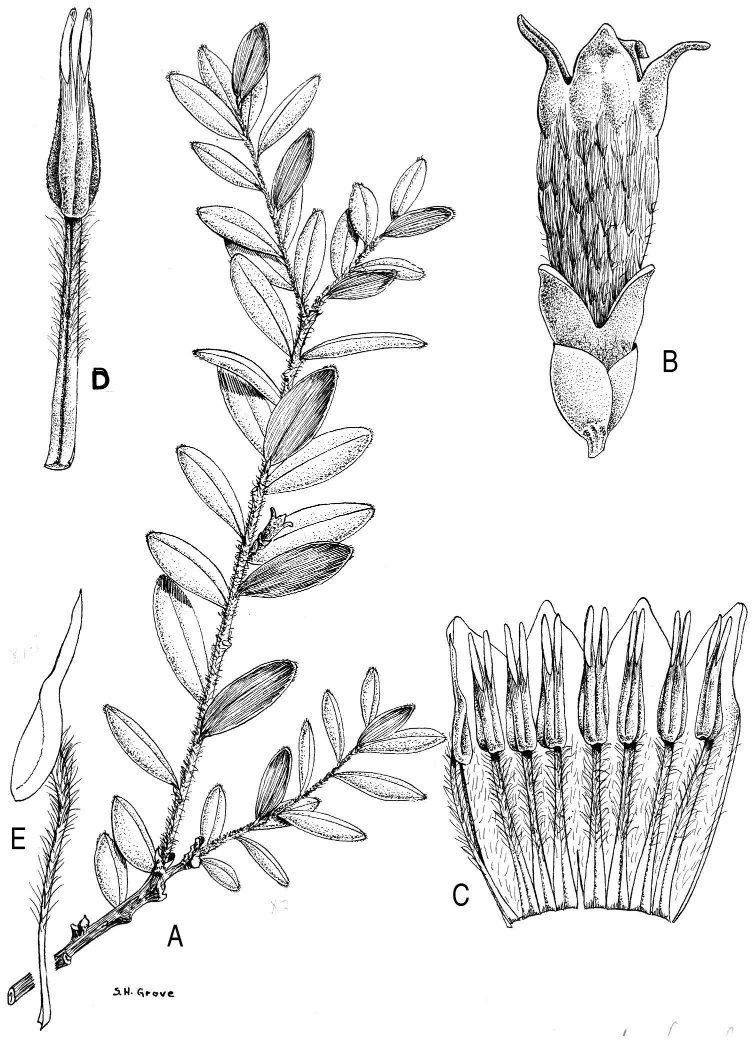
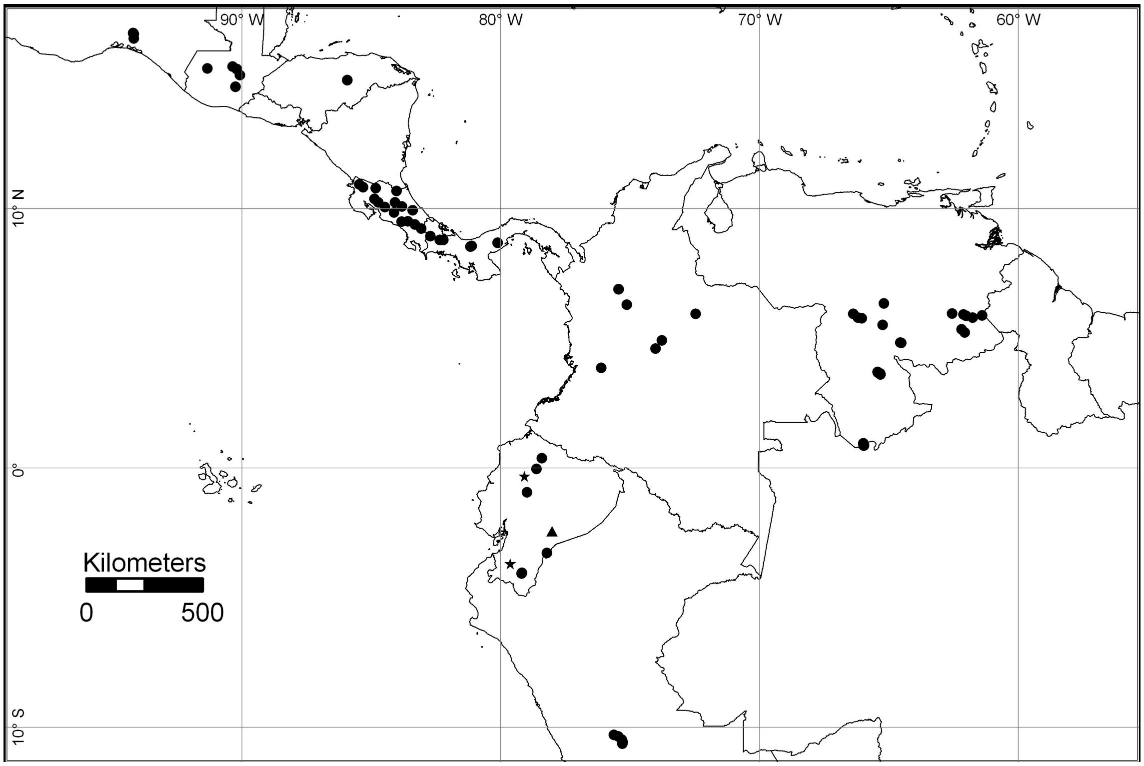


Fig. 20. Illustration of *Disterigma humboldtii.* **A.** Branch; **B.** Flower with differentiated apical bracteoles; **C.** Open corolla exposing the stamens; **D.** Adaxial view of a stamen; **E.** Lateral view of a stamen (*Steyermark 48535*, F). Originally published as *D. mayanum.* Modified from Flora of Guatemala, Part 8(2), fig. 27 (1966).

coriaceous and sometimes succulent, ovate, elliptic or rarely obovate, 0.6–2(–2.5) x (0.2–)0.3–0.8(–1.3) cm, basally obtuse or cuneate, marginally entire or rarely crenulate towards apex, slightly revolute towards base, apically ciliolate or ciliate with deciduous eglandular hairs, apically subacute, obtuse, or rarely blunt acute, drying wrinkled, adaxially and abaxially glabrate or rarely pilosulose with eglandular hairs and sometimes with glandular hairs, the venation adaxially obscure or hyphodromous with the midvein impressed, abaxially obscure, hyphodromous, or 3-nerved with the midvein raised. Axillary **solitary flowers** and rarely 2–3-flowered fascicles; bracts 5–8, chartaceous, ovate or transverse-elliptic, 0.4–2 x 0.6–2.2 mm, marginally eciliate or minutely ciliolate with eglandular hairs, apically obtuse, abaxially glabrous; pedicel 0.7–1.5(–2) mm long, reduced and hidden by overlapping bracts or rarely evident or at least with a portion of it not completely obscured by overlapping bracts, glabrate with eglandular or glandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping entire calyx tube or to upper limb, covering 40–85(–100)% of calyx, obovate, ovate, or reniform, 1.8–4(–4.8) x 1.6–4 mm, marginally eciliate or sometimes ciliolate with minute eglandular hairs, apically obtuse, the surface smooth and often keeled, abaxially glabrous or glabrate with eglandular hairs at base, adaxially glabrous. **Flowers** 4-merous. Calyx aestivation valvate, campanulate, 3–4.8(–5.5) mm long; tube angled, 1.1–2 mm long, abaxially glabrous or glabrate with eglandular or glandular hairs; limb 1.7–3.3 mm long, abaxially glabrous or glabrate (especially apically) with eglandular hairs, adaxially glabrous; lobes triangular, (1–)1.3–2.5 x (0.8–)1–1.8 mm, marginally eciliate or rarely ciliolate with eglandular hairs, apically acute; sinuses acute (V-shaped). Corolla pink or white, thin-fleshy, bistratose, tubular or urceolate, (4.5–)6.5–13.5 mm long, 2–3.5 mm diam., 1.3–2.8 mm wide at throat, abaxially glabrate with eglandular or glandular hairs, adaxially glabrous (especially in South America, although the presence of indumentum may vary within the same population) or glabrate; lobes 0.7–1.5 x 0.8–1.3 mm, apically acute, adaxially rugose. Stamens 8, (4–)6.5–11.8 mm long, included or rarely the tips exserted; filaments distinct, straight, more or less linear with parallel sides or broader at base, (2.5–)4–7.5 mm long, abaxially and adaxially glabrate, pilose, or pilulose; anthers distinct, papillae only on thecae; thecae 1–1.5(–1.8) mm long, with or without basal appendages; tubules 2, distinct, 1.3–2.5(–3.1) mm long, dehiscing introrsely by longitudinal slits, 0.9–1.1 mm long. Ovary 4-locular; style 5.7–10(–12) mm long, exserted. **Berry** white (few unconfirmed reports of light purple fruits; fruiting specimens have not been collected in Central America), more or less spherical, the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo color unknown.



Map 9. Geographic distribution of *Disterigma humboldtii* ●*, D. leucanthum* ▲, and *D. micranthum* ★.

Distribution and ecology. *Disterigma humboldtii* is the second most collected species of the genus, and 85% of the collection events come from Central America, mainly from Costa Rica (71%), along with some representatives from Panama, Mexico, Guatemala, and Honduras. In South America, this species is found scattered in Colombia, Venezuela, Ecuador, and Peru (Map 9). It grows in premontate and montane cloud forests between (1000-)1500-3500 m. Flowering specimens have been found year-round and fruiting specimens year-round except for January and April.

Etymology. This species was named in honor of the explorer, A. von Humboldt.

Representative specimens examined. MEXICO. Oaxaca: Mun. San Miguel Chimalapa, Cima del Cerro Salomón, al NW de Benito Juárez, 1880 m, 13 Feb 1986 (fl) *Ishiki 1406* (NY); Mun. San Miguel Chimalapa, Cerro Baúl, en línea recta al N de San Pedro Tapanatepec, 1900 m, 19 Jul 1985 (fl). *Wendt et al. 5037* (NY); Mun. Santa María Chimalapa, Puerto de los Duendes, entre Cerro Quetzal y Cerro Solomón, 1800-1900 m, 22 Jul 1985 (fl). *Wendt et al. 5094* (CAS, MO).

GUATEMALA. Alta Verapaz: Mun. San Juan Chamelco, montaña Caquipec, Chicacnab I, 2200 m, 4 Nov 1999 (fl), *Förther et al. 10447* (BM, NY); Chamá to Cobán, 1000 m, 23 Aug 1920 (fl), *H. Johnson 645* (F, US). **Baja Verapaz:** entre Quetzal y Purulhá, 8 dec 1993 (fl), *Castillo et al. 2099* (B, F); Unión Barrios, 9 Mar 1972 (fl), *Contreras 11199* (BM, CAS, DUKE, LL, NY); Chilasco, 6 km E on Concepción road, 28 Jul 1971 (fl), *Contreras 10906* (DUKE, LL, NY); near Tres Rostros in W end of Sierra de las Minas, 2000 m, 23 Feb 1945 (st), *Sharp 45249* (GH). **El Progreso:** Sierra de las Minas, between Finca Piamonte and summit Volcán Santa Luisa, 2400-3333 m, 5 Feb 1942 (fl), *Steyermark 43534* (F, NY). **Huehuetenango:** Cerro Huitz, between Barillas and Mimanhuitz, Sierra de los

Cuchumatanes, 1600-2600 m, 14 Jul 1942 (fl), *Steyermark 48535* (A, F). **Zacapa:** between Loma El Picacho and Cerro de Los Monos, 2000-2600 m, 16 Jan 1942 (fl), *Steyermark 42817* (F).

HONDURAS. Olancho: top of La Picucha de PN de Agalta, 13 km NNW of Catacamas, 2350 m, 2 Jun 1992 (fl), *D'Arcy 18084* (MO), *Mejía 147* (DUKE, MO).

COSTA RICA. Alajuela: 15 km from Vara Blanca on road to Volcán Poás, 2500-2600 m, 31 Dec 1973 (fl), *Almeda et al. 2210* (DUKE); Monteverde Reserve, trail El Valle, 1600 m, 26 Oct 1985 (fr), *Haber 3174* (MO); Monteverde Cloud Forest Reserve, Peñas Blancas river valley, 950-1100 m, 27 Jul 1986 (fl, fr), *Haber et al. 5797* (MO); San Ramón, Los Angeles, Reserva Forestal San Ramón, 1000 m, 4 Dic 1993 (st), *G. Herrera 6761* (F); San Ramón, Los Angeles, Reserva Biológica Alberto M. Brenes, 1300 m, 14 Oct 1994 (st), *G. Herrera et al. 7371* (F); Cerro Azahar, headwaters of Río San Pedro, 1400-1500 m, 14 May 1983 (fl), *Liesner et al. 15591* (MO, NY, WIS); road out of San Ramón, beyond Angeles Norte, 1100-1200 m, 15 Dec 1974 (fl), *Luteyn et al. 4279* (DUKE, NY); cantón San Ramón, R. F. San Ramón, Cordillera de Tilarán, Lon Angeles Norte, 1100 m, 6 Jun 1995 (fl), *Morales 4428* (MO); road San Ramón-Balsa, 14 km N of bridge over Quebrada Volio, 900-1000 m, 29 Aug 1979 (fl), *Stevens 13751* (DUKE, F, LL, MO, NY); PN Poás, 2500 m, 13 Aug 1978 (fl), *Wilbur 27709* (DUKE). **Cartago:** Reserva Río Macho, 3 de Junio, Cordillera de Talamanca, 2625 m, 19 Oct 1989 (fl), *Crow 7396A* (F, MO); Cerro de la Muerte, Cordillera de Talamanca, 2690 m, 5 May 1985 (st), *Horn SPH210* (UC, WIS); road from La Trinidad to Hacienda El Volcán Turrialba, 2400-2600 m, 25 Dec 1974 (fl), *Luteyn 4520* (DUKE); slopes on property of ICE hydroelectric plant over Río Orosi, 1300-1800 m, 13 Dec 1974 (fl), *Luteyn et al. 4234* (DUKE), 1300-1800 m, 20 Dec 1974, *Luteyn et al. 4399* (DUKE); Turrialba, PN Barbilla, cuenca del Matina, sendero Barthon Cerro Akata, 1600 m, 7 Mar 2001 (fl), *E. Mora 1854* (NY); Cerro de la Carpintera, 1500 m, Feb 1924 (st), *Standley 34326* (US); Cerro Asunción, 3200 m, 8 Feb 1988 (fl), *Widmer 960* (NY); Cerro Cuerici, 2900 m, 16 Aug 1989 (fl), *Widmer 811* (NY); S El Empalme, 2300 m, 4 Jul 1976 (fl), *Wilbur 19874* (DUKE). **Guanacaste:** Rincon de la Vieja, PN Santa Maria, 1800-1900 m, 8 Apr 1984 (fl), *Baker SM6* (BM); Río Chiquito de Arenal, Tilaran, San Bosco river valley, 1000-1300 m, 28 Aug 1986 (fl), *Haber 5584* (MO); Río Chiquito de Tilaran, Río Negro, 1450 m, 1 Jul 1986 (fl), *Haber et al. 5164* (MO); cantón Liberia, PN Guanacaste, Volcán Cacao, 1200-1600 m, 12 Jul 1996 (fl), *J. F. Morales et al. 5484* (NY). **Heredia:** PN Braulio Carrillo, 1990 m, 2 Sep 1992 (fl), *Boyle 1047* (DUKE); area Gallito, Reserva Forestal Cordillera Central Volcánica, 2020 m, 13 Mar 1984 (fl), *Cowan 4550* (NY, TEX); PN Braulio Carrillo, Río Bajo de Honduras, La Palma, 1150 m, 23 Jan 1983 (fl), *Garwood et al. 406* (BM); Vara Blanca de Sarapiquí, 1500-1700 m, Sep 1937 (fl), *Skutch 2345* (L); Cerros de Zurquí, NE of San Isidro, 2000-2400 m, 3 Mar 1926 (fl), *Standley & Valerio 50820* (US); S of PN Braulio Carrillo, above Sacramento y San José de la Montaña, 2500-2700 m, 24 Jul 1980 (fl), *Wilbur 29617* (DUKE); Volcán Barba, 2200-2800 m, 3 May 1971 (fl), *Wilbur 14051* (DUKE, LL, MICH, MO); Cerro Chompipe, 1800-2000 m, 21 Dec 1974 (fl), *Wilbur & Luteyn 18605* (DUKE). **Limón:** Cordillera de Talamanca, Kámuk massif, 3000-3200 m, 17-18 Sep 1984 (fl), *Davidse et al. 29281* (DUKE, MO); Cordillera de Talamanca, Valle de Silencio, 2350-2450 m, 8 Sep 1984 (fl), *Davidse et al. 28569, 28709* (MO). **Puntarenas:** Cordillera de Talamanca, cantón Pérez Zeledón, PI La Amistad, 2600-2800 m, 6 Apr 1995 (fl), *Aguilar & Garrote 3891* (NY), 2450 m, 20 Sep 1996 (fl), *J. F. Morales & Quesada 5801* (NY); Reserva Biológica Monteverde, Ojo de Agua Arancibia, 1300-1500 m, 3 Oct 1989 (fl, fr), *E. Bello 1328* (MO); Cordillera de Talamanca, Cerro Echandi, 3050-3160 m, 22 Aug 1983 (fl), *G. Davidse et al. 23897* (MO, NY); PN Braulio Carrillo, 3 Mar 1994 (fl), *Alverson 2988* (COL). **San José:** cantón Pérez Zeledón, cuenca Térraba-Sierpe, Estación Cuericí, 2800-2900 m, 24 Sep 1996 (fl), *Gamboa 713*

(MO); cantón Dota, R.F. Los Santos, cuenca del Savegre, R. F. Río Macho, 3000 m, 24 Jun 1997 (fl), *Gamboa 1536* (MO); cantón Desamparados, Altos del Tablazo, 1700-1980 m, 23 Apr 1994 (fl), *J. F. Morales 2717* (NY); La Palma, 1600 m, 3 Feb 1924 (fr), *Standley 32973* (US); about 7 km NE of Cascajal and about 1.6 km NE of Lecheria Juncos, 1650 m, 3 Jul 1976 (st), *Wilbur 19817* (DUKE); trail between Alto La Palma and Baja La Hondura, 1300-1480 m, 13 Jul 1976 (fl), *Wilbur 20361* (DUKE, NY); Cerro Danser, WSW of Aserri, 2100-2300 m, 18 Feb 1978 (fl), *Wilbur 24512* (DUKE).

PANAMA. Bocas del Toro: Robalo trail, N slopes of Cerro Horqueta, 1800-2000 m, 5-7 Aug 1947 (fl), *Allen 4986* (F, MO, US); Valle del Silencio, 8-10 Aug 1979, *Antonio 1630* (NY, PMA); slopes of Cerro Itamut, 3100 m, 4 Mar 2006 (fl), *Knapp & Monro 9878* (BM, NY), 3200 m, 12 Mar 2006 (fl), *Knapp & Monro 9977* (BM). **Chiriquí:** Bajo Mono-Robalo trail, W slopes of Cerro Horqueta, 1520-2130 m, 27 Jul 1947 (fl), *Allen 4845* (F, MO, NY, S, US); distrito Rancimiento, Jurutungo, alrededores de Cerro Pando, de Los Quetzales hasta hito fronterizo, 1940-2385 m, 22 Sep 1926 (fl), *Aranda 3126* (PMA); distrito Renacimiento, Jurutungo, entre La Quijada, del Diablo y la cima de Cerro Pando, 2315 m, 25 Sep 1996 (fl), *Galdames 3400* (F, MO, PMA); Cerro Pate Macho, above Cerro Pate Alto, 2200 m, 15 Mar 1982 (fl), *Knapp et al. 4242* (DUKE, MO); Boquete, PI La Amistad, La Pila region, Cerro Puna-Las Nubes road, trail El Retoño, 2100-2256 m, 21 Jan 2003 (fl), *Luteyn & P. Pedraza 15571* (AAU, COL, INB, K, MEXU, MO, NY, PMA, US), *15572* (NY, PMA), *15573* (COL, INB, MO, NY, PMA); Guadalupe Arriba, above Cerro Punta, 2100 m, 23 Jul 1985 (fl), *Nevers 6032* (MO); Bajo Chorro, 1900 m, 20-22 Jul 1944 (fl), *Woodson & Schery 684* (MO, NY). **Coclé:** summit of Cerro Gaital, N of El Valle, 1000-1400 m, 10 Jul 1982 (fl), *Knapp et al. 5997, 5978* (MO); summit of Cerro Gaital, N of El Valle. **Veraguas:** summit of Cerro Tute, N of Santa Fé, from trail, that begins 0.7 km N of the Escuela Agricola de Alto Piedra, 1450 m, 18 Feb 1996 (fl), *Luteyn 14871*

(DUKE, NY, PMA); summit of Cerro Arizona, N of Santa Fé, 1450 m, 6 Oct 1998, *Luteyn et al. 15284* (PMA, NY).

COLOMBIA. Antioquia: Mun. Yarumal, vereda El Cedro, Altos de Ventanas, 2000 m, 9 Jul 2004 (fl), *P. Pedraza et al. 1069* (AAU, COL, HUA, MO, NY), *1070* (COL, CUVC, HUA, MO, NY), *1075* (AAU, COL, CUVC, HUA, MO, NY); Mun. Guatepé, NNE of Guatapé, vereda Santa Rita, Finca Montepinar, 1850 m, 20 Nov 1986 (fl), *Zarucchi 4167* (COL, HUA, MO, NY). **Boyacá:** Buenavista, headwaters of Río Pauto, ridge of Quebrada Laja (Quebrada Colorada), 2700 m, 10 Nov 1944 (fl), *Fosberg 22237* (NY, UC, US). **Cundinamarca:** Guadalupe, Bogotá, 2850 m, s.d. (fl), *Bro. Daniel 13* (NY); near Guasca, 3100 m, 31 May 1941 (fl), *Haught 5791* (COL, P, UC, US). **Valle del Cauca:** Hoya del Río Guadalajara, 2500-2550 m, 27 Feb 1969 (fl), *Cuatrecasas et al. 27591* (COL, NY, US).

VENEZUELA. Amazonas: Cerro Neblina, S slopes of Cañón Grande, 1900 m, 30 Nov 1984 (fl), *Croat 59472* (MO, NY, US); Atures, Serranía Yutajé, cumbre del Cerro Yutajé, Cañon Yutajé, 1800 m, 21 Mar 1988 (fl), *Hube 12615* (NY, US); Atabapo, Cerro Marahuaca, 2700 m, 12 Oct 1988 (fl), *Liesner 24691* (MO, NY), 2685 m, 15 Jan 1981 (fl), *Maguire et al. 65670* (NY), 2480-2500 m, 1-2 Feb 1982 (fl), *Steyermark et al. 126016* (NY). **Bolivar:** distrito Piar, Apáraman tepuí, 2100 m, 27 Mar 1987 (fl), *Holst 3709* (MO, NY); distrito Cedeño, Serranía Guanay, en las altiplanicies mas E del Río Parguaza, 1700 m, 20-28 Oct 1985 (fl), *Huber 11030* (NY, US); Meseta del Jaua, cabeceras del Río Marajano, afluente del Cácaro, 1750-1800 m, 20 Nov 1989 (fl), *Hube 12987* (NY); Ptari tepuí, 1600-2000 m, 17 Dec 1952 (fl), *Maguire & Wurdack 33893* (NY); distrito Piar, Macizo de Chimantá, NE del tepuí Acopán, 1950 m, 8-11 Feb 1985 (fl), *Pipoly et al. 7180* (NY); Auyán tepuí, 1800 m, 28 Aug 1983 (fl), *Prance & Huber 28291* (MO, NY, US), 14 May 1964 (fl), *Steyermark 93886* (L, NY, US); distrito Piar, Murisipan tepuí, 1700 m, 26 May 1986 (fl), *Steyermark et al. 132119* (MO, NY);

Cerro Venamo, cerca de los límites con la Guyana Inlgesa, 95-1150 m, 29-30 Dec 1963 (fl), *Steyermark et al. 92342* (L, NY, US).

ECUADOR. Cotopaxi: Pilaló, 3000 m, 1-3 May 1959 (fl), *Harling 4923* (L, S); cantón Sigchos, 2840 m, 21 Jul 2003 (fl), *J. Ramos et al. 6412* (NY). **Imbabura:** carretera Cotacachi-Apuela, 3000 m, 21 Dec 2003 (fl), *P. Pedraza & C. Pedraza 1008* (NY, QCA, QCNE). **Loja:** PN Podocarpus, 2700-3300 m, 16 Aug 2004 (fl, fr), *P. Pedraza & N. R. Salinas 1202* (AAU, COL, MO, NY, QCA, QCNE), 2700-3300 m, 17 Aug 2004 (fl, fr), *P. Pedraza & N. R. Salinas 1212* (COL, MO, NY, QCA, QCNE). **Loja/Zamora-Chinchipe:** Loja-Zamora road, 2700 m, 31 Dec 1978 (fl), *Luteyn et al. 6566* (NY). **Morona-Santiago:** Cordillera de Huaracayo, E of Cordillera del Cóndor and Río Coangos, 1760 m, 19 Mar 2001 (fl, fr), *Neill et al. 13068* (NY). **Pichincha:** Carretera Quito-Nono-Mindo, camino Viejo, 2600 m, 10 Dec 2003 (fl, fr), *P. Pedraza & C. Pedraza 961* (NY, QCA, QCNE).

PERU. Pasco: Prov. Oxapampa, PN Yanachaga Chemillén, abra La Esperanza, 2800 m, 23 Mar 2003 (fl), *Monteagudo et al. 4779* (USM); Prov. Oxapampa, distrito Villa Rica, PN Yanachaga-Chemillén, Abra Villa Rica, 2300 m, 14 Jun 2005 (fl, fr), *E. Ortiz et al. 693* (HOXA, MO, NY, USM); Prov. Oxapampa, distrito Huancabamba, PN Yanachaga-Chemillén, Milpo, 2900 m, 1 Feb 2005 (fr), *E. Ortiz et al. 275* (HOXA, MO, USM); Prov. Oxapampa, distrito Oxapampa, PN Yanachaga-Chemillén, Chacos, camino hacia la antena, 2380 m, 16 Jun 2006 (fl, fr), *P. Pedraza et al. 1614* (COL, NY, USM).

Disterigma humboldtii is characterized by its leaves subacute, obtuse, or rarely blunt acute; by its solitary flowers with the pedicel usually reduced and hidden by the overlapping bracts; by its differentiated apical bracteoles enveloping the entire calyx tube or up to the upper limb; by its corollas white, tubular or urceolate, (4.5–)6.5–13.5 mm long, with equally length variable stamens; by its stamens with the thecae papillate; and by its white berries and embryos (fruiting specimens have not been collected in Central America). Unlike the adaxially puberulous corollas of *D. alaternoides*, a species frequently thought to be close to *D. humboldtii* (Luteyn, 1996; Smith, 1933; Wilbur, 1992), the corollas of *D. humboldtii* are adaxially glabrous in South America (although inconspicuous hairs may be found within the same population) or mostly glabrate with minute hairs in Central America (sometimes inconspicuous). These two taxa are discussed in more detail in *D. alaternoides*.

The linear variation in leaf and flower size observed in *Disterigma humboldtii* is reflected in the number of synonimyzed taxa, each one of them originally describing a different combination of traits (i.e., long corollas with small leaves, short corollas with large leaves, small corollas with small leaves, etc.), but all essentially with the same floral characteristics (see Fig. 20 for an example of *D. mayanum*). Differences in size are likely to be shaped by micro-environmental factors, thus *D. ecuadorense* and *D. pilosum* are here synonymized. The external indumentum can also be shaped by the environment or it can be manifested differently with age; for example, the pilulose indumentum of *D. pilosum* have been also found in representative specimens of *D. humboldtii* on the young shoots, but not in the mature branches.

Local names and uses. This species is known as “Muras” in Morona-Santiago (Ecuador).

18. Disterigma leucanthum A. C. Sm., Mem. New York Bot. Gard. 8(1): 50. 1952. Type. Ecuador. Morona-Santiago: Cordillera Cutucú, ridge S and W of Río Itzintza, 1525-1800 m, 17 Nov 1944 (fl), *Camp E-1344* (holotype, US; isotypes, F, NY). Photo NY neg. 9891 ex NY.

Epiphytic **shrubs**. Young branchlets ridged, more or less smooth, glabrate, the hairs inconspicuous, eglandular, and white, the mature branches glabrous. **Leaves** 0–2 per cm, spirally arranged, diffuse or patent; petiole 1.5–2.2 mm long, glabrate, the hairs inconspicuous, eglandular; lamina ovate or elliptic, 1.2–2.8 x 0.7–1.6 cm, basally obtuse, marginally entire, slightly revolute, apically ciliolate with minute eglandular hairs, apically obtuse or acute, adaxially glabrous or glabrate with inconspicuous eglandular hairs over the midvein, abaxially glabrate with glandular hairs, the venation adaxially 3- or 5-nerved with the midvein impressed or raised, abaxially hyphodromous with the midvein raised. Axillary **solitary flowers** and rarely 2-flowered fascicles; bracts 5–7, chartaceous, ovate, 0.7–1.5 x 0.9–1.4 mm, marginally ciliolate with inconspicuous eglandular hairs, apically obtuse, abaxially glabrate with inconspicuous eglandular hairs; pedicel 1.7–3 mm long, evident or at least with a portion of it not completely obscured by overlapping bracts, puberulous with eglandular and glandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping entire calyx tube, covering 30–47% of calyx, obovate or transverse-elliptic, 1.5–2 x 2.6–4 mm, marginally ciliate with eglandular or glandular hairs, apically truncate (less often subtruncate), the surface slightly pustulate, abaxially densely puberulous or glabrate in cultivation, the hairs eglandular, adaxially glabrous. **Flowers** 4-merous. Calyx aestivation imbricate, campanulate, (3.5–)4.2–6.5 mm long; tube angled, 1.2–2.5 mm long, abaxially densely puberulous or glabrate in cultivation, the hairs eglandular; limb (2–)3–4 mm long, abaxially densely puberulous or glabrate with eglandular hairs, adaxially glabrate with minute eglandular hairs; lobes ovate, (2–)2.5–3.8(–4.5) x (1.5–)2–3.2(–3.5) mm, marginally ciliate with eglandular hairs, apically acute; sinuses obscured by the overlapping bases of the imbricate lobes (sometimes pressing makes the lobes spread). Corolla pink or white, thick-fleshy, bistratose, urceolate, (5.5–)6–9 mm long, 3.7 mm diam. (1.8–2.3 mm in dry), 3 mm wide at throat (1.5–2.3 mm in dry), abaxially densely puberulous (especially distally) or glabrate in cultivation, the hairs eglandular or glandular, adaxially glabrate at least on the lobes; lobes 0.9–2 x 0.8–1.3 mm, apically acute, adaxially rugose. Stamens 8, (4.5–)5.8–6.4 mm long, exserted or included; filaments distinct, straight, more or less linear with parallel sides, 2.2–3 mm long, abaxially glabrous or glabrate in cultivation, adaxially puberulous distally; anthers distinct, papillae only on thecae, some with few hairs at base; thecae (1.3–)1.7–2 mm long, without basal appendages; tubules 2, distinct, 1.9–2.6 mm long, dehiscing introrsely by longitudinal slits, 0.6–0.7 mm long. Ovary 4-locular; style (5–)6.3–9.7 mm long, exserted. **Berry** unknown.

Distribution and ecology. *Disterigma leucanthum* is a rare species only known from very few collections from Cordillera Cutucú and Cordillera del Cóndor, in the eastern Ecuadorian province of Morona-Santiago (Map 9). This species grows in premontane cloud forests between 1000-1800 m, apparently on sandy soils. Flowering specimens have been found in September, November, and December.

Etymology. The species name makes reference to the white corollas.

Representative specimens examined. ECUADOR. Morona-Santiago: Cordillera del Cóndor, 1200 m, Aug 1976 (fl), *Argent C12881* (E, from living material at The Royal Botanic Garden Edinburgh, Acc. No. 762392 P10), 1200 m, 29 Sep 2003 (fl), *Cubey 2* (E, from living material at The Royal Botanic Garden Edinburgh, Acc. No. 19762392*D); Limón Indanza, Cordillera del Cóndor, Cerro Chuank Naint, 1130 m, 20 Dec 2005 (fl), *Kajekai et al. 283* (NY); Limón Indanza, Cordillera del Cóndor, Cerro Shuar Yunkumanas, Asociación Nunkui, Cerro Chuank Naint, 1150 m, 19 Dec 2005 (fl), *C. Morales et al. 1606* (NY).

The type collection of *Disterigma leucanthum* has distinctive flowers with the calyces and corollas densely puberulous abaxially; the calyx aestivation imbricate with the sinuses obscured by the overlapping bases of the imbricate lobes (sometimes pressing makes the lobes spread); the calyx lobes ovate and adaxially glabrate; and the corolla adaxially glabrate. Also characteristic of the species is the pedicel evident or at least with a portion of it not completely obscured by the overlapping bracts, and the differentiated apical bracteoles with the surface minutely pustulate. However, the floral indumentum in other collections, including specimens from cultivated plants (*Argent C12880, C12881, Cubey 2*), is glabrate instead of puberulous. Unfortunately, the known herbarium specimens of this species are so few that at the moment it is not possible to discern which represents the typical condition. Additional collections from Los Tayos [*Argent C12880* (E)] and from Valle del Río Pastaza, near El Topo [*Camp E-1684-5* (NY, US), *E-2410* (NY)], differ from the typical *D. leucanthum* in not having calyx lobes overlapping so strongly. Collections from Huila (Colombia) [*Luteyn 4966* (COL, L, NY) and *Lozano 4145* (COL, WIS)] could belong here or to a new species, but unfortunately, the flowering material is too deficient to justify the inclusion of such a disjunct population.

Conservation status. *Disterigma leucanthum* is known from few collections with a relatively restricted distribution area in eastern Ecuador. It was not until 2005 that new collections were added to the last known from 1976, and in 2003, a living collection was known to be at the Royal Botanic Garden of Edinburgh. *Disterigma leucanthum* is threatened by logging and colonization, and in the IUCN red list of plants endemic to Ecuador it is categorized as VU D2 (Pedraza-Peñalosa et al., in press).

19. Disterigma micranthum A. C. Sm., Mem. New York Bot. Gard. 8(1): 52. 1952. Type. Ecuador. El Oro: Moro-moro region, about 21 miles W of Portovelo, 1035-1280 m, 7 Oct 1944 (fl), *Camp E-616* (holotype, NY; isotype, fragment US ex NY). Photo NY neg. 9892 ex NY, photo US neg. 3434 ex NY.

(Fig. 10 E)

Epiphytic or terrestrial **shrubs**, scandent or erect, about 1 m tall. Young branchlets ridged, more or less smooth, villosulous, the hairs eglandular and brown, the mature branches indumentum similar but glabrate. **Leaves** 4–5 per cm, apparently distichous, diffuse; petiole 1 mm long, glabrate, the hairs eglandular; lamina ovate or elliptic, 0.4–1 x 0.3–0.4 cm, basally cuneate, marginally entire, apically ciliolate with eglandular hairs, apically subacute or blunt acute, adaxially glabrous, abaxially glabrate with glandular hairs, the venation adaxially and abaxially obscure. Axillary **solitary flowers**; bracts 4–5, chartaceous, ovate or elliptic, 0.6–1.5 x 0.6–1.1 mm, marginally eciliate, apically obtuse, abaxially glabrous; pedicel 1–2 mm long, reduced and hidden by overlapping bracts, glabrous; differentiated apical bracteoles 2, distinct, chartaceous, enveloping to upper half of calyx lobes or entire calyx, covering 54–93% of calyx, elliptic or transverse-elliptic, 2–3 x 2–3 mm, marginally eciliate, apically obtuse, the surface smooth, abaxially and adaxially glabrous. **Flowers** 4-merous. Calyx aestivation valvate, campanulate, 2.3–3 mm long; tube terete, 0.9–1.2 mm long, abaxially glabrate with glandular hairs; limb 1.3–2.1 mm long, abaxially and adaxially glabrous; lobes triangular, 0.9–1.5 x 0.8–1.1 mm, marginally eciliate; sinuses acute (V-shaped). Corolla white, thin-fleshy, bistratose, urceolate, 3–4.5 mm long, 3 mm diam., 2 mm wide at throat, abaxially glabrate with minute and very few glandular hairs, adaxially glabrous; lobes 0.9 x 0.6 mm, apically acute, adaxially rugose. Stamens 8, 3–3.5 mm long, included;

filaments distinct, straight, broader at base, 1.8–2.3 mm long, abaxially and adaxially pilulose; anthers distinct, papillae on both thecae and tubules; thecae 0.7–0.8 mm long, with or without basal appendages; tubules 2, distinct, 0.6–0.8 mm long, dehiscing introrsely by longitudinal slits, 0.4–0.5 mm long. Ovary 4-locular; style 3.4–3.5 mm long, exserted. **Berry** white, more or less spherical, 4.5–5.6 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo white.

Distribution and ecology. *Disterigma micranthum* is only known from two populations (three collections altogether) in the Ecuadorian Andes (Map 9). The type specimen is from the Moro-Moro (south-western Ecuador) region were it was recollected in 2004. There, is a reserve located there now and the species was only found in a dense patch of secondary vegetation bordering the reserved area next to a major road. The second known population was recorded in 1980 on the old road to Santo Domingo de los Colorados, in the province of Pichincha. This species grows in low altitude premontane cloud forest, between 900-1600 m. Flowering specimens have been collected in August and October, and fruiting specimens in August.

Etymology. The name of this species makes reference to its very small flowers.

Specimens examined. ECUADOR. El Oro: región de Moro-Moro, a lo largo del borde de la Reserva Forestal Buenaventura (Fundación Jocotoco), cerca de 10 km después de Piñas, en la vía a Machalá, 900-1100 m, 19 Aug 2004 (fl, fr), *P. Pedraza & N. R. Salinas 1229* (AAU, COL, E, HUA, LPB, MO, NY, QCA, QCNE, US). **Pichincha:** Chillogallo-Santo Domingo road, below Chiriboga, 16 km from the new road, 1600 m, 13 Aug 1980 (fl), *Holm-Nielsen. et al. 24811* (F, K, MO, NY).

Disterigma micranthum is distinguished by having very small flowers (3-4.5 mm long), with very small stamens (3-3.5 mm long), and tubules under 1 mm long; its terete calyx tube is also characteristic (Fig. 10 E). *Disterigma micranthum* belongs to a group of taxa that are closely related and that exhibit great vegetative and reproductive variation; they are *D. dendrophilum* and *D. noyesiae* (see Table 12)*,* with *D. cryptocalyx* and *D. humboldtii*, probably more distantly related*.* Although it is possible to find morphological features that characterize each one of these species, the differences between them are not that many, except when comparing species with extreme morphologies, such as *D. micranthum* and *D. cryptocalyx*.

Table 12. Summary of differences between *Disterigma micranthum*, *D. dendrophilum,* and *D. noyesiae*

Characters	***D. micranthum***	***D. dendrophilum***	***D. noyesiae***
Leaf apex	Subacute, blunt acute	Acute to long acuminate	Subacute, blunt acute, acute, acuminate
Pedicel conspicuousness	Hidden by overlapping bracts	With at least a portion of it evident	With at least a portion of it evident or sometimes hidden
Differentiated apical bracteoles calyx coverage	54-93%	50-65%	Usually extending up to 2.2 mm beyond the calyx or rarely as long as the calyx
Calyx tube in cross section	Terete	Angulate (only known in dry)	Angulate
Corolla shape and length	Urceolate, 3-4.5 mm long	Tubular, 4.4-5.6 mm long	Tubular or urceolate, 4-10(-11) mm long
Stamens length	3-3.5 mm long	(4-)4.4-5 mm long	4.0-8.0(-9.1) mm long
Anthers length	1.3-1.5 mm long	2.5-3 mm long	(2.1-)2.5-4.8 mm long
Tubule length	0.6-0.8 mm long	1.5-2 mm long	1-2.4 mm long
Anther papillae	On both theca and tubule	On theca	On theca

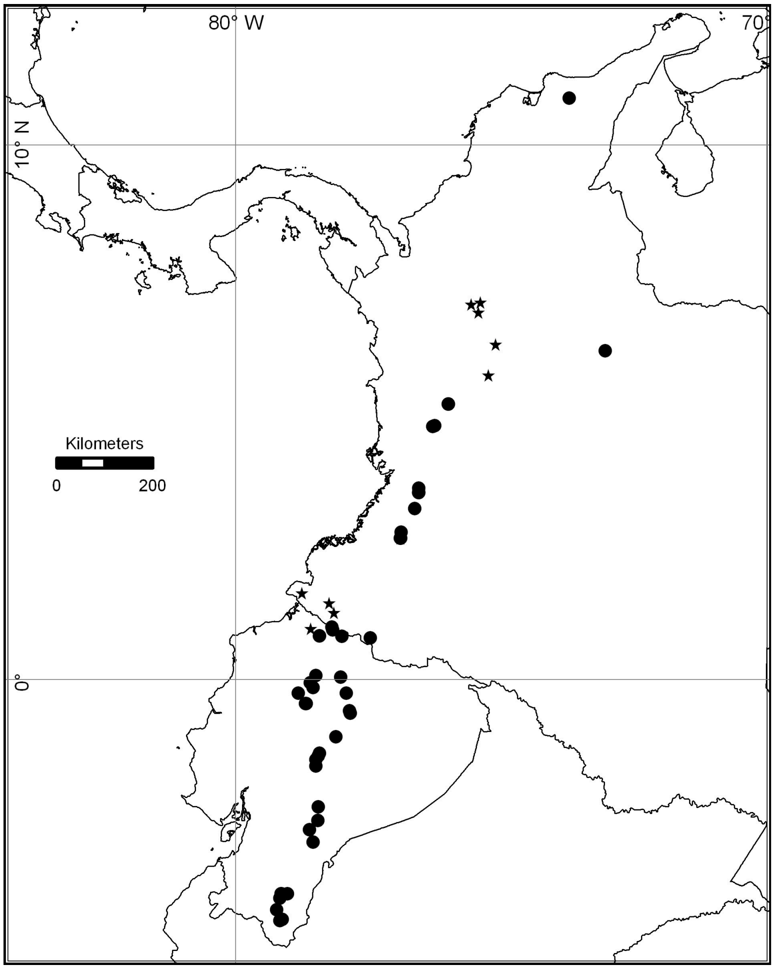
Conservation status. *Disterigma micranthum* is only known from two disjunct populations, one from Pichincha (ca. Santo Domingo de los Colorados) and the other from El Oro (ca. Moro-Moro). It was not re-collected since 1980 until 2004, when it was found in the type locality (Moro-Moro), in the Reserva Forestal Buenaventura (Fundación Jocotoco). There, the species was found forming a large patch among secondary vegetation, along the border of the reserve facing the main road; however, in a quick exploration of the reserve no additional populations were found within the protected area (Pedraza, obs. pers.). Colonization, agriculture, and mining are the main threats in this region. In the IUCN red list of plants endemic to Ecuador it is categorized as EN B1 ab(iii) (Pedraza-Peñalosa et al., in press).

20. Disterigma noyesiae Luteyn, Fl. Ecuador 54: 272. 1996. Type. Ecuador. Carchi: 9 km E of El Chical, 12 Nov 1988 (fl), *Dorr & Barnett 6072* (holotype, NY; isotypes, AAU n.v., CAS, QCA n.v., QCNE n.v.). The sheets at AAU, QCA, and QCNE were not found.

Epiphytic or terrestrial **shrubs**, scandent or erect, 0.3–4 m tall. Young branchlets ridged, more or less smooth, villous or villosulous, the hairs eglandular and brown, the mature branches indumentum similar but glabrate. **Leaves** 3–11 per cm, apparently distichous, diffuse or patent; petiole 0.5–1.6(–2) mm long, glabrous or glabrate, the hairs eglandular or glandular; lamina ovate or elliptic, 0.4–2(–2.4) x 0.3–1(–1.5) cm, basally cuneate or obtuse, marginally entire, apically ciliolate with eglandular hairs, apically acute or acuminate or sometimes subacute or blunt acute, adaxially glabrous or glabrate with minute eglandular hairs, abaxially glabrate with glandular hairs, the venation obscure or 3-nerved on both sides, the midvein adaxially impressed and abaxially raised.

Axillary **solitary flowers** and rarely 2-flowered fascicles; bracts 5–8, chartaceous, ovate, elliptic, or transverse-elliptic, 0.6–3.2 x 0.6–2.7 mm, marginally eciliate or sometimes apically ciliolate with minute eglandular hairs, apically obtuse, abaxially glabrous; pedicel 1–4(–5) mm long, evident or at least with a portion of it not completely obscured by overlapping bracts, or sometimes reduced and hidden by overlapping bracts, glabrate or rarely glabrous, the hairs eglandular or glandular; differentiated apical bracteoles 2, distinct, chartaceous, enveloping entire calyx (92–100% of calyx) or extending beyond calyx (0.5–2 mm beyond the calyx), elliptic or suborbicular or transverse-elliptic, 2.4–6(–7) x 2.6–7.5 mm, marginally eciliate or apically ciliate with eglandular hairs, apically obtuse (and usually splitting when large), the surface smooth, abaxially and adaxially glabrous. **Flowers** 4-merous. Calyx aestivation valvate, campanulate to cylindric, (2–)2.3–5.2 mm long; tube weakly angled, 0.8–3.6 mm long, abaxially glabrous or glabrate with glandular hairs; limb 0.8–2.5 mm long, abaxially and adaxially glabrous; lobes triangular, 0.4–2.2 x 0.5–2.2 mm, marginally eciliate, apically acute; sinuses acute (V-shaped) or rarely rounded (U-shaped). Corolla pink or white, thin-fleshy, bistratose, tubular or urceolate (inflated at the middle), 4–10(–11) mm long, (2.7–)4–4.4 mm diam., (1.6–)3–3.2 mm wide at throat, abaxially glabrate with glandular hairs, adaxially glabrous; lobes 0.6–1.6 x 0.8–2 mm, apically acute, adaxially rugose. Stamens 8, (3.6–)4–8(–9.1) mm long, included or sometimes the tips exserted; filaments distinct, straight, more or less linear with parallel sides or broader at base, (2–)2.5–5.2 mm long, abaxially and adaxially pilulose or puberulous; anthers distinct, papillae only on thecae; thecae 1–2.4 mm long, basally appendaged; tubules 2, distinct, 1.1–2.8 mm long, dehiscing introrsely by longitudinal slits, (0.4–)0.6–1.5 mm long. Ovary 4-locular; style 4–9.9 mm long, exserted (the style many times remain enclosed by the enveloping bracteoles after the corolla is shed; when the fruit is maturing it falls off and the bracteoles spread out). **Berry** white, more or less spherical, 6–12 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo white.

Distribution and ecology. The herbarium specimens of *Disterigma noyesiae* come from all over Ecuador, but it is also known from central and southern Colombia, with only a few other scattered collections in the north (Map 10). This species has great altitudinal variation, growing in premontane and montane cloud forests, between 1000-3500 m. Flowering specimens have been collected year-round except it January and March, and fruiting specimens year-round except it January.



Map 10. Geographic distribution of *Disterigma noyesiae* ● and *D. pseudokillipiella* ★.

Etymology. This species was named after Jessie Smith Noyes.

Representative specimens examined. COLOMBIA. Cauca: PNN Munchique, Mun. El Tambo, vereda La Romelia, 1950 m, 25 Jul 1993 (fl), *F. González 2822* (COL), 2640 m, 20 Jul 1993 (fl), *F. González et al. 2794* (COL, PSO), 2600-2800 m, 5 Aug 1980 (fl), *Lozano 3652* (COL), 2500 m, 8 de Aug 2004 (fl), *P. Pedraza & Giraldo 1178* (CAUP, COL, NY), *1166* (COL, NY); PNN Munchique, km 60-65 along El Tambo-20 de Julio road, 2500-2560 m, 29 Apr 1979 (fl), *Luteyn et al. 7502* (AAU, CAUP, COL, MO, NY); PNN Munchique, Mun. El Tambo, entre La Romalia y La Gallera, 1700-2640 m, 7 Aug 2004 (fl), *P. Pedraza & Giraldo 1155* (CAUP, COL, CUVC, HUA, MO, NY). **Magdalena:** Sierra Nevada de Santa Marta, transecto Alto Río Buriticá, 3300 m, 9 Aug 1977 (fl), *Jaramillo-M. et al. 5445* (COL), 2700 m, 2 Aug 1977 (fl), *Jaramillo-M. et al. 5351* (COL). **Nariño:** Mun. Ipiales, corregimiento de La Victoria, Río Chingual, 2400-2600 m, 18 Apr 1995 (fl), *B. R. Ramírez 7306* (HUA). **Risaralda:** Mun. Apía, vereda Tatamá, Reserva Karagabí (Grupo GER), 3200 m, 13 Jul 2004 (fl), *P. Pedraza & C. Pedraza 1077* (AAU, COL, CUVC, HUA, MO, NY), *1080* (COL, CUVC, NY), 3200 m, 14 Jul 2004 (st), *P. Pedraza & C. Pedraza 1089* (COL). Santander: Mun. Encino, Reserva Biológica Cachalú, 1900-2200 m, 15 Jul 2002 (fl), *N. R. Salinas et al. 94* (COL). **Valle del Cauca:** Mares, 1970-2000 m, 13 Mar 1947 (fr), *Cuatrecasas 23766* (A, F, US); carretera Anselmanuevo-San Jose del Palmar, 1990 m, 25 Aug 1976 (fl, fr), *Forero et al. 2024* (COL), 1870-1950 m, 19 Apr 1979 (fl), *Luteyn et al. 7268* (AAU, COL, CUVC, MO, NY); Mun. Cali, Finca Zingara, carretera Cali-Buenaventura, corregimiento de la Elvira, 1900 m, 29 Oct 1995 (fl), *Giraldo-Gensini & Olver 487, 697* (NY), 1900 m, 2 Jun 1996 (fl), *Giraldo-Gensini & Olver 710* (NY); San Antonio, W of Cali , 1900-2350 m, 26 Feb-2 Mar 1939 (fl, fr), *Killip & García-Barriga 33876* (A, BM, COL, NY, US); cuenca del Río Cali, cerca de Peñas Blancas, 23 Jan 1963 (fl), *López-Figueiras 8355* (US); corregimiento El Boquerón, vereda El Brillante, Cerro del Inglés en la Serranía de los Paraguas, 2100 m, 22 Jul 2004 (fl, fr), *P. Pedraza & C. Pedraza*

1117 (AAU, CAUP, COL, CUVC, FMB, HUA, MO, NY, QCA, US), 2100 m, 23 Jul 2004 (fl), *P. Pedraza & C. Pedraza 1120* (COL); Mun. de la Cumbre, corregimiento de Bitaco, Reserva Agua Bonita, 1700-1900 m, 10 Dec 1998 15 Dec 1998 (fl), *W. Vargas 5382* (HUA); Mun. La Cumbre, corregimiento de Bitaco inspección de policia Chicoral, Reserva de la Sociedad Civil Agrícola-Himalaya, 2000-2220 m, 18 May 2006 (fl), *A. Zuluaga 287* (COL).

ECUADOR. Carchi: Tulcán-Maldonado road, near Maldonado, 2275 m, 23 May 1993 (fl), *Boyle & Bradford 1920* (MO, NY), 2550 m, 5 Aug 1976 (fl), *Ollgaard & Balslev 8480* (AAU, MO, NY), 2000 m, 20 May 1991 (fl), *W. Palacios & Rubio 7300* (MO, NY, QCNE), 2300 m, 16 Dec 2003 (fl), *P. Pedraza & C. Pedraza 973* (AAU, COL, E, MO, NY, QCA, QCNE), *977* (NY); El Chical-Tulcán road, 34 km E of El Chical, 2900 m, 10 Aug 2004 (fr), *Croat & Hannon 93218* (NY); parroquia Maldonado, Tulcán to El Chical road, Páramo del Angel, 2256 m, 2 Feb 1995 (fl, fr), *A. Ortiz et al. 400* (NY); Espejo, El Gualtal, cresta del Cerro Golondrinas Hembra, 3000 m, 21 Aug 1994 (fl), *W. Palacios & Clark 12497* (MO, NY), *W. Palacios & Clark 12570* (MO); carretera Tulcán-Maldonado, después del caserio El Laurel, antes del Páramo del Angel, 2800 m, 21 Dec 2003 (fl), *P. Pedraza & C. Pedraza 994* (COL, NY, QCA, QCNE); carretera Tufiño-Maldonado, 2300 m, 16 Dec 2003 (fl), *P. Pedraza & C. Pedraza 974,* (COL, NY, QCA); al N de El Chical, trocha de Piedras Blancas a El Pailón-Gualpi-San Marcos-Tobar Donoso, 1050 m, 17 Dec 2003 (fl), *P. Pedraza & C. Pedraza 989* (AAU, COL, MO, QCA, QCNE, US). **Chimborazo:** Baños-Riobamba road, 24 Apr 1971 (fl), *Lugo 1813* (GB, MO, NY); 3-4 km from Puela, 10 Oct 1968 (fl), *Lugo 571* (GB, NY). **Esmeraldas:** cantón San Lorenzo, road Lita to El Cristal, on finca of Dr. La Lama, 1220-1350 m, 13 May 1992 (fl), *Luteyn & Quelal 14619* (B, NY), *14643*

(NY). **Imbabura:** vicinity of Laguna la Virgen, on ridge S of Río Clavadero, E of Cayambe Peak, 2650 m, 26 Jul 1944 (fr), *Wiggins 10464* (CAS). **Loja:** crest of the Cordillera de Zamora, E of Loja, 3050 m, 2 Jul 1944 (fl, fr), *Camp E-74* (NY, US); Vilcabamba-Valladolid road, S of Vilcabamba, 2450 m, 29 Jul 2004 (fr), *Croat 92619* (NY); E of Loja, 2850 m, 15 May 1965 (fl), *Knight 874* (WIS); road Loja-Zamora, 3050 m, 17 Jul 1967 (fl), *Wrigley 118* (NY, WIS). **Morona-Santiago:** on the trail from Sevilla de Oro to Mendez, Tambo Chontal to Tambo Consuelo, 1700-2400 m, 16 Dec 1944 (fl), *Camp E-1595* (NY); Méndez-Paute road, SW of Méndez, 1943 m, 12 Jul 2004 (fr), *Croat et al. 90857* (NY); vía Plan de Milagro-Gualaceo, near Tinajillas, 2100-2200 m, 6 Feb 1989 (fl), *W. Palacios & Werff 3728* (MO, NY). **Napo:** end of Salcedo-Napo road, near junction of rivers Langoa and Mulatos. 2500 m, 25 Jun 1983 (fl, fr), *Brandbyge 42188* (MO, NY, QCA); Cantón El Chaco, Río Oyacachi, main trail between Oyacachi and El Chaco, 2400 m, 24 Dec 1996 (fl, fr), *Clark et al. 3648* (MO, NY); W of Cosanga, 2000 m, 11 Feb 1980 (fl), *Harling & Andersson 16451* (GB, K, NY); Quijos, Reserva Ecológica Antisana, Cordillera de los Guacamayos, 2300 m, 12-14 Jan 1999 (fl), *Vargas & Narváez 3493* (NY); Cerro Antisana, NE of Borja, 1667 m, 5 Aug 1960 (fl, fr), *Grubb et al. 1232* (K, NY). **Pichincha:** W of Aloag on road to Santo Domingo de los Colorados, 2700 m, 12 Aug 1976 (fl), *Argent & Burbridge 527* (A, E, L, NY); between Nono and Nanegal, 2300 m, 11 Aug 1955 (fl), *Asplund 17289* (B, K, L, LL, NY, S); Cerro Pugsi, NW slope of Volcán Pichincha, 3020 m, 27 Sep 1980 (fl), *Bleiweiss 1140* (NY); bosque Protector Pasochoa, trail to top of Pasochoa, 3000-3500 m, 16 Nov 1990 (fr), *Cerón-M. & Alarcón 2300* (MO, NY); Reserva Geobotánica Pululahua, sector Moras Pungo-Papa Tena, 2900-3100 m, 17 Aug 1988 (fl), *Cerón-M. & Cerón 4436* (NY); Andes of Quito, 2400 m, s.d. (fl), *Jameson 83* (BM, E, P); Quito, 1850 (fl), *Jameson 802* (BM, K, OXF, P); Quito-Nono-Puerto Quito road, NNW of Nono, 2184-2244 m, 29 Apr 1978 (fl, fr), *Luteyn & Lebrón-Luteyn 5854* (COL, NY, QCA), 2700 m, 10 Dec

2003 (fl, fr), *P. Pedraza & C. Pedraza 959* (AAU, COL, MO, NY, QCA, QCNE); antigua carretera a Santo Domingo de los Colorados, pasando por Chiriboga, 2100 m, 23 Dec 2003 (fr), *P. Pedraza & C. Pedraza 1010* (NY, QCA); carretera Panamericana Quito-Santo Domingo de los Colorados, 2650 m, 24 Dec 2003 (fl, fr), *P. Pedraza & C. Pedraza 1011* (AAU, COL, MO, NY, QCA, QCNE). **Tungurahua:** Cordillera de Llangnates, near junction of Río Golpe and Río Sangarinas (Desaguadero), 3000 m, 25 Sep 1939 (fl, fr), *Asplund 9871* (NY, S); NW slopes of Tungurahua, 2500 m, 28 Apr 1951 (fl), *Bell 754* (BM, NY); Baños, 15 Oct 1968 (fl, fr), *Lugo 608* (F, GB, MO, NY, S, US); 2100-3000 m, May 1858 (fl, fr), *Spruce 5403* (BM, CGE, E, F, GH, K, L, NY, OXF, P, S). **Zamora-Chinchipe:** PN Podocarpus, 2600 m, 21 Nov 1998 (fl), *Cornejo & Bonifaz 6710* (NY); Zamora-Loja road, 16 km from the Estación Científica San Francisco, 2770 m, 25 Jul 2004 (fr), *Croat 92142* (NY); Loja-Zamora road, 2770 m, 19-20 Apr 1973 (fl), *Holm-Nielsen et al. 3941* (L); Yangana-Valladolid road, 2600 m, 9 May 1997 (fl), *Lewis 3269* (K, NY), 2500 m, 6 May 1987 (fl), *Werff & W. Palacios 9368* (MO, NY). **Without province:** Sep 1881 (fl), *Sodiro s.n.* (P).

Without country. Nueva Granada, Nevado, Río Hacha, Feb 1842 (fr), *Linden 1627* (BM, F, OXF, P).

When *Disterigma noyesiae* was described by Luteyn (1996), based on one specimen from El Chical (Carchi), the species was circumscribed by plants with leaves ovate-subrotund and small (4-5.5 mm long), with equally small flowers (calyx ca. 1.5 mm long, corolla 3.7-4.3 mm long), and with the differentiated apical bracteoles enclosing the calyx and the lower half of the corolla. However, plants with bracteoles extending beyond the calyx (sometimes combined with flowers with bracteoles just covering the entire calyx) and with equally smaller or gradually larger flowers are much more widespread in Carchi, and in Ecuador in general. The size and shape of the leaves could vary within the same area (e.g., Tulcán-Maldonado road) and independently of the flower size variation, and consequently it is not regarded as a good specific character. Furthermore, if you move north from the border between Ecuador and Colombia, the size variation in the corolla and leaves gradually increases. For all these reasons, the concept of *D. noyesiae* is here expanded to embrace a wider morphological variation and geography, including specimens identified as potential hybrids between *D. alaternoides* and *D. cryptocalyx*, and, *D. acuminatum and D. cryptocalyx* for Ecuador (Luteyn, 1996). Molecular analyses have not shown signs of hybridization, and the putative parental species of these hybrids were not found occurring near the areas where *D. noyesiae* was collected.

The morphological variation of *Disterigma noyesiae* is difficult to interpret, especially when you look at the extremes of the gradient. Nevertheless, this species can be characterized by its differentiated apical bracteoles with smooth surfaces, covering the entire calyx and often extending beyond it up to 2 mm; by its calyx cylindric-campanulate and angulate at the tube; by its corollas adaxially glabrous; by its stamens with filaments pilulose on both sides; and by its papillae only developed on the thecae. The differences between *D. noyesiae* and other species have already been discussed in *D. cryptocalyx* and in Table 12. The large-leaved specimens of *D. noyesiae* can be separated from *D. humboldtii* because of the leaf apex (mostly acute to acuminate vs. subacute, blunt acute, or obtuse, respectively), the calyx coverage of the differentiated apical bracteoles [100% up to 2 mm beyond the calyx vs. (40-)50-90%], and the conspicuousness of the pedicel (at least partially evident vs. reduced and hidden by the bracts).

21. Disterigma ollacheum Pedraza, **sp nov.** Type. Peru. Puno: Prov. Carabaya, ruta Ollacheum-San Gabán, entre Ollacheum y la central hidroeléctrica, 13˚46’ 59.9”S, 72˚28’21.5”W, 1800-2500 m, 14 May 2005 (fl, fr), *P. Pedraza et al. 1528* (holotype: USM; isotypes: AAU, COL, CUZ, F, K, LPB, MO, NY, QCA, US).

(Fig. 21)

Species nova foliis crassis, in sicco rugosis, ellipticis vel raro suborbicularibus, in apice obtusis, prominenter apiculatis, floribus maximam partem solitariis, pedicello 1.5-4.5 mm longo, manifesto vel minimum ex parte per bracteas imbricatas non omnino occulto, bracteolis apicalibus glabris, floribus 5-meris, aestivatione calycis valvata, tubo calycis acuti-angulato, sinubus acutis, corolla pallide viridi vel cremea incrassato-carnosa urceolata, adaxialiter glabra, thecis tubulisque papillosis, fructibus purpuratis, embryone seminis alba distincta.

Shrubs growing over rock outcrops or inside rock cracks, prostrate and decumbent, or erect, up to 0.6 m tall. Young branchlets ridged, more or less smooth, glabrate or puberulous, the hairs white, minute, eglandular and glandular, the mature branches glabrous. **Leaves** 0–4 per cm, spirally arranged, diffuse; petiole 1.1–2.6 mm long, glabrate, the hairs eglandular and glandular; lamina succulent and drying wrinkled, elliptic or rarely suborbicular, (0.9–)1.3–2.5 x (0.5–)0.7–1.2 cm, basally obtuse, marginally entire, apically ciliolate or ciliate with eglandular hairs (especially in young leaves), apically obtuse and prominently apiculate, adaxially glabrous or glabrate in young leaves with eglandular and glandular hairs, abaxially glabrate with glandular hairs, the venation obscure or hyphodromous on both sides, the midvein adaxially impressed and abaxially raised. **Axillary solitary flowers** and sometimes 2-flowered fascicles; bracts 3–6, chartaceous, ovate, 0.8–2 x 1–2 mm, marginally ciliolate with minute and few eglandular and glandular hairs, apically obtuse, abaxially glabrous; pedicel 1.5–4.5 mm long, evident or at least with a portion of it not completely obscured by overlapping bracts, glabrous or glabrate with eglandular and glandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping the base of calyx tube or the entire calyx tube, covering 36–50% of calyx, transverse-elliptic, 1.8–2.7 x 3–4 mm, marginally ciliolate with eglandular hairs or minute glandular hairs, apically truncate or sometimes obtuse, the surface smooth, abaxially and adaxially glabrous. **Flowers** 5-merous. Calyx aestivation valvate, campanulate, 4.2–5.5 mm long; tube sharply angled with the angles sometimes looking like very small wings in herbarium specimens, 1.7–2.5 (–3) mm long, abaxially puberulous with eglandular or glandular hairs; limb (2.3–) 2.5–3 mm long, abaxially puberulous with eglandular or glandular hairs, adaxially glabrous; lobes triangular, 1.3–1.8 x 1.5–3 mm, marginally eciliate, apically acute; sinuses acute (V-shaped). Corolla light green or cream-colored, thick-fleshy, very hard and leathery in both fresh and dry material, bistratose, urceolate, (6.6–)7–8.5(–9) mm long, 5.3–6 mm diam., 3.3–4 mm wide at throat, abaxially and adaxially glabrous; lobes 1.1–1.5 x 1.1–1.7 mm, apically acute, adaxially rugose. Stamens 10, 5.1–6.2 mm long, included; filaments distinct, straight, more or less linear with parallel sides, 2.9–3.5 mm long, abaxially glabrous, adaxially puberulous distally; anthers distinct, papillae on both thecae and tubules; thecae 1.6–2.2 mm long, without basal appendages; tubules 2, distinct, 1.7–2 mm long, dehiscing introrsely by longitudinal slits, 0.8–1.2 mm long. Ovary 5-locular; style 6.7–7.7 mm long, included. **Berry** purple, more or less spherical, 6–8.3 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo white.

Distribution and ecology. *Disterigma ollacheum* is known from southern, Peru, around Ollachea (Puno), and from Tabina, a locality that probably belongs to the same province (Map 11). The species has a wide altitudinal range between

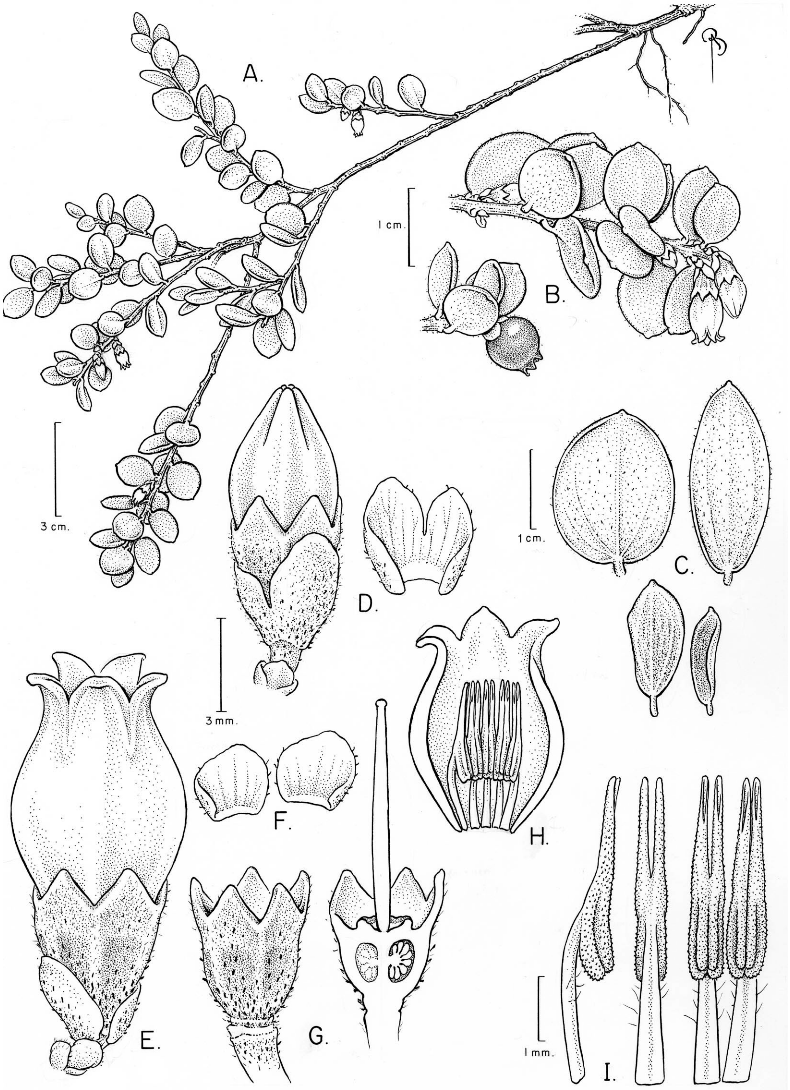
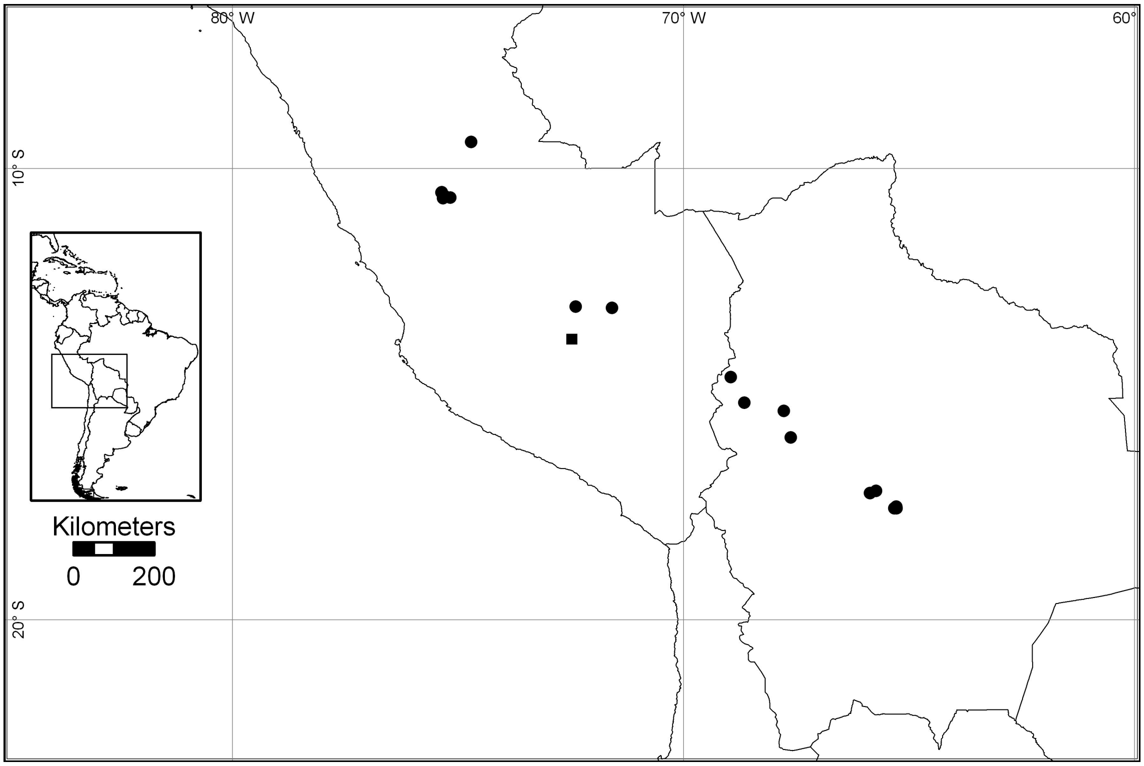


Fig. 21. Illustration of *Disterigma ollacheum*. **A.** Branch showing caulinar roots; **B.** Details of branches bearing fruits and solitary axillary flowers; **C.** Examples of leaf shapes, the lower ones are from the young shoots; **D.** Floral bud showing rarely fused bracteoles; **E.** Flower with differentiated apical bracteoles clasping the calyx; **F.** Differentiated apical bracteoles; **G.** Calyx with the bracteoles removed, external view showing the sharp angles and longitudinal section; **H.** Longitudinal section of the corolla; **I.** Lateral, abaxial, and adaxial views of the stamens (A-I: *P. Pedraza 1528*, NY; C: *P. Pedraza 1532*, NY).

(1800-)2100-3600 m, growing epilitic in puna and motane vegetation, over rocky outcrops. Flowering specimens have been collected in May, June and August, and fruiting specimens in May. The flowers of *D. ollacheum* are visited by bumblebees and hummingbirds (*Boeke 2983);* additionally, an intricate ant nest (*PP 1534*, undetermined) was found in its root system, in the narrow layer between the rock and the humus.



Map 11. Geographic distribution of *Disterigma ollacheum* ■ and *D. ovatum* ●.

Etymology. The species is named after the town of Ollacheum (Puno, Peru), in which vicinity it is found.

Specimens examined. PERU. Puno: Prov. Carabaya, 3 km S of Ollacheum, 13 Aug 1980 (fl), *J. D. Boeke & S. Boeke 2983* (COL, CUZ, MO, NY, USM); Tabina, Jun 1954 (fl), *Lechler 2113a p.p.* (K, NY); Prov. Carabaya, ruta

Ollacheum-San Gabán, entre Ollacheum y la central hidroeléctrica, 1800-2500 m, 14 May 2005 (fl, fr), *P. Pedraza et al. 1527* (AAU, COL, CUZ, NY, USM), *1532* (CUZ, NY).

Disterigma ollacheum is characterized by having leaves succulent that dry wrinkled, elliptic or rarely suborbicular, and with the apex obtuse and prominently apiculate; pedicels relatively long and evident, or at least with a portion of it not completely obscured by overlapping bracts; flowers 5-merous; calyx tube sharply angled and sometimes looking shortly winged in herbarium specimens; corolla light green or cream-colored, leathery, urceolate, and adaxially glabrous; papillae on both thecae and tubules; and by having berries purple with the seed embryos white. *Disterigma ollacheum* has leaves similar in size and shape to those of *D. ovatum*, as well as flowers equally solitary and 5-merous. Nevertheless, these two species can be easily separated with careful observations and their major differences are summarized in Table 13.

Table 13. Summary of differences between *Disterigma ollacheum* and *D. ovatum*

Characters	***D. ollacheum***	***D. ovatum***
Leaf texture	Coriaceous & succulent	Coriaceous
Leaf margin drying	Not revolute	Slightly revolute at base
Pedicel length & conspicuousness	1.5-4.5 mm, with at least a portion of it evident	0.9-1.5 mm, reduced and hidden by overlapping bracts
Bracteoles marginal hairs	Eglandular & minute glandular	Eglandular
Calyx tube in cross-section	Sharply angled	Terete
Corolla color	Light green or cream	White or pink
Corolla indumentum abaxial/adaxial	Glabrous/Glabrous	Glabrate/Glabrate, rarely even on lobes
Anthers papillae	On thecae & tubules	On thecae
Seed embryo	White	Green

22. Disterigma ovatum (Rusby) S. F. Blake, J. Wash. Acad. Sci. 16: 365. 1926. *Vacciniopsis ovata* Rusby, Bull. Torrey Bot. Club 20: 434, pl. 170. 1893.. Type. Bolivia. "Cochabamba: vicinity of Cochabamba" [sheets marked *Bang 876* read either vic. Cochabamba and 1891, or, Zongo and 1890 or 1891, alternatively], 1891 (fl), *Bang 876* (holotype, NY; isotype, C n.v., E, F n.v., G (x2), GH n.v., K n.v., MICH, NY (2x), US (2x)). The GH and K sheets were not found.

Thibaudia vitis-idaea Griseb. in Smith, Brittonia 1(4): 221.1933, pro. syn., nom. Illegit, on *Lechler 2113* at G.

Epiphytic or terrestrial **shrubs**, scandent or erect, up to 3 m tall. Young branchlets usually with a mucilaginous exudate distally, ridged, more or less smooth, puberulous or glabrate, the hairs eglandular, white, the mature branches indumentum similar. **Leaves** 0–4 per cm, spirally arranged, diffuse; petiole 2–3.5 mm long, glabrate or puberulous, the hairs eglandular; lamina elliptic, or less often obovate or ovate, 1.2–2.4(–3.5) x 0.6–1.2(–1.9) cm, basally obtuse or cuneate, marginally entire, slightly revolute towards base, apically ciliolate with eglandular hairs (especially in young leaves), apically obtuse and usually prominently apiculate, adaxially glabrous or glabrate in young leaves with eglandular or glandular hairs, abaxially glabrate with glandular hairs, the venation hyphodromous on both sides, the midvein adaxially impressed and abaxially raised. Axillary **solitary flowers** and rarely in 2(–3)-flowered fascicles; bracts 4–6, chartaceous, ovate, 0.8–2.4 x 0.9–2.8 mm, marginally eciliate, apically obtuse, abaxially glabrous; pedicel 0.9–1.5 mm long, reduced and hidden by overlapping bracts, glabrous or glabrate with glandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping the base of calyx tube or the entire calyx tube, covering 40–60% of calyx, ovate or elliptic, 2–3.5 x 2.3–3.9 mm, occasionally marginally ciliolate with minute eglandular hairs (apically), apically obtuse, the surface smooth and keeled, abaxially and adaxially glabrous. **Flowers** 5-merous, rarely corollas 4- or 6-lobed, or calyces appearing to be 4-lobed because a lobe is reduced or because two adjacent lobes are much smaller and closer. Calyx aestivation valvate, campanulate, (3.8–)4.5–5.3(–5.7) mm long; tube terete, (1.8–)2–2.5(–2.7) mm long, abaxially glabrate with glandular hairs; limb (2–)2.5–3.2 mm long, abaxially glabrate or glabrous with eglandular hairs, adaxially glabrous; lobes triangular, 1.5–2(–2.5) x 1.4–1.7 mm, sometimes ciliolate with eglandular hairs, apically acute; sinuses acute (V-shaped). Corolla pink or white, thick-fleshy, bistratose, urceolate, (5.6–)6.5–7.5(–9) mm long, 3.7–6 mm diam., 2.3–4 mm wide at throat, abaxially glabrate with glandular hairs, adaxially glabrate, rarely even on the lobes; lobes (1.1–)1.5–2 x 1.2–1.5 mm, apically acute, adaxially rugose. Stamens 10, (4.8–)5.5–6.7 mm long, included; filaments distinct, straight, more or less linear with parallel sides, (2.5–)2.7–3.5 mm long, abaxially and adaxially puberulous distally; anthers distinct, papillae only on thecae, at times with a couple of long hairs at base; thecae 1.3–1.8 mm long, basal appendages present or not; tubules 2, distinct, 1.6–2.1(–2.6) mm long, dehiscing introrsely by longitudinal slits, 0.8–1.1 mm long. Ovary 5-locular; style 6.8–7.8 mm long, exserted. **Berry** violet to almost black, more or less spherical, 6–7 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo green.

Distribution and ecology. *Disterigma ovatum* is found in the central Andes, more specifically in the regions of Huánuco, Pasco, and Cusco in Peru, as well as in the departments of La Paz and Cochabamba in Bolivia (Map 11). This species grows in cloud forests between (1800-)2000-3500(-3800) m. It is locally abundant and has been recorded in both primary and secondary vegetation, as well as on roadsides and pasture lands with remnant forest. Flowering specimens have been found in January, March-May, July, September, and October, and fruiting specimens in April-June and August-October. Bumblebees have been seen visiting its flowers (*P. Pedraza et al. 1503, 1505, 1516*).

Etymology. The species name makes reference to the ovate shape of some leaves.

Representative specimens examined. PERU. Cusco: Prov. Paucartambo, Kosñipata, trocha Unión, 3415 m, 9 Oct 2003 (fl, fr), *H. Qquellón et al. 70* (CUZ, USM), 1850 m, 26 Oct 2003 (st), *H. Qquellón 115* (CUZ); Prov. Paucartambo, Kosñipata, predio Waykicha [Wayquecha], 3000 m, 25 Sep 2003 (fl), *H. Qquellón et al. 41* (CUZ); 2850 m, 6 May 2005 (fl), *P. Pedraza et al. 1516* (AAU, COL, LPB, MO, NY); Prov. La Convención, Katarompanaki, campamento II, trochas 2 y 4, 1800 m, 2-3 May 2004 (fl, fr), *Salinas-R. et al. 6875* (CUZ); Prov. La Convención, Tingkarani, campamento II, trocha Imperita, 2180 m, 9-10 May 2004 (fl), *Salinas-R. et al. 7310* (CUZ); Prov. Paucartambo, distrito Challabamba, PN Manú, Trocha Erickson, 3490 m, 5 May 2005 (st), *Salinas-R. et al. 7613* (COL, USM), 2660 m, 5 May 2005 (fl, fr), *Salinas-R. et al. 7622* (COL, CUZ, MO, NY, USM). **Huánuco:** SW slope of Río Llullacichis watershed, Cerros del Sira, camp 6, 2205 m, 30 Jul 1969 (fl), *Dudley 13496* (NA). **Pasco:** Prov. Oxapampa, PN Yanachaga-Chemillén, 1800 m, 16 Jan 2005 (fl), *E. Ortiz et al. 211* (HOXA, HUSA, MO, NY, USM), 2800 m, 12 Mar 2005 (fl), *E. Ortiz & Mateo 391* (HOXA, MO, USM), 2400-2500 m, 16 Mar 2005 (st), *E. Ortiz & Mateo 473* (HOXA, MO), 29 May 2005 (fl), *E. Ortiz et al. 648* (HOXA, NY, USM), 2315 m, 14 Jun 2005 (fr), *E. Ortiz et al. 695* (HOXA, MO, NY, USM), 2360-2800 m, 27 Sep 2005 (fr), *E. Ortiz et al. 993* (HOXA, MO, NY, USM), 2380 m, 16 Jun 2006 (fr), *P. Pedraza et al. 1611* (NY, USM). **Puno:** Sachapata, Aug 1954 (fr), *Lechler 2581* (K).

BOLIVIA. Cochabamba: Prov. Chapare, Cochabamba 54 km hacia Villa Tunari, 2750 m, 30 Apr 1979 (fl), *St. G. Beck 1417* (L, LPB, NY); Prov. Chapare, km 90-103, Cochabamba to San Antonio-Chapare, 3500 m, Apr 1961 (fl), *M. Cárdenas 63* (BOLV, US), *6004* (US); Prov. Carrasco, Sehuencas, 2100 m, 1 May 1993 (fl), *P. Ibisch & C. Ibisch 93.0136* (LPB), 2100 m, 13 Sep 1993 (fl), *P. Ibisch & C. Ibisch 93.1001* (LPB); Cuchicanchi pass, 3000 m, 13-21 Apr 1892 (fl), *Kuntze s.n.* (NY); Prov. Chaparre, carretera Cochabamba a Villa Tunarí, cerca de la presa Corani, 3300 m, 7 Apr 2005 (fl, fr), *P. Pedraza et al. 1500* (COL, LPB, MO, NY), *1501* (AAU, COL, F, LPB, MO, NY, US), 1760 m, 8 Apr 2005 (fl, fr), *P. Pedraza et al. 1502* (COL, LPB, NY); Prov. Carrasco, carretera entre Monte Puncu y Sehuenca, hacia el PN Carrasco, 2868 m, 9 Apr 2005 (fl, fr), *P. Pedraza et al. 1503* (COL, LPB, MO, NY)*, 1504* (LPB, NY)*, 1505* (COL, LPB, MO, NY). **La Paz:** Prov. Nor Yungas, Puerto Linares, 39 Kms hacia Caranavi, después de La Cumbre, 1410 m, 10 Mar 1979 (fl), *St. G. Beck 474* (L, LPB); Bautista Saavedra, ANMI Apolobamba, Ininlaya, subiendo por Siata por senda de incienseros, 2275 m, 27 Apr 2005 (fr), *Fuentes et al. 7393* (NY); Prov. Franz Tamayo, entre la senda de Chuncani a Tokuaque, 8 Sep 2001 (fl), *Orellana & Quispe 1876b* (LPB); Prov. Nor Yungas, 13.7 km NW of San Pedro on road through Inca-huara-Mejillones and along trail to 12 de Octubre, 1500 m, 15-16 Jan 1983 (fl), *Solomon 9283* (LPB, NY).

Although the specific epithet of *Disterigma ovatum* makes reference to its ovate leaves, elliptic leaves are more common throughout all its distributional range. This species can be differentiated from the rest of the genus by having leaves apically obtuse and usually prominently apiculate, with their margins becoming slightly revolute towards base after drying; flowers mostly 5-merous, but rarely looking 4-lobed because one of the calyces lobes is very small or because two adjacent lobes are so shifted one next to the other that they give the impression of being one; corolla pink or white, thick-fleshy, urceolate, and adaxially glabrate; and berries violet to almost black, with the embryos of the seeds green. The type collection diverges from the typical *D. ovatum* in having smaller flowers and corollas with hairs even on the lobes.

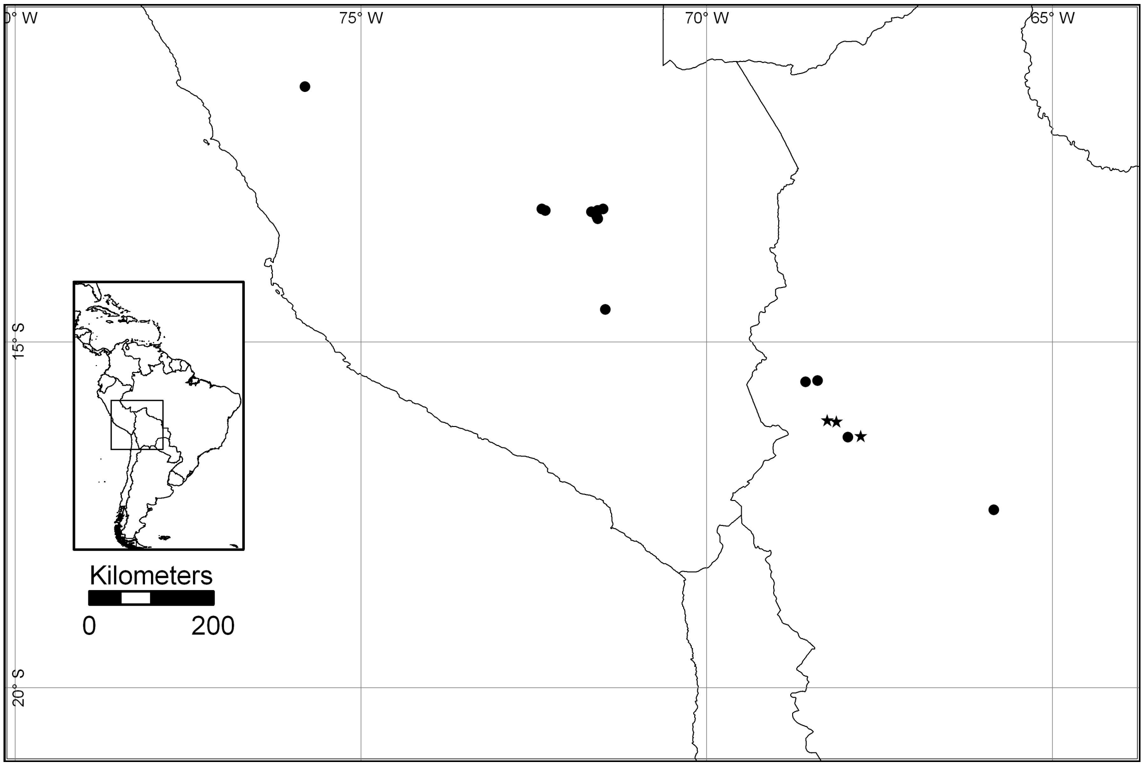
The overall morphology of *Disterigma ovatum* recalls that of *D. ollacheum* and their major differences are presented in Table 13. Smith (1933) related *D. ovatum* to *D. alaternoides* but they differ from each other in many ways; for example *D. ovatum* has 5-merous flowers and green seed embryos, while *D. alaternoides* has 4-merous flowers and white seed embryos.

23. Disterigma pallidum A. C. Sm. Brittonia 1: 222. 1933. Type: Bolivia. La Paz: Nor Yungas, Unduavi, 3300 m., Nov. 1910 (fl, fr), *Buchtien 2982* (holotype, NY; isotype, NY, US (2x)). Photo NY neg. 9893 and 9894 ex NY.

Epiphytic or terrestrial **shrubs**, erect, 0.75–3 m tall. Young branchlets ridged, more or less smooth, puberulous, the hairs eglandular or glandular, white, the mature branches indumentum similar but glabrate. **Leaves** 2–4 per cm, apparently distichous, diffuse; petiole 1.6–3.6 mm long, glabrate, the hairs eglandular or glandular; lamina elliptic or at times ovate, 0.9–1.8 x 0.47–0.95 cm, basally obtuse or cuneate, marginally entire, slightly revolute towards base, apically ciliolate with eglandular hairs (especially in young leaves), apically obtuse and shortly apiculate, sometimes acute or obtuse, adaxially glabrate with eglandular hairs, abaxially glabrate with glandular hairs, the venation adaxially hyphodromous with the midvein impressed, abaxially obscure. Axillary **solitary flowers** and rarely 2-flowered fascicles; bracts 4–6, chartaceous, ovate, 0.7–1.6 x 0.7–1–6 mm, marginally eciliate, apically obtuse or acute, abaxially glabrous; pedicel 0.7–1.3 mm long, reduced and hidden by overlapping bracts, glabrate with glandular hairs; differentiated apical bracteoles fused by one of their ends into 1, very rarely a couple of flowers with 2 bracteoles, chartaceous, enveloping entire calyx tube or sometimes just the base of the calyx tube, covering 29–50% of calyx, ovate or transverse-elliptic, (1.3–)1.5–3.4 x (2–)3–4.6 mm, marginally ciliolate with eglandular hairs, apically obtuse and emarginate, or obcordate, the surface smooth with one or two diffuse keels, abaxially and adaxially glabrous. **Flowers** 4-merous. Calyx aestivation valvate, cylindric, (4.7–)5.5–7.5 mm long; tube terete, 2.4–3.1 mm long, abaxially glabrate with eglandular or glandular hairs; limb 2.8–4.9 mm long, abaxially glabrate with eglandular hairs, adaxially glabrous; lobes triangular, 1.6–2.8 x 0.9–1.8 mm, marginally eciliate, apically acuminate and drying darker; sinuses rounded (U-shaped). Corolla bright pink, thick-fleshy, bistratose, tubular, (9.9–)11.9–15 mm long, 3–3.6 mm diam., 2.1–2.5 mm wide at throat, abaxially and adaxially glabrous; lobes 1.7–2.4 x 1.1–2 mm, apically acute, adaxially smooth. Stamens 8, (8.7–)11–13.5 mm long, included; filaments distinct, straight, more or less linear with parallel sides, (6.7–)8.7–11 mm long, abaxially glabrous, adaxially glabrate distally; anthers distinct, papillae on both thecae and tubules; thecae (1.5–)1.9–2 mm long, without basal appendages; tubules 2, distinct, (1.1–)1.4–1.7 mm long, dehiscing introrsely by longitudinal slits, (0.8–)1–1.3 mm long. Ovary 4-locular; style 12–13 mm long, exserted. **Berry** purple, more or less spherical, 5–6.7 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo color unknown.

Distribution and ecology. *Disterigma pallidum* is endemic to the department of La Paz, in Bolivia, more specifically, to the area of Cotapata-Coscapa-Chuspipata, on both the new and old roads to Coroico, as well as in the valley of the river Zongo (Map 12). This species grows between 2950-3500 m, in montane cloud forests (ceja de montaña) or in the transition to humid puna (yungas in

Bolivia). It is frequently associated with *Sphagnum* and has been recorded growing in both primary and secondary vegetation, as well as along roadsides. Flowering specimens have been found in January-July and November-December, and fruiting specimens in March-April and November.



Map 12. Geographic distribution of *Disterigma pallidum* ★ and *D. pernettyoides* ●.

Etymology. The species name probably makes reference to the pink flowers (*pallidus*= pale).

Specimens examined. BOLIVIA. La Paz: Prov. Murillo, Valle del Zongo, 3150 m, 7 Apr 1979 (fl), *St. G. Beck 1149* (L, LPB) 2950 m, 26 Nov 1994 (fl, fr), *St. G. Beck 22326* (LPB, NY), 3140 m, 2 Mar 2000 (fl, fr), *Luteyn et al. 15440* (BOLV, CUZ, K, LPB, NY, TEX), 3341 m, 14 Apr 2005 (fl, fr), P. *Pedraza et al. 1506* (LPB, MO, NY, COL), *1507* (AAU, LPB, MO, NY, COL, US), 3000 m, 17 Mar 1984 (fl, fr), *Solomon 11943* (LPB, MO, NY), 3200 m, 20 Feb 1987 (fl), *Solomon 16102* (BOLV, LPB, MO, NY), 3200 m, 4 Apr 1987 (fl), *Solomon 16485* (LPB); Prov. Nor Yungas, 34 km de la cumbre hacia Coroico, Chuspipata, 3100 m, 1 Jan 1983 (fl), *St. G. Beck 7804* (L, LPB, NY); Prov. Nor Yungas, Unduavi, 3300 m, Nov 1910 (fl, fr), *Buchtien 2983* (CAS, GH, L, NY, US, WIS); Prov. Nor Yungas, Cotapata about 13 km E of Unduavi along road to Yolosa, 3100 m, 7 May 1990 (fl), *Luteyn & Dorr 13538* (AAU, COL, LPB, NY, USM); Prov. Nor Yungas, trail to Río Coscapa, 5.6 km W of Cotapata, 3300-3500 m, 5 May 1990 (fl), *Luteyn & Dorr* 13475 (BOLV, LPB), 13591 (AAU, COL, MO, NY); Prov. Nor Yungas, Cotapata about 11 km NE of Unduavi, 3100 m, 22 Dec 1983 (fl), *Solomon & Moraes 11404* (LPB, MO, NY); Prov. Nor Yungas, 1.2 km E of Cotapata on road between Unduavi and Chuspipata, 3100 m, 26 Jun 1986 (fl), *Solomon 15365* (K, LPB, MO, NY).

Disterigma pallidum is easily distinguished for having only one differentiated apical bracteole as a result of the fusion of the original pair by one of their ends; the resulting bracteole has the apex emarginate or obcordate. Rarely flowers with two distinct bracteoles (a handful among all examined specimens) can be found. Additionally, *D. pallidum* can also be characterized by its leaves apparently distichous, with the apex obtuse and shortly apiculate; its calyces with the apex of the lobes often drying darker and with rounded sinuses; its corollas long, tubular, and bright pink; and by its purple berries. In the description given above, the flower dimensions within parentheses correspond to those of the original description, which are smaller than the average observed throughout all the distribution of the species. It is also important to note that the original description erroneously accounted for two differentiated apical bracteoles instead of one.

Although *Disterigma pallidum* has a distinctive combination of characters and can be singled out because of its bracteoles, it superficially looks like a small-leaved form of *D. alaternoides* or *D. humboldtii*, two species that despite being widespread, are less frequent in the central Andes where *D. pallidum* grows. *Disterigma pallidum* can be easily differentiate from *D. alaternoides* and *D. humboldtii* because its corollas are bright dark pink (vs. white to light pink in the other species), and because of its longer calyces [(4.7-)5.5-7.5 mm vs. (2.5-) 3.5-5.5 mm], corollas [(9.9–)11.9–15 mm vs. (5.2)7-9(-10) mm], and stamens [(8.7–)11–13.5 mm vs. (4.5-)5-7(-8) mm].

24. Disterigma panamense Standl., Fieldiana Bot. 22: 365. 1940. Type. Panamá. Darién: Cana-Causí trail, Chepigana, 1680 m, 15 Mar 1940 (fl), *Terry 1564* (holotype, F).

Disterigma luteynii Wilbur, Bull. Torrey Bot. Club 101: 248. 1974, **syn. nov.** Type. Panama. Panamá: summit of Cerro Jefe and along the road between Cerro Azul and Cerro Jefe, 1000 m, 21 Jun 1972 (fl), *Luteyn 3206* (holotype, DUKE; isotypes, F, MO).

Epiphytic **shrubs**, wiry and scandent. Young branchlets ridged, pubescent, the hairs eglandular, and light brown, the mature branches indumentum similar but glabrate. **Leaves** 6–10 per cm, apparently distichous, diffuse or rarely patent; petiole 0.8–1.5 mm long, glabrate or puberulous, the hairs eglandular or glandular; lamina oblanceolate or obtrullate, (0.8–)0.9–1.5 x 0.2–0.4(–0.5) cm, basally cuneate, marginally entire, apically ciliolate with minute eglandular hairs (especially in young leaves), apically blunt acute or sometimes acute, adaxially glabrate with minute eglandular hairs over the base and the midvein, abaxially glabrate with glandular hairs, the venation adaxially obscure or hyphodromous with the midvein impressed, abaxially 3-nerved with the midvein raised. Axillary and subterminal, **solitary flowers**; bracts 2–6 or occasionally completely absent when the flowers subterminal, chartaceous, ovate, 0.8–1.5 x 0.7–2.1 mm, marginally minutely ciliolate with eglandular hairs, apically obtuse, abaxially glabrous; pedicel 0.5–2 mm long, reduced and hidden by overlapping bracts, glabrate with eglandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping entire calyx tube or to part of calyx lobes, covering 42–70% of calyx, ovate or transverse-elliptic, 1.5–2.2(–3) x 2.1–3.6 mm, marginally ciliolate with eglandular hairs, apically obtuse, the surface smooth, abaxially glabrous or rarely glabrate with eglandular hairs, adaxially glabrous. **Flowers** 4-merous. Calyx aestivation imbricate, campanulate, (2.8–)3–3.6(–4.2) mm long; tube terete, 0.9–1.5 mm long, abaxially glabrous; limb 1.8–2.8 mm long, abaxially glabrous or rarely apically glabrate with eglandular hairs, adaxially glabrous; lobes triangular, 1.4–2(–2.5) x 1–1.6 mm, marginally ciliolate with eglandular hairs, apically acute; sinuses acute (V-shaped). Corolla white, sometimes with pink hue, thin-fleshy, bistratose, tubular or narrowly urceolate, 5.6–6(–6.5) mm long, 2.1–2.5 mm diam., ca. 1.8 mm wide at throat, abaxially glabrous, adaxially glabrate with very few hairs, sometimes as short as 0.15 mm long, and especially concentrated on the lobes; lobes 1.3-1.5 x 1–1.4 mm, apically acute, adaxially rugose. Stamens 8, 5–5.3(–6) mm long, included; filaments distinct, straight, more or less linear with parallel sides, 2.2–3.5 mm long, abaxially and adaxially puberulous (apically); anthers distinct, papillae only on thecae or also on the tubules (especially at base) and then inconspicuous; thecae not basally prognathous, 1–1.5 mm long, with or without basal appendage; tubules 2, distinct, 1.6–2.2 mm long, dehiscing introrsely by longitudinal slits, 0.4–0.8 mm long. Ovary 4–locular; style 4.5–6 mm long, exserted or included. **Berry** white, 5.6–7.8 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seeds with embryo white.

Distribution and ecology. This rare species is known from few collections from central and western Panama, from one collection from Chocó in Colombia, and from another collection from Carchi in Ecuador (Map 8). It grows in shrubby vegetation in the tropical rainforest and premontane cloud forest, between 660-1675 m. Flowering specimens have been found year-round and fruiting specimens have been found in January, April, October, and December.

Etymology. This species was named after the type collection that came from Panama.

Specimens examined. PANAMA. Darién: Serranía de Pirre, along headwaters of Río Escucho Ruido, about 16 km N of Alto de Nique, 1530-1550 m, 27 Jul 1976 (fl), *Croat 37917* (DUKE, MO); Cerro Pirre, top of peak just S of Pirre, 10-20 Jul 1977 (st), *Folsom 4510* (MO); Cuasi-Cana trail between Cerro Campamento and La Escalera to Páramo, E of Tres Bocas, 30 Apr 1968 (fl, fr), *Kirkbride Jr. & Duke 1282* (MO, NY). **Panamá:** Cerro Jefe, 1000 m, 9 Feb 1978 (fl), *Almeda & Nakai 3444* (CAS), 1000 m, 6 May 1985 (fl), *Carrasquilla 2091* (MO, NY, PMA), 1000 m, 20 Jan 1984 (fl, fr), *H. W. Churchill 4283* (MO), 1000 m, 29 Dec 1984 (fl), *Correa et al. 4566* (PMA), 11 Apr 1977 (st), *D'Arcy 11386A* (MO), 11 Apr 1977 (fl), *Folsom et al. 2520* (DUKE, MO), 800-1000 m, 3 Aug 1977 (fl), *Folsom & Hartman 4643* (MO), 1000 m, 4 Apr 1982 (fl), *Huft & Knapp 1719* (MO), 1000 m, 5 Jun 1973 (fl), *Luteyn & Kennedy 3950* (DUKE, F, GH, MICH, MO), 900-1000 m, 3 Feb 1996 (fl), *Luteyn 14797* (CAS, K, NY, PMA, TEX), 900-1000 m, 10 Oct 1998 (fl), *Luteyn et al. 15291* (NY, PMA), 900-1000 m, 23 Jan 2003 (fl, fr), *Luteyn & P. Pedraza 15574* (COL, NY, PMA)*, 15575* (COL, NY, PMA), *15576* (COL, INB, MO, NY, PMA), 850-900 M, 12 Jul 1986 (fl), *McDonagh et al. 50* (BM), 750-800 m, 8 Jul 1987 (fl), *McPherson 11193* (MO), 8 Oct 1974 (fr), *Mori & Kallunki 2382* (MO), 1000 m, 10 Dec 1974 (fl, fr), *Mori & Kallunki*

3610 (MO), 1000 m, 18 Dec 1974 (fl), *Nee 13971* (MO, WIS), 850-900 m, 7 Oct 1980 (fl), *Sytsma 1487* (MO, NY), 850-900 m, 29 Oct 1980 (fl, fr), *Sytsma 2006* (MO), 850-900 m, 7 Oct 1980 (fr), *Sytsma 1439* (MO, NY), 900-1000 m, 27 Jan 1966 (fl, fr), *Tyson et al. 3266* (MO), 1000 m, 8 Jan 1975 (fl), *Wilbur & Luteyn 19467* (DUKE), 9 Feb 1978 (fl), *Wilbur 24112* (DUKE, F, MO, NY).

COLOMBIA. Chocó: alturas de Nique and ridge to SW, 1250-1500 m, 31 Dec 1980 (fl), *Hartman 12475* (MO).

ECUADOR. Carchi: N of San Marcos, trail to Río San Juan, 660 m, 18 Jan 1983 (fl), *Barfod 41470* (NY, QCA).

Although the populations of *Disterigma panamense* with narrow leaves may slightly recall the leaves of *D. hammelii,* the differences between them are many. *Disterigma panamense* is easily separated because its leaves are apparently distichous, and oblanceolate or obtrullate; its solitary flowers are axillary and subterminal; its calyx aestivation is imbricate and its calyx sinuses are acute; its corollas are white, short, tubular or narrowly urceolate, and adaxially glabrate; and because its fruits and seed embryos are white.

Disterigma luteynii and *D. panamense* are not sufficiently differentiated one from the other to be considered different species; they have overlapping floral and vegetative dimensions and share many important morphological characters such as leaf shape and apex, position of the solitary flowers, bracteole appearance and arrangement on the pedicel, floral merosity, and calyx aestivation among others. Therefore the status of *D. luteynii*, being the most recent name, can no longer be maintained. However, some specimens described under *D. luteynii*, a species thought to be endemic to Cerro Azul and Cerro Jefe in the province of Panama, differ from the rest of *D. panamense* in usually having leaves shorter (3 or less times longer than broader vs. 5 or at least 3 times longer than broader respectively) and wider [(0.2-)0.30.4(-0.5) cm vs. 0.2-0.3(0.4) cm], the calyx limb shorter (1.8-2.0 mm vs. 2.5-2.8 mm long), and the calyx lobes shorter [1.4-1.7 mm vs. 2(-2.5) mm]. The relatively larger leaves from Cerro Jefe come from a premontane cloud forest with many small trees and shrubs and unusually open canopy.

Local names and uses. This species is known as “Pasino” in Carchi (Ecuador), where the plant is crushed into paste that is placed on the forehead to treat fever.

25. Disterigma pernettyoides (Griseb. ex Wedd.) Nied., Bot. Jahrb. Syst. 11: 224. 1889. *Vaccinium pernettyoides* Griseb. ex Wedd., Chlor. And. 2: 179, pl. 73. 1857. Type. Perú. Tabina [“Andes de Cuzco y Carabaya” in the protologue], s.d. (fl), *Lechler 2113a p.p.* (holotype, P; isotype, G) [the holotype has two labels, one reads *Lechler 2113* and the other reads *Lechler 2113a*, which is the collection cited in the protologue]. The type is a mixed collection with the *Lechler 2113a p.p.* at K and NY being *D. ollacheum*.

(Fig. 22)

Terrestrial **shrubs**, prostrate and decumbent, or erect, 0.1–1 m tall. Young branchlets ridged, more or less smooth, puberulous, the hairs eglandular, light brown, the mature branches indumentum similar but glabrate. **Leaves** (4–)6–13 per cm, spirally arranged, ascending, diffuse, and some patent; petiole 1–1.6 mm long, glabrate, the hairs eglandular; lamina narrowly elliptic, narrowly oblong, or rarely lanceolate, 0.5–1.1 x 0.2–0.4 cm, basally obtuse, marginally crenulate and eciliate, apically acute or subacute, adaxially glabrate with eglandular hairs, abaxially glabrate with glandular hairs, the venation adaxially hyphodromous with the midvein impressed, abaxially obscure or hyphodromous with the midvein raised. Axillary **solitary flowers** and rarely 2-flowered fascicles; bracts 5–8, chartaceous, ovate, 0.6–2.5 x 0.7–2.5 mm, marginally eciliate, apically obtuse, abaxially glabrous; pedicel 1.5–2.4(–3) mm long, evident or at least with a portion of it not completely obscured by overlapping bracts, glabrate with eglandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping entire calyx tube, covering 45–58% of calyx, ovate, elliptic, or suborbicular, 2.2–4.4 x 2.3–4.4 mm, marginally eciliate, apically obtuse, the surface smooth, abaxially and adaxially glabrous. **Flowers** 4-merous (rarely few corollas 5-merous). Calyx aestivation valvate, campanulate, 4.6–6.3 mm long; tube terete or slightly angled, 2–2.4 mm long, abaxially glabrate with eglandular or glandular hairs; limb 2.5–3.7 mm long, abaxially puberulous with eglandular hairs (apically), adaxially glabrous; lobes triangular, 2–3 x 1–2 mm, marginally eciliate, apically acute; sinuses acute (V-shaped). Corolla white (sometimes with pink hue under intense sunlight conditions), thin-fleshy, bistratose, campanulate, (10–)11.5–17 mm long, 7.5–10 mm diam., 5.5–8.7 mm wide at throat, abaxially glabrous or occasionally glabrate with eglandular hairs, adaxially glabrous; lobes 2.8–4 x 2.8–5.2 mm, apically acute, adaxially slightly rugose at apex. Stamens 8, 7.3–9.2 mm long, included; filaments distinct, weakly geniculate and sometimes hard to notice it in pressed material, broader at base, 4.4–6 mm long, abaxially puberulous, adaxially puberulous distally; anthers distinct, papillae on both thecae and tubules; thecae 1.7–2.2 mm long, without basal appendages; tubules 2, distinct, 1.6–2 mm long, dehiscing introrsely by longitudinal slits, 0.9–1.5 mm long. Ovary 4-locular; style 7.6–11.5 mm long, included. **Berry** white, more or less spherical, 4–10 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo white.

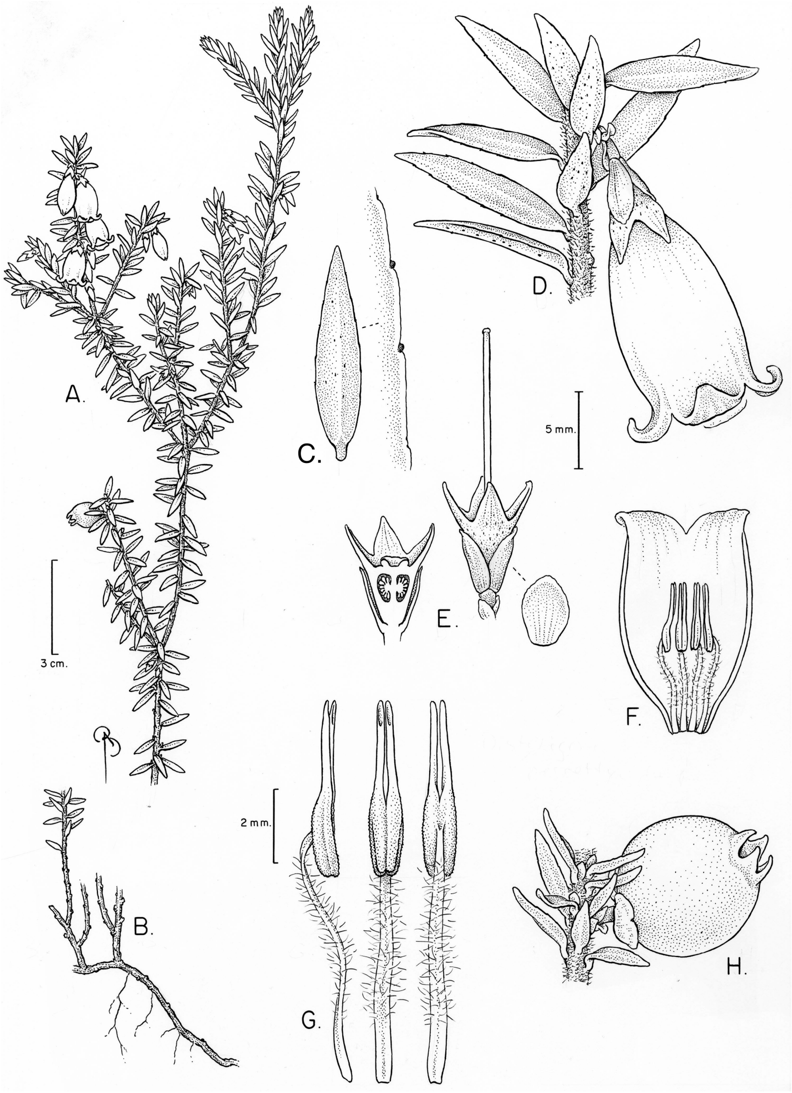


Fig. 22. Illustration of *Disterigma pernettyoides*. **A.** Branch; **B.** Detail showing caulinar roots; **C.** Leaf showing the crenulate margin; **D.** Detail of a solitary axillary flower; **E.** External view and longitudinal section of the calyx and inferior ovary, with the differentiated apical bracteoles; **F.** Longitudinal section of the corolla; **G.** Lateral, adaxial, and abaxial views of the stamens showing softly geniculate filaments. **H.** Fruit (A: *Vuilleumier 364*, NY; B: *Luteyn 6382,* NY; C-H: *P. Pedraza* et al. *1550,* NY).

Distribution and ecology. *Disterigma pernettyoides* is restricted to the central Andes, to the departments of La Paz and Cochabamba in Bolivia, and to the Peruvian regions of Cusco and Junín (Map 12). The species distribution could extend as northern as San Martín, but unfortunately the specimens from the region are sterile and *D. codonanthum* cannot be ruled out [e.g., *Young 1932* (USM)]. This species grows between 2000-3900 m, in the montane cloud forest, the yungas (páramo yungeño) of Bolivia, and in the Peruvian humid puna. It is frequently associated with *Sphagnum* and has been recorded growing in both primary and secondary vegetation, as well as on roadsides. Flowering and fruiting specimens have been found all year-round.

Etymology. Probably named that way because its small and crenulate leaves recall those of *Pernettya* (Ericaceae).

Specimens examined. PERU. Cusco: Prov. Paucartambo, Tres Cruces, PN Manú, 3470 m, 18 Sep 2002 (fl), *Ackerman & Salinas-R. 351* (NY), 3600 m, 5 May 1990 (fl), *Cano E. 3499* (USM), 3600 m, 5 May 1990 (fl), *Cano E. 3500* (F, USM), 3290-3500 m, 7 Dec 1978 (fl, fr), *Luteyn & Lebrón-Luteyn 6382* (CAS, F, GB, MO, NY, USM), 3600 m, 4 Jun 1960 (fl), *C. Vargas 13314* (CUZ); Prov. Paucartambo, PN Manú, Acanacu [Acjanaco], 3900 m, 5 May 1939 (fl), *Balls B6703* (BM, E, F, NA, NY, UC, US), 3380-3400 m, 28 Apr 1990 (fl), *Cano E. 3118* (F, USM), 3450 m, 2 May 1990 (fl), *Cano E. 3346* (USM), 3550-3450 m, 3 Mar 1991 (fl, fr), *Cano E. 4512* (F, USM), 3300-3600 m, 6 May 2005 (fl, fr), *Salinas-R. et al. 7625* (COL, CUZ, MO, NY), 3700 m, 13 Nov 1986 (fl), *Tupayachi-H 37* (NY), Jun 1937 (fl, fr), *C. Vargas 308* CUZ, F, MO, NY, US); Prov. Paucartambo, entre Acjanaco y Esperanza, PN Manú, 2950 m, 14 Feb 1990 (fl), *Cano E. 2899* (F); Prov. Paucartambo, PN Manu, Conga, 3500-3600 m, 19 Jul 1990 (fl, fr), *Cano E.*

3882 (USM); Prov. Paucartambo, PN Manu, Acjanaco, trocha Ericsson, 3400-3450 m, 20 Mar 1992 (fl), *Cano E. & Aguilar 5176* (USM), 3250-3350 m, 1 Sep 1990 (fl), *Cano E. & Young 4062* (F, USM), 3487 m, 5 May 2005 (fl, fr), *Salinas-R. et al. 7615* (COL, CUZ, NY); Prov. Paucartambo, along road between Paucartambo and Shintuya (to Puerto Maldonado), 1-2 km below entrance to PN Manú, 3230 m, 5 Oct 1995 (fl, fr), *Croat 78168* (MO, NY); Prov. Paucartambo, Valle del Pilcopata, roadside above Pillahuata, 3000-3500 m, 15 Dec 1983 (fl), *Foster & Wachter 7535* (NY, F, USM), 3150 m, 22-23 Nov 1962 (fl), *C. Vargas 13960* (CUZ, US); Tres Cruces, PN Manú, NW of Paucartambo-Pilcopata road, 3330-3500 m, 29 Jun 1978 (fl), *Gentry et al. 23476* (F, MO), 3500-3600 m, 25 Oct 1984 (fl, fr), *Maas et al. 6175* (MO, NY, USM), 2000 m, 4 Apr 1987 (fl), *Nuñez 7745* (CUZ, F, MO, NY); paso de Tres Cruces, Cerro de Cusilluyoc, PN Manú, 3600-3800 m, 3 May 1925 (fl, fr), *Pennell 13905* (GH, NY, US, USM, S); Prov. Paucartambo, Kosñipata, trocha Unión, 3415 m, 4 Oct 2003 (fl), *H. Qquellón et al. 46* (CUZ, USM); Prov. Paucartambo, Kosñipata, predio Wayquicha, 3000 m, 25 Sep 2003 (fl), *H. Qquellón et al. 38* (USM); Valle de Pillahuata, cerca de las montañas de Paucartambo, Aug 1931 (fl, fr), *F. L. Herrera 3338* (US), 2800 m, 20 Jul 1936 (fl), *West 7079* (MO, UC), 3000 m, 12 Dec 1952 (fl), *Woytkowski 29* (NY, USM); Convención, Ollantaytambo-Quillabamba road, beyond the Abra Málaga, 3360-3550 m, 26 Jun 2006 (fl, fr), *Luteyn et al. 15706* (NY, USM); Prov. Paucartambo, km 115 NE from Huambutio, NE of Paucartambo, 2955 m, 8 Dec 1978 (fl), *Luteyn & Lebrón-Luteyn 6411* (MO, NY, USM); Prov. La Convención, carretera Ollantaytambo-Santa Teresa, después de San Luis y antes de Carrizales, 2950 m, 21 May 2005 (fl), *Pedraza et al. 1550* (CUZ, USM, COL, MO, NY, QCA, US); Prov. Paucartambo, Toccozochayoc, 3100 m, 17 Dec 1952 (fl), *Woytkowski 105* (USM). **Junín:** Prov. Tarma, Huasahuasi, 3400 m, 20 Mar 1994 (fl), *G. J. León 552* (NY).

BOLIVIA. Cochabamba: Prov. Chapare, km 104 on road from Cochabamba to Chapare and Villa Tunari, 3025 m, 17 Feb 1971 (fl, fr), *Hawkes et al. 4444* (MO); 104 km camino al Chapare, 3100 m, 6 Dec 1966 (fl)*, Steinbach 577* (F, GH, MICH, MO, NY, S, UC, US, WIS). **La Paz:** Yungas, 1890 (fl), *Bang 708* (BM, E, F, GH, MO, NY, US); Prov. Nor Yungas, cerca de 25 km después de la cumbre, 3480 m, 9 Feb 1980 (fl), *St. G. Beck 2849* (L, LPB, NY); Prov. Nor Yungas, pasando Unduavi hacia Cotapata, 3200 m, 3 May 1993 (fl), *St. G. Beck 19973* (LPB, NY); Prov. Nor Yungas, Unduavi, cerca de 2 km hacia Chuspipata, 3200 m, 29 Jun 2002 (fl), *St. G. Beck 27847* (LPB); Prov. Nor Yungas, PN Cotapata, cerca Unduavi, 3300-3450 m, 16 Sep 1997 (fl), *Berg 5173* (NY), 3450-3550 m, 7 Oct 1997 (fl), *Berg 5296* (LPB), 3250 m, 21 Oct 1982 (fl), *Solomon 8648* (MO, NY); Prov. Nor Yungas, La Paz-Coroico, 3130 m, 22-28 Jan 1983 (fl, fr), *Besse et al. 1738* (SEL, NY), 30 Mar 1977 (fl), *Boeke 1392* (LPB, NY); 3200 m, 4 Mar 2000 (fl, fr), *Luteyn et al. 15441* (LPB, NY); Prov. Nor Yungas, around Unduavi, 3400 m, 1907 (fl), *Buchtien s.n.* (L), 3300 m, Nov 1910 (fl), *Buchtien 100* (BM, E, F, GH, NY), *Buchtien 273* (F), 3300 m, Nov 1910 (fl), *Buchtien s.n.* (F, L), 3400 m, Oct 1931 (fl), *Buchtien 743* (F, GH, LPB, US), 3000-3200 m, 16 May 1991 (fl) *Feuillet 15019* (LPB), 3150 m, 27 Oct 1973 (fl), *Graf 226* (NY), 3100 m, 10 Oct 1982 (fl), *Menhofer X-1585* (LPB), 3030 m, Oct 1885 (fl), *Rusby 2022* (BM, E, F, GH, MO, NY, P, US, WIS), 3300 m, 19 Jul 1982 (fl), *Solomon & Daly 8013* (LPB, NY), 3100 m, 22 Dec 1983 (fl), *Solomon & Moraes 11438* (LPB, MO, NY); Prov. Nor Yungas, 4 km E of Unduavi Nuevo, mule trail of Rusby, 3300 m, 20 Mar 1988 (fl, fr), *Grifo & Solomon 1006* (MO, NY); Prov. Nor Yungas, Río Coscapa trail, near 3 km NE of Unduavi, W of Cotapata, 3420-3480 m, 30 Apr 1988 (fl), *M. Lewis 88334* (LPB, MO, NY); 3300-3500 m, 5 May 1990 (fl, fr), *Luteyn & Dorr 13502* (CAS, CUZ, LPB, MO, NY, TEX); Prov. Nor Yungas, carretera La Paz-Coroico, trocha en frente de la intersección con la carretera a Chulumani, 3420 m, 15 Apr 2005 (fl, fr), *Pedraza et al. 1508* (AAU, COL, LPB, MO, NY, US); Prov. Nor Yungas, entre la intersección de Chulumani y los caminos nuevo y viejo a Coroico, 3120 m, 15 Apr 2005 (fl, fr), *Pedraza et al. 1509* (COL, LPB, NY), *1511* (COL, LPB, NY); Cocopunco, 3030 m, 24-29 Mar 1926 (fl), *Tate 364* (LPB, NY); Prov. Nor Yungas, Hichuloma, an abandoned railroad station just across the border with Prov. Murillo, off the road from La Paz-Coroico, 3300 m, 18 Nov 1967 (fl), *Vuilleumier 364* (GH, LPB, NY, TEX); Prov. Larecaja, Mapiri trail (trek from Ingenio to Mapiri), 3100-3600 m, 21 Jul 2002 (fl), *Clark & Barrientos 6644* (LPB, NY); Prov. Larecaja, along trail from Mapiri to Soratá, between Tararani and Yani, 3000-3500 m, s.d. (fl), *Krukoff 11479* (NY), *Krukoff 11487* (F, NY), *11494* (NY); Prov. Larecaja, Mapiri, 3030 m, Apr 1886 (fl) *Rusby 2027* (NY). **Without province:** entrada de los Yungas, 2700 m, s.d (fl), *Girault s.n.* (USM); Jolapampa, 25 Sep 1902 (fl), *Williams 1557* (NY).

Disterigma pernettyoides is characterized by its leaves numerous, narrow (2-4 mm), and marginally crenulate; its pedicels evident or at least with a portion of it not completely obscured by the overlapping bracts; its corollas white, campanulate, and long [(10–)11.5–17 mm long]; its stamens weakly geniculate; and by its white fruits and seed embryos. The field notes on the herbarium voucher specimens sometimes suggest that the corolla turns pink or rose after anthesis, however that is not the case. The pink hue of the corollas of *D. pernettyoides* is not different from the one observed in the other species of the genus as a protection against intense solar radiation; in fact, the coloration is not always uniform or present, and it can already be found in floral buds. The morphological similarities of *D. pernettyoides* with other species are discussed under *D. codonanthum* (Table 11).

Local names and uses. This species is known as “Tarma” or “Perla-Perla” in Junín (Peru), and as “Winkiko” in the Bolivian yungas.

26. Disterigma pseudokillipiella Luteyn, Fl. Ecuador 54: 85. 1996. Type. Colombia. Antioquia: road to San Fermín de Briceño, about 25 km N of Yarumal, 1525-1830 m, 26 May 1984 (fl), *Luteyn et al. 10758* (holotype, NY; isotypes, AAU n.v., CAS, COL n.v., HUA n.v., JAUM n.v., K, MEXU n.v., MO). The sheets at AAU, COL, and HUA were not found

Epiphytic or terrestrial **shrubs**, scandent. Young branchlets ridged, more or less smooth, pubescent or puberulous, the hairs eglandular, light brown, the mature branches indumentum similar but glabrate. **Leaves** 0–5 per cm, spirally arranged, ascending or diffuse; petiole 1–2 mm long, glabrate, the hairs eglandular; lamina elliptic or lanceolate, 0.9–2.8 x 0.2–0.5 cm, basally obtuse or attenuate, marginally entire, apically ciliolate with eglandular hairs, apically acute or acuminate, adaxially glabrous or glabrate with eglandular hairs, abaxially glabrate with glandular hairs, the venation adaxially hyphodromous with the midvein impressed, abaxially obscure or hyphodromous with the midvein raised. Axillary and subterminal **solitary flowers**; bracts 1-8 or occasionally completely absent when the flowers subterminal, chartaceous, ovate, 1–2.2 x 0.9–3 mm, often inconspicuously ciliate with eglandular hairs, apically acute, abaxially glabrous or glabrate with inconspicuous eglandular hairs; pedicel 0.5–2.5 mm long, reduced and hidden by overlapping bracts, glabrous or glabrate with eglandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping entire calyx tube or to part of calyx lobes, covering 46–62% of calyx, ovate, 2.5–3.4 x 3–4 mm, marginally ciliolate with eglandular hairs, apically obtuse, the surface softly longitudinally striate (rarely smooth in pickled specimens), abaxially glabrous or glabrate with inconspicuous eglandular hairs, adaxially glabrous. **Flowers** 4-merous. Calyx aestivation valvate, campanulate, 4.2–6 mm long; tube terete, 1.2–1.8 mm long, abaxially glabrous; limb 3–4.5 mm long, abaxially and adaxially glabrous; lobes triangular, 2–4 x 1–1.8 mm, marginally ciliolate with eglandular hairs, apically acute; sinuses acute (V-shaped). Corolla light green or white, usually with pink hue on lobes, thin-fleshy, bistratose, urceolate (basally inflated), 6.6–9.1 mm long, 2.8–5 mm diam., 1.5–2.6 mm wide at throat, abaxially glabrous or glabrate with inconspicuous eglandular and glandular hairs, adaxially glabrate; lobes 0.9–1.3 x 0.8–2 mm, apically acute, adaxially rugose. Stamens 8, 6.5–7.4 mm long, exserted or at times included; filaments distinct, straight, more or less linear with parallel sides or broader at base, 3.5–5 mm long, abaxially puberulous or rarely glabrate, adaxially puberulous; anthers distinct, papillae only on thecae; thecae 1.4–2.2 mm long, without basal appendages; tubules 2, distinct, 1.7–2.8 mm long, dehiscing introrsely by longitudinal slits, 0.7–1.1 mm long. Ovary 4–locular; style 7.8–8.2 mm long, exserted. **Berry** white, depressed (wider than taller), 5.5–6.5 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo color unknown.

Distribution and ecology. *Disterigma pseudokillipiella* is found in the cordilleras Central and Occidental of Colombia, and in northern Ecuador in the provinces of Esmeraldas and Imbambura (Map 10). This rare species grows between 300-2500 m, in the montane and premontane cloud forest, as well as in the transitional zone to the tropical rain forest. It has been recorded growing in both primary and secondary vegetation, as well as on roadsides. Flowering specimens have been found all year-round, except for February, and fruiting in January, March, June, and September.

Etymology. The epithet makes reference to the genus *Killipiella* (named after the botanists E. P. Killip), now a synonym of *Disterigma*.

Specimens examined. COLOMBIA. Antioquia: Mun. Yarumal/Briceño, 2 km de la Troncal Caribe, via Santa Ana-Briceño, 1710-1980 m, 13 Aug 1992 (fl), *Gómez & Callejas 759B (*HUA, NY), 1710-1980 m, 18 Sep 1992 (fl, fr), *Gómez et al. 792* (NY), 1800-2000 m, 29 Jan 1993 (fl, fr), *Gómez & Callejas 867* (NY); Mun. Yarumal, 2 km from the Yarumal-Ventanas road junction with Santa Ana-Briceño turn-off, near Quebrada San Fermín, 1800-2000 m, 31 Oct 1996 (fl), *Luteyn et al. 14994* (NY); Mun. Guatapé, 9 km NE of Guatapé, vereda Santa Rita, finca Montepinar, 1800-1850 m, 13 Apr 1989 (fl), *Luteyn & Callejas 12506* (NY); Medellín-Sonsón road, 15-16 kms NE of Sonsón towards Argelia, 2440-2530 m, 27 Mar 1979 (fl), *Luteyn & Lebrón-Luteyn 7159* (AAU, COL, HUA, K, MO, NY, PSO); Medellín-Sonsón road, 9-11 kms SE of La Unión, 2377-2440 m, 26 Mar 1979 (st), *Luteyn & Lebrón-Luteyn 7120* (NY); Mun. Yarumal, vereda El Cedro, sector Altos de Ventanas, 1-3 km de la carretera al Cedro desde la Troncal del Caribe, 1700-1800 m, 9 Jul 2004 (fl), *P. Pedraza et al. 1066* (COL, CUVC, FMB, HUA, NY), *1068* (COL, CUVC, HUA, NY). **Cauca:** Mun. El Tambo, PNN Munchique, 2500-2560 m, 26 Apr 1979 (fl), *Luteyn et al. 7501* (CAUP, COL, NY), 2200-2640 m, 8 Aug 2004 (fl), *P. Pedraza & Giraldo 1167* (CAUP, COL, HUA, NY). **Chocó:** Mun. San José del Palmar, hoya del Río Torito (afluente del Río Hábita), 850-950 m, 15 Mar 1980 (fl, fr), *Forero et al. 7344* (COL, NY). **Nariño:** Mun. Barbacoas, El Diviso, 800 m, 10 Jun 1980 (fr), *Salazar de Benavides 2295* (PSO); Mun. Tumaco, corrigimiento Guayacana, 300 m, 20 Mar 1980 (fl), *Salazar de Benavides 9327* (PSO); Mun. Barbacoas, corregimiento de Junín, a 3 km del pueblo, 1300 m, 16 Jun 1988 (fl, fr), *Salazar de Benavides 9962* (PSO).

ECUADOR. Esmeraldas: Lita-Alto Tambo road, km 5-18, 750 m, 18 Jan 1987 (fl, fr), *Dodson et al. 16860* (MO). **Imbabura/Esmeraldas:** carretera Lita-Alto Tambo-San Lorenzo, 750 m, 20 Dec 2003 (fl, fr), *P. Pedraza & C. Pedraza 999* (COL, E, MO, NY, QCA), *1000* (COL, NY, QCA).

Without country. Growing at The New York Botanical Garden (Acc. No. 1035/2004), 1 Nov 2006 (fl), *P. Pedraza 1617* (NY).

Disterigma pseudokillipiella recalls the narrow-leaved forms of *D. stereophyllum* and *D. styphelioides*. They have in common the presence of solitary flowers, the numerous bracts overlapping and hiding the reduced pedicel, the differentiated apical bracteoles usually covering part of the calyx lobes and with the surface softly striate, the 4-merous flowers, and the white berries. However, *D. pseudokillipiella* has a unique combination of morphological features and it is characterized by its narrow and long leaves (3 or more times longer than broader), its axillary and subterminal solitary flowers, its differentiated apical bracteoles enveloping the entire calyx tube to the lower half of the calyx lobes, its calyx valvate with acute sinuses, and its corollas urceolate and light green or white. The major differences between this species and other morphologically similar species are summarized in Table 14.

Table 14. Summary of differences between *Disterigma pseudokillipiella*, *D. stereophyllum,* and *D. styphelioides*

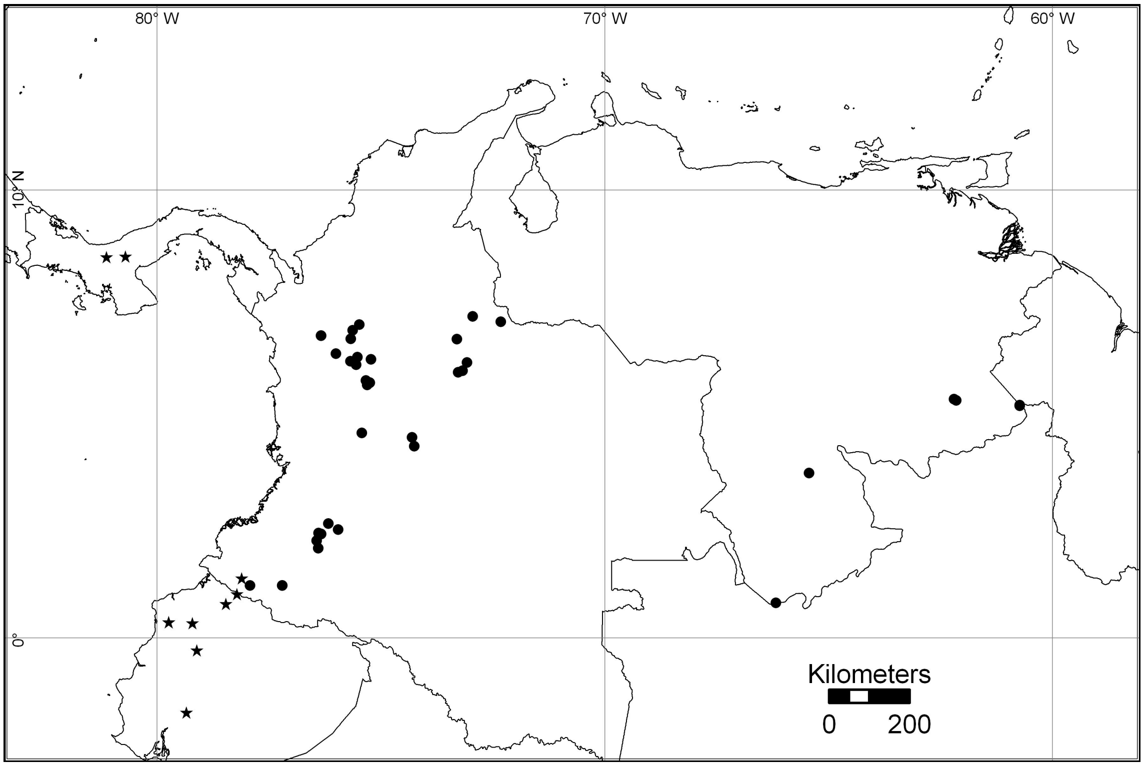
Characters	***D. pseudokillipiella***	***D. stereophyllum***	***D. styphelioides***
Leaf shape	Elliptic or lanceolate	Elliptic or oblanceolate, rarely ovate	Lanceolate
Leaf dimensions	0.9-2.8 X 0.2-0.5 cm	0.9-2.9 X0.3-1.3 cm	2-4.4 x 0.5-0.9 cm
Leaf venation abaxially	Hyphodromous or obscured	Hyphodromous or 3-nerved	Midvein and secondary veins parallely nerved
Solitary flower	Axillary and terminal	Axillary and terminal	Axillary
Apical bracteoles calyx coverage	46-62%	58-76%	72-100%
Calyx aestivation & sinus shape	Valvate & acute	Imbricate & obscured by overlapping calyx lobes bases	Imbricate & obscured by overlapping calyx lobes bases
Corolla shape	Urceolate	Urceolate	Tubular
Staminal filaments	Distinct	Distinct	Some fused & some distinct
Calyx lobes at fruit maturity	Spreading, lobes white	Converging into a cone, lobes green	Converging into a cone, lobes green

27. Disterigma staphelioides (Planch. ex Wedd.) Nied., Bot. Jahrb. Syst. 11: 210. 1889. *Vaccinium staphelioides* Planch. ex Wedd., Chlor. And. 2: 180. 1857. Type: Colombia. Cauca: Popayán, Páramo de Guanacas, s.d. (fl), *Hartweg 1214*, (holotype, P; isotype, B†, BM, C, CGE (x2), G, K (x2), fragment L ex K, NY, fragment NY ex K, OXF, P). Photo F neg. 4642 ex B†, photo NY neg. s.n. ex P.

Disterigma cuspidatum (Planch.) Nied., Bot. Jahrb. Syst. 11: 210. 1889, **syn. nov.** *Vaccinium cuspidatum* Planch. ex Wedd., Chlor. And. 2: 180. 1857. Type. Colombia. Tolima, s.d. (fl), *Goudot 3* (holotype, P; isotype, fragment F ex P, G, K, fragment L ex P, fragment NY ex K, OXF). Photo F neg. 38269 ex P, photo NY neg. 10531 ex K.

Terrestrial **shrubs**, scandent, prostrate and decumbent, erect, or 0.5–3 m tall. Young branchlets not ridged, more or less smooth, villous, the hairs eglandular and often wavy, the mature branches indumentum similar but villous or glabrate. **Leaves** 9–14 per cm, apparently distichous, patent to reclinate; petiole 0.5–1.6 mm long, glabrate or puberulous, the hairs eglandular; lamina a little succulent, ovate, (0.5–)0.6–0.8(–1) x (0.2–)0.4–0.5 cm, basally cordate or obtuse, marginally entire or rarely inconspicuously crenulate towards apex, apically ciliolate with eglandular hairs, sharply acuminate, long-acuminate, or rarely acute at apex, adaxially glabrous or glabrate with eglandular hairs, abaxially glabrate with glandular hairs, the venation adaxially obscure, abaxially hyphodromous or 3-nerved with the midvein raised. Axillary **solitary flowers**; bracts 4–5, chartaceous, ovate or transverse-elliptic, 2–3.2 x 1.6–3.6 mm, marginally ciliate with eglandular hairs, apically obtuse and cuspidate, abaxially glabrous; pedicel 1.2 mm long, reduced and hidden by overlapping bracts, minutely villosulous with eglandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping to part of calyx lobes, covering 63–87% of calyx, ovate, 3.2–5.6 x 3.2–4 mm, marginally ciliate with eglandular hairs, apically obtuse and cuspidate or acuminate, the surface smooth, abaxially and adaxially glabrous. **Flowers** 4-merous. Calyx aestivation valvate, campanulate, (5–)5.6–7.1 mm long; tube terete, (1.3–)1.6–2 mm long, abaxially glabrous; limb (3–)3.6–5.3 mm long, abaxially and adaxially glabrous; lobes triangular, (2.8–)3.6–5.2 x (1–)1.2–1.6 mm, marginally ciliate or ciliolate with eglandular hairs, apically acuminate or long-acuminate; sinuses rounded (U-shaped). Corolla white, thin-fleshy, bistratose, urceolate (inflated at the middle), (5–)7–9.5 mm long, 2.4–3.6 mm diam., 1.6–2.4 mm wide at throat, abaxially glabrate with eglandular hairs, adaxially glabrous; lobes (1.2–)2–2.8 x (0.8–)1.2–1.6 mm, apically acute, adaxially rugose (at least on the margins or apex). Stamens 8, (5.5–)7.1–7.6 mm long, exserted; filaments distinct, straight, broader at base, 3.5–4 mm long, abaxially and adaxially pilose; anthers distinct, papillae only on thecae; thecae 1–1.6 mm long, without basal appendages; tubules 2, distinct, (1.4–)2–2.4 mm long, dehiscing introrsely by longitudinal slits, 2 mm long. Ovary 4-locular; style (5.5–)6.5–7.9 mm long, exserted; nectary rarely with few hairs. **Berry** purple, more or less spherical, 5.2 mm diam. (immature), the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo white.

Distribution and ecology. *Disterigma staphelioides* is widespread in the northern Andes from Monte Roraima in the border of Guyana, Brazil and Venezuela, going through the three Colombian cordilleras as far south as Nariño (Map 13). This species grows between 1500-3500 m, in the montane and premontane cloud forest, as well as in the subpáramos and páramos. It has been recorded growing in both primary and secondary vegetation, as well as on roadsides. Flowering specimens have been found year-round and fruiting in March, May-August.



Map 13. Geographic distribution of *Disterigma staphelioides* ● and *D. utleyorum* ★.

Etymology. The meaning of the name of this species remains unknown as it was not indicated when published and no Greek or Latin roots seem to appropriately fit.

Representative specimens examined. COLOMBIA. Antioquia: Mun. Medellín, cerca de 130 kms hacia Yarumal, pasando Santa Rosa, cerca de San José de la Montaña, 27 Jun 1986 (fl), *St. G. Beck 13075* (LPB); Mun. San Antonio del Prado, vereda Potreritos, estribaciones del Alto el Romeral, 2600-2760 m, 12 Jul 2004 (fl), *J. C. Betancur & J. Betancur 10908* (COL, NY); Piedras Blancas, 2550 m, 13 Jul 1957, *Cabrera 101* (MEDEL, PMA); bosque bajo de la cumbre de

Las Palmas, camino Medellín-El Retiro, 2500 m, 18 Oct 1946 (fl), *Fajardo 36* (CAS, COL, MEDEL, US), 2500 m, 22 Sep 1946 (fl), *Gärtner 30* (COL, MEDEL, US), 2500 m, 18 Oct 1946 (fl), *Gutiérrez 1112* (COL, MEDEL, MICH, UC); Mun. Sonsón, La Soledad, camino a Río Verde de los Montes, camino antiguo Sonsón-Río Verde, 2400-2500 m, 9 Apr 1994 (fl), *Gómez et al. 1027* (HUA, NY); Yarumal-Valdivia road, 2160 m, 22 Mar 1979 (fl), *Luteyn et al. 7045* (COL, NY); Sonsón, vereda la Palmita, trail to Páramo de las Palomas, ca. 7 km NNE turnoff to Río Verde along Sonsón-Río Verde road, 2525-2750 m, 8 Apr 1988, *Luteyn et al. 11980* (AAU, COL, HUA, MO, NY, PSO); Medellín-Sonsón road, NE of Sonsón towards Argelia, 2530-2680 m, 27 Mar 1979 (fl), *Luteyn & Lebrón-Luteyn 7136* (AAU, CAS, COL, E, HUA, K, MO, NY, PSO, QCA, US); Mun. Frontino, corregimiento Nutibara, Nutibara-La Blanquita road, region murrrí, alto de Río Cuevas, 6 Apr 1989 (fl), *Luteyn & Sylva 12498* (CAS, HUA, NY), 1220-2130 m, 7 Jun 1989 (fl, fr), *Luteyn & Sylva 13281* (NY); Mun. Belmira, corregimiento Labores, 2650 m, 30 Jul 1983 (fl), *M. Pérez 107* (HUA); Urrao, vía hacia Caicedo, alto de Caicedo km 108, 2720 m, 4 Dec 1984, *Orozco et al. 1352* (COL); Mun. Sonsón, carretera que conduce de Sonsón a Nariño, en el área conocida como el Páramo, 2450-2800 m, 5 Jul 2004 (fl, fr), *P. Pedraza & C. Pedraza 1062* (AAU, COL, CUVC, HUA, FMB, MO, US, VEN); Medellín, Laguna Guarne, 2500 m, 7 Dec 1946, *Uribe-Uribe 1401* (COL, MEDEL); Mun. Sonsón, km 12 of road Sonsón-Nariño, 2630 m, 6 Dec 1986 (fl), *Zarucchi & Bedoya 4453* (HUA, MO, NY, US), *4454* (COL). **Bolivar:** bellow Páramo el Chaquiro, 2800-3100 m, 24 Feb 1918 (fl), *Pennell 4431* (NY). **Cauca:** Mun. Puracé, PNN Puracé, entre Pilimbalá y el Volcán Puracé, 3500-4300 m, 14 Nov 2004, *J. C. Betancur et al. 11219* (CAUP, COL); PNN Puracé, sector Paletará, 2900-3000 m, 19 Oct. 1987 (fl), *Duque 672* (COL), 3050-3150 m, 4 Mar 1979 (fl), *Luteyn & Lebrón-Luteyn 6952* (AAU, CAUP, COL, MO, NY); Mun. Coconuco, Valle de Paletará, PNN Puracé, 3050 m, 29 Jul 1980 (fl, fr), *Lozano 3470* (COL, NY); 26 km E of Totoró, 2950 m, 6 May 1984 (fl, fr), *Luteyn et al. 10208* (AAU, COL, HUA, JAUM MO, NY, US); along Coconuco road just outside entrance of PNN Puracé, 2987 m, 4 Mar 1979 (fl, fr), *Luteyn & Lebrón-Luteyn 6926* (COL MO NY); Mun. Puracé, Valle del Paleterá, vía Itsnos, cerca del Valle de los Frailejones, 9 Aug 2004 (fl), *P. Pedraza & Gómez 1247* (COL, HUA, NY). **Cundinamarca:** Páramo de Sibaté, 3750 m, 19 May 1981 (fl), *Iglesias 232* (COL); Bogotá-Usme road, Páramo de Chisacá, 3375-3450 m, 17 May 1979 (fl), *Luteyn et al. 7778* (COL). **Huila:** San José de Isnos, El Marmol, PNN Puracé, 2800 m, 24 Jul 1980 (fl), *Lozano 3412* (COL); La Plata, Arrabal, 2380 m, 1 Oct 1984 (fl), *Lozano et al. 4379* (COL, F). **Nariño:** Mun. Pasto, Páramo del Tábano, 17 Jun 1976, *André 2975 p.p.* (B, NY), 3100 m, 4 May 1967 (fl), *Guarín-M. 573* (PSO); Reserva Bilógica La Planada, 7 km S of Chucunés, along Las Vieja trail, 1800-1900 m, 5 Aug 1990 (fl), *Luteyn & Sylva 13843* (AAU, COL, MO, NY, PSO, QCA). **Norte de Santander:** Alto del Venado entre Samaria y Toledo, 2300-2400 m, 31 Oct 1941 (fl), *Cuatrecasas et al. 12814* (COL, F, US). **Putumayo:** lado S de la Laguna de La Cocha, páramo de Santa Lucia, 2900-3100 m, 9 Jan 1941 (fl), *Cuatrecasas 11865* (COL, US). **Santander:** Mun. Gámbita, vereda El Volcán, 2100 m, 11 Nov 1981 (fl), *Caro 35* (COL); Mun. Charalá, corregimiento de Virolín, camino al Olival, 1700 m, 8 Dec 1978 (fl), *Díaz-P. 1687* (COL); headwaters of Quebrada Chiriviti, W of Galán, 2700 m, 5 Sep 1944 (fl), *Fassett 25699* (NY, US), *Fassett 25702* (COL); Mun. Tona, vereda Guarumales, 1800 m, 9 Apr 2001 (fl), *Galindo et al. 414* (COL); Encino, Reserva Biológica Cachalú, 1900-2200 m, 15 Jul 2002 (fl), *N. R. Salinas et al. 108,* (COL, NY). **Tolima:** road to Nevado del Tolima, NNW of Ibagué, beyond Juntas, 2500-2750 m, 16 May 1984 (fl), *Luteyn et al. 10588* (CAS, NY). **Without department:** s.d., *Hartweg 4642* (NY).

GUYANA. Cuyuni-Mazaruni: Roraima trail, 1390 m, Feb 1982 (fl), *Kerby 485* (E).

VENEZUELA. Bolivar: Chimantá Massif, base of upper falls of Río Tirica above summit camp, 1940 m, 7 Feb 1955 (fl), *Steyermark & Wurdack 566* (F, NY, US). **Amazonas:** Venezuela-Brazil border, Cerro Neblina, 1900-2100 m, 17 Apr 1984 (fl), *Gentry & Stein 46730* (MO, NY); Cerro de la Neblina, Río Yatua, 1500-1700 m, 13 Jan 1954 (fl), *Maguire et al. 37257* (NY, US); Cerro de la Neblina, 6.5 km SSW of base camp, S extension of range, 1600 m, 18 Apr 1984 (st), *Stein et al. 1641* (MO, NY); Mun. Atabapo, Cerro Marahuaca, meseta SE, quebrada Yekuana, 2560 m, 10-12 Oct 1983 (fl), *Steyermark 129524* (MO, NY). **Bolivar:** Monte Roraima, 2300 m, 2 Nov 1973 (fl), *Persaud 177* (K, NY); Monte Roraima, SW slopes, 2180 m, Jan 1939 (fl), *Pinkus 131* (NY, US); Mun. Piar, Macizo del Chimantá, cabeceras orientales del Caño Chimantá, 2000 m, 26-29 Jan 1983 (fl), *Steyermark et al. 127988* (F, MO, NY, US); Mun. Piar, Macizo del Chimantá, altiplanicie en la base meridional de los farallones superiores del Apacará Tepui, 2200 m, 30 Jan-1 Feb 1983 (fl), *Steyermark et al. 128305* (MO, NY). **Mérida:** distrito Rivas Dávila, La Sabana, cerca de Pico Horma, 2850 m, 8 Aug 1970 (fl), *Ruiz-Terán & López-Figueiras 592* (L, NY). **Without department:** s.d., *Stübel 216* (F).

The study of the specimens of *Disterigma staphelioides* and *D. cuspidatum* revealed that there is no clear cut boundary between them when using the characters proposed by Smith (1933). Although the apical bracteoles of *D. cuspidatum* are distinctively long-acuminate and mostly obtuse to subacute in *D. staphelioides*, acute bracteoles also occur in some flowers of the type specimens of *D. staphelioides*. The apex of the differentiated apical bracteoles is not considered to be significant enough to grant species distinction, and the other suggested diagnostic characters that would be more significant at the specific level, e.g., corolla dimension, occur with either obtuse or acuminate bracteoles. The basonyms of both names, *Vaccinium staphelioides* and *V. cuspidatum*, were published in the same issue and on the same page. However, the description of *V. cuspidatum* is very brief and only consists of two non-specific characters (characters shared by may other species). On the other hand, the description of *V. staphelioides* is not only detailed, but it also explicitly identifies a type collection and therefore it is here regarded as the most appropriated basonym for the species. It is worthy to mention that *V. staphelioides* was validly published by Weddell in *Chloris Andina* using a name provided by Planchon in an unpublished manuscript. There is no doubt that Weddell provided the valid publication of the name but when Niedenzu made the combination for *Disterigma staphelioides* in 1889, he incorrectly attributed *V. staphelioides* to Planchon, an omission found in later works.

Disterigma staphelioides is distinguished by its leaves apparently distichous, numerous, small, ovate, and usually apically acuminte and pricking; its long (almost as long as the limb), narrow, and acuminate calyx lobes; its rounded calyx sinuses; its urceolate and adaxially glabrous corollas; and its purple berries with white seed embryos. Vegetatively, *D. staphelioides* is similar to *D. dendrophilum* and *D. acuminatum,* but can be differentiated from the others because its calyces are 5 mm long or more (vs. up to 3.6 mm long in the other species), its calyx lobes are more than 3 mm long (vs. up to 2 mm long), its sinuses are rounded (vs. acute), its corollas are (5-)7-9.5 mm long (up to 6 mm long), and its stamens are at least 5.5 mm long (vs. up to 5 mm long).

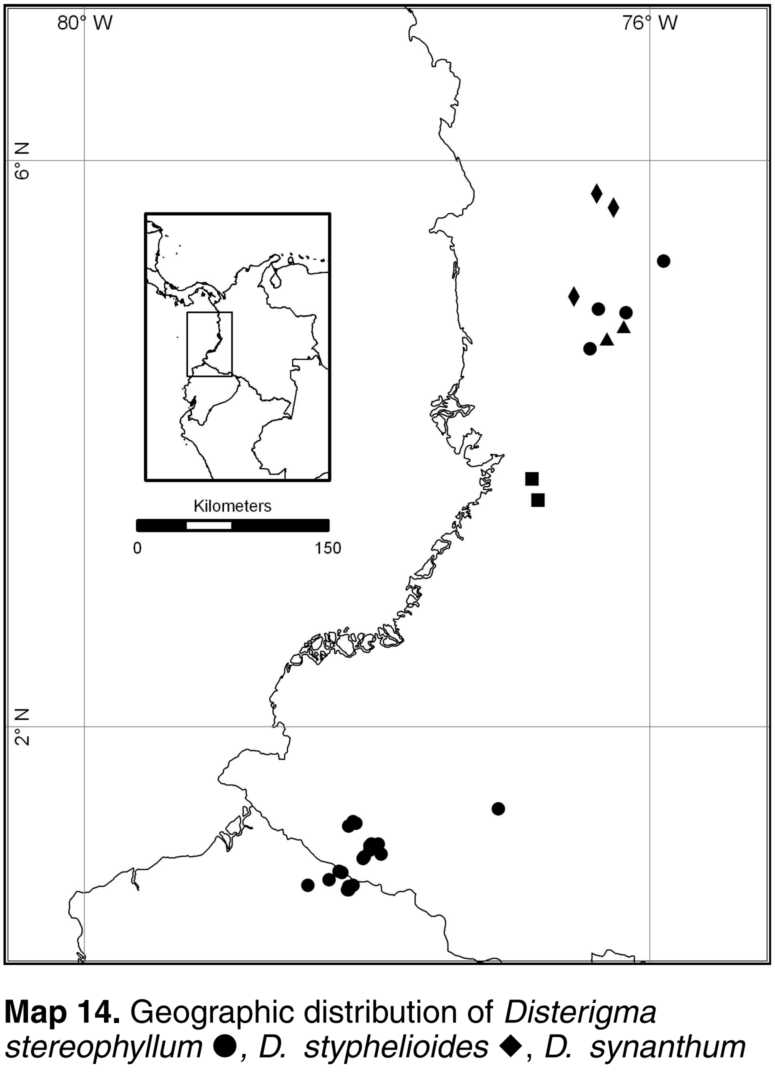
Here it is suggested that *Callejas & Roldán 10590* (HUA, NY) from Colombia (Antioquia), and *Maguire 33324* (NY, US), *Steyermark & Wurdack 1156* (F, NY, US), and *Steyermark 58713* (A, F) from Venezuela (Chimantá and Roraima), could be of hybrid origin from crosses between *D. staphelioides* and *D. humboldtii*. These specimens fell out of the expected variation within the species by a character or two. Their leaves are ovate to elliptic, with an apex acute, blunt acute, or subacute, and their margin crenulate or entire; their calyx lobes are shorter than average, just 2-3 mm long; and their corollas are adaxially puberulous or glabrous. Populations from both paternal species co-exist in the area where these unusual collections came from; additional fieldwork there would be necessary to conduct detailed molecular and morphological studies.

28. Disterigma stereophyllum (A. C. Sm.) Luteyn, Fl. Ecuador 54: 276. 1996. *Killipiella stereophylla* A. C. Smith, Contr. U.S. Natl. Herb. 29(8): 357. 1950. Type. Colombia. Nariño: W slope of the Cordillera Occidental, Ricaurte, 1300 m, 18 Apr 1941 (fl), *Sneidern 612* (holotype, F; isotypes, L n.v., MICH, NY, fragment US). Photo F neg. 52535 ex F, photo NY neg. 9673, 10500, and 13027.

(Fig. 10 F)

Epiphytic or terrestrial **shrubs**, scandent. Young branchlets ridged, more or less smooth, mostly glabrate or puberulous, the hairs inconspicuous, eglandular, white, the mature branches glabrous. **Leaves** 3–6 per cm, spirally arranged, diffuse or patent; petiole 1–3 mm long, glabrate, the hairs inconspicuous, eglandular; lamina elliptic, oblanceolate, or rarely ovate, 0.9–2.9 x 0.3–1.3 cm, basally obtuse or truncate, marginally entire, apically ciliolate with eglandular hairs, apically acute, adaxially glabrous or the young leaves glabrate with inconspicuous eglandular hairs over the midvein, abaxially glabrate with minute glandular hairs, the venation adaxially hyphodromous with the midvein impressed, abaxially hyphodromous or 3-nerved with the midvein raised. Axillary and subterminal **solitary flowers**; bracts 7–9, chartaceous, ovate or elliptic, 0.8–3.4 x 1–3 mm, occasionally marginally ciliate with eglandular hairs, apically obtuse, abaxially glabrous or rarely glabrate with inconspicuous eglandular hairs; pedicel 0.8–1.5(–2.5) mm long, reduced and hidden by overlapping bracts, glabrate with minute glandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping to lower half of calyx lobes, covering 58–76% of calyx, ovate, elliptic, or suborbicular, (3–)4.4–6 x (3–)4.4–6 mm, marginally ciliolate with minute eglandular hairs, apically obtuse, the surface softly longitudinally striate (smooth in most of the pickled material), abaxially glabrous or sometimes glabrate with inconspicuous eglandular and glandular hairs, adaxially glabrous. **Flowers** 4-merous. Calyx aestivation imbricate, campanulate, (5–)5.5–8.7 mm long; tube slightly angled, 1.2–2 mm long, abaxially glabrate with minute glandular hairs; limb (3.8–)4.3–7.1 mm long, abaxially glabrate with inconspicuous eglandular and glandular hairs, adaxially glabrous; lobes elliptic [triangular in only a few flowers from Ansermonuevo (Valle del Cauca, Colombia)], (3.5–)4–5.3(–6.5) x (1.2–)2.2–3.5(–4.4) mm, marginally ciliolate with eglandular hairs, apically obtuse and apiculate or very rarely subacute and apiculate; sinuses obscured by the overlapping bases of the imbricate lobes (the lobes spread when the calyx lobes are triangular). Corolla pink or white, thick-fleshy, not bistratose, urceolate (inflated in the middle), (6–)7.5–10(–11.5) mm long, 4–4.4 mm diam., 1.5–2 mm wide at throat, abaxially glabrous or glabrate with glandular hairs, adaxially glabrate; lobes 1–1.6 x 1–1.5 mm, apically acute, adaxially rugose. Stamens 8, (5.6–)7–8(–8.2) mm long, included; filaments distinct, straight, obtriangular, (3.3–)3.6–5 mm long, abaxially glabrous or rarely glabrate with inconspicuous hairs, adaxially pubescent; anthers distinct but tightly packed, papillae only on thecae; thecae 1.3–1.9(–2.2) mm long, without basal appendages; tubules 2, distinct, (2–)2.2–2.6(–3.1) mm long, dehiscing introrsely by longitudinal slits, 0.9–1.5(–1.7) mm long. Ovary 4-locular; style 7.6–8.8 mm long, exserted. **Berry** white, more or less spherical, 6.5–7.5 mm diam., the persistent calyx lobes converging and overlapping, green; seed embryo white.

Distribution and ecology. *Disterigma stereophyllum* is found in the northern western Andes from Chocó (Colombia) to Carchi (Ecuador), or in the western limit of the Chocó biogeographic region (Map 14). This rare species grows between 750-2100(-3000) m, in the montane and premontane cloud forest, as well as in the transitional zone to the lowland rainforest. It has been recorded growing in both primary and secondary vegetation, as well as on roadsides and pastureland with remnant vegetation. Flowering specimens have been found all year-round, and fruiting in December-February and July-August.



Map 14. Geographic distribution of *Disterigma stereophyllum* ●*, D. styphelioides* ◆, *D. synanthum* ■*,* and *D. verruculatum* ▲.

Etymology. *Stereophyllum* comes from the Greek word *stereos* that mean hard, solid, or thick, perhaps as a reference to the coriaceous leaves of this species.

Representative specimens examined. COLOMBIA. Chocó: Mun. San José del Palmar, vereda Portachuelo, Finca Barro Blanco, 1300 m, 15 Jan 1983 (fl, fr), *Díaz-P. 3577* (COL); hoya del Río Torito (afluente del Río Hábita), fincal Los Guadales, 730-830 m, 2 Mar 1980 (fl), *Forero et al. 6485*3, 3 Mar 1980 (fl), *Forero et al. 6579* (COL, MO, NY); Ansermanuevo-San José del Palmar road, from Chocó to Valle border,10 km W towards San José del Palmar, 1524-2050 m, 15 May 1984 (fl), *Luteyn et al. 10546* (CAS, COL, K, NY); Mun. San José del Palmar, Ansermonuevo-San José del Palmar road, 1850-1975 m, 19 Apr 1979, *Lutyen et al. 7299* (COL, NY), 1200-1500 m, 20 Apr 1979 (fl, fr), *Luteyn et al. 7310* (AAU, COL, CUVC, MO, NY). **Nariño:** Reserva Natural La Planada, 1800 m, 20 Feb 1993 (fl), *Agudelo et al. 2931* (COL), 1800 m, Nov 1993 (fl), *Amaya 305* (COL), 1780-1800 m, 28 Jul 1988 (fr), *Croat 69642* (PSO)*, 71180* (PSO), 1800 m, 4 Jan 1989 (fl), *Gentry et al. 64484* (PSO), 1850-1870 m, 8 Oct 1997 (fl), *Luteyn et al. 15206* (COL, NY), 1850 m, 24-25 Feb 1979 (fl), *Luteyn & Lebrón-Luteyn 6816* (AAU, CAS, CAUP, COL, CUVC, E, HUA, K, MO, NY, PSO, QCA, US), 1800-1900 m, 7 Aug 1990 (fl, fr), *Luteyn & Sylva 13916* (COL, NY, PSO), 1900 m, 28 Nov 1976, *Salazar de Benavides 758* (PSO) *8832* (NY, PSO), *10804* (PSO), 1850 m, 27 Dec 2003 (fl, fr), *N. R. Salinas et al. 420* (COL, NY), 1800 m, 25 Jul 1994 (fl), *Tupac-O. & Ríos 407* (PSO), Jul 1995 (fl), *W. Vargas 7374* (MEDEL); Mun. Barbacoas, Reserva Natural Río Ñambí, 1300 m, 9 Aug 1992 (fl), *Arias 116* (PSO), 1300-1350 m, 1-8 Dec 1993 (st), *Gómez et al. 935* (COL, HUA, NY), 1300-1500 m, 1-12 Dec 1993 (fl), *Gómez et al. 978* (COL); Altaquer-Junín road, about 3 km W of Altaquer, near bridge over Río Nembi, 1100 m, 25 Feb 1979 (fl, fr), *Luteyn & Lebrón-Luteyn 6839* (CAS, COL, L, MO, NY, QCA, TEX, US); Mun. Mallama, La Alegría, puente el Tablón, 1500-1600 m, 20 Dec 1995 (fl), *B. R. Ramírez & M. S. González 9265* (PSO); Mun. Barbacoas, El Mirador-Cuyambé, 1400 m, 5 Dec 1986 (fl), *Salazar de Benavides 7542* (PSO), 1800 m, 7 Sep 1994 (fl), *Tupac-O 413* (PSO); Mun. Barbacoas, corregimineto Altaquer-Nembí, 1350 m, 6 Jul 1987 (fl), *Salazar de Benavides 8056* (PSO). **Risaralda:** Mistrato, entre los corregimientos de Geguadas y Puerto de Oro, bosque de Pisones, 1550 m, 2 Apr 1993, *J. L. Fernández et al. 9721* (COL).

ECUADOR. Carchi: alrededores de Maldonado, 1500 m, 5 Sep 1981 (fl), *Balslev 1980* (NY); Cerro Golondrinas hembra, 3070 m, 24 Jul 1994 (fl), *Boyle et al. 3376* (NY), 3000 m, 21 Aug 1994 (fl), *W. Palacios & Clark 12530* (NY), 3000 m, 21 Aug 1994 (fl), *W. Palacios & Clark 12535* (NY); vicinity of El Chical, along road to Carmen, departing main road El Chical-Piedras Blancas, 1435-1500 m, 17 Feb 2005 (fr), *Croat 94772* (NY); SW of the finca of Rafael Quindis, 1930-2100 m, 28 Nov 1987 (fl), *Hoover & Womley 1855* (MO); vicinity of El Chical, 12 km below Maldonado, along Río San Juan, 1200 m, 26 May 1978 (fl), *Madison et al. 4558* (F, NY, SEL); N de El Chical, trocha que conduce de Piedras Blancas a El Pailón-Gualpi-San Marcos-Tobar Donoso, 1050 m, 17 Dec 2003 (fl, fr), *P. Pedraza & C. Pedraza 988* (AAU COL MO NY QCA QCNE); Reserva Indígena Awa, Centro El Baboso, parroquía Tobar Donoso, 1800 m, 17-27 Aug 1992 (fl, fr), *Tipaz et al. 1994* (MO, NY).

Disterigma stereophyllum is well differentiated because its solitary flowers are axillary or subterminal; its differentiated apical bracteoles, which envelope up to the lower half of the calyx lobes, are softly striate; its calyx aestivation is imbricate and the calyx sinuses are obscured by the overlapping bases of the imbricate lobes; its calyx lobes are elliptic, long, apically apiculate, and obtuse or subacute; its filaments are obtriangular; its white fruits when mature are crowned by the converging and overlapping green calyx lobes; and because its seed embryos are white. Although more or less characteristic, the leaves of this species vary widely in size, even within the same plant. Often, the leaves on long shoots or in the branches that carry new growths are half the size of the regular leaves. Another morphological variation is that of the calyces of some of the specimens from the vicinity of Ansermonuevo (Valle del Cauca, Colombia) (i.e., *Luteyn et al. 7299, 7310, Díaz-P. 3577*); the calyx lobes of some flowers are more triangular than elliptic and consequently not wide enough to cause their bases to imbricate and obscure the calyx sinuses at anthesis (although the aestivation remains imbricate). Perhaps this feature has been fixed in some individuals with the help of the apparently low population density observed for this species. For a discussion about the morphological similarities of this species with others see Table 14 under *D. pseudokillipiella*.

Local names and uses. This species is known as “Chaquilulo” in Nariño (Colombia).

29. Disterigma styphelioides (A. C. Sm.) Pedraza, **comb. nov.** *Killipiella styphelioides* A. C. Sm. J. Wash. Acad. Sci. 33: 243. 1943. Type. Colombia. Chocó: Corcovado region, upper Río San Juan, ridge along Yeracüí Valley, 200-275 m, 24-25 Apr 1939 (fl), *Killip 35222* (holotype, US).

(Fig. 23)

Epiphytic **shrubs**. Young branchlets ridged, more or less smooth, puberulous, the hairs eglandular, brown, the mature branches indumentum similar but glabrous or glabrate. **Leaves** 1–3 per cm, spirally arranged, diffuse or patent; petiole 2–3.5 mm long, glabrate, the hairs eglandular; lamina lanceolate, 2–4.4 x 0.5–0.9 cm, basally obtuse, marginally entire, apically ciliolate with eglandular hairs (especially in young leaves), apically acute, adaxially glabrous or glabrate with inconspicuous eglandular hairs over the midvein, abaxially glabrate with minute glandular hairs, the venation hyphodromous adaxially with the midvein impressed, abaxially with the secondary veins marked and parallel. Axillary **solitary flowers**; bracts 6–9, chartaceous, ovate, elliptic, or suborbicular, 1.6–8 x 1.2–4 mm, marginally ciliate with eglandular and glandular hairs, apically obtuse or acute, abaxially glabrous; pedicel 2–2.8 mm long, reduced and hidden by overlapping bracts, glabrate with eglandular and glandular hairs; differentiated apical bracteoles 2, distinct, chartaceous, enveloping to upper half of calyx lobes or entire calyx, covering 72–100% of calyx, ovate or elliptic, 6.3–9.5 x 3.5–4.5 mm, marginally ciliate with eglandular and glandular hairs, apically acute, the surface softly longitudinally striate (more or less smooth in pickled material), abaxially and adaxially glabrous. **Flowers** 4-merous. Calyx aestivation imbricate, campanulate, 8.5–10 mm long; tube terete, 2.2–3 mm long, abaxially glabrate with inconspicuous glandular hairs; limb 6–7 mm long, abaxially and adaxially glabrous; lobes oblong-lanceolate, 5.7–6 x 1.2–2.1 mm, marginally ciliate with eglandular and glandular hairs, apically acute; sinuses obscured by the overlapping bases of the imbricate lobes. Corolla white, thick-fleshy, bistratose, tubular (but lobes very deep and spreading perpendicularly), 9–12 mm long, 2 mm diam., 2 mm wide at throat, abaxially glabrate, with glandular hairs, adaxially glabrous; lobes 5–6.2 x 1–1.2 mm, apically acute, adaxially smooth. Stamens 8, 9.5–11.5 mm long, exserted about half of their length; filaments distinct or connate into a tube, not all the filaments connate in the same extent, straight, more or less linear with parallel sides, 3–4 mm long, abaxially glabrous, adaxially inconspicuously glabrate; anthers distinct, papillae on both thecae and tubules but especially conspicuous on the tubules; thecae 2.4–2.5 mm long, with a prominent basal appendage; tubules 2, distinct, 4.7–6.5 mm long, dehiscing introrsely by longitudinal slits, 1.5–2.5 mm long. Ovary 4–locular; style 11.2–13.2

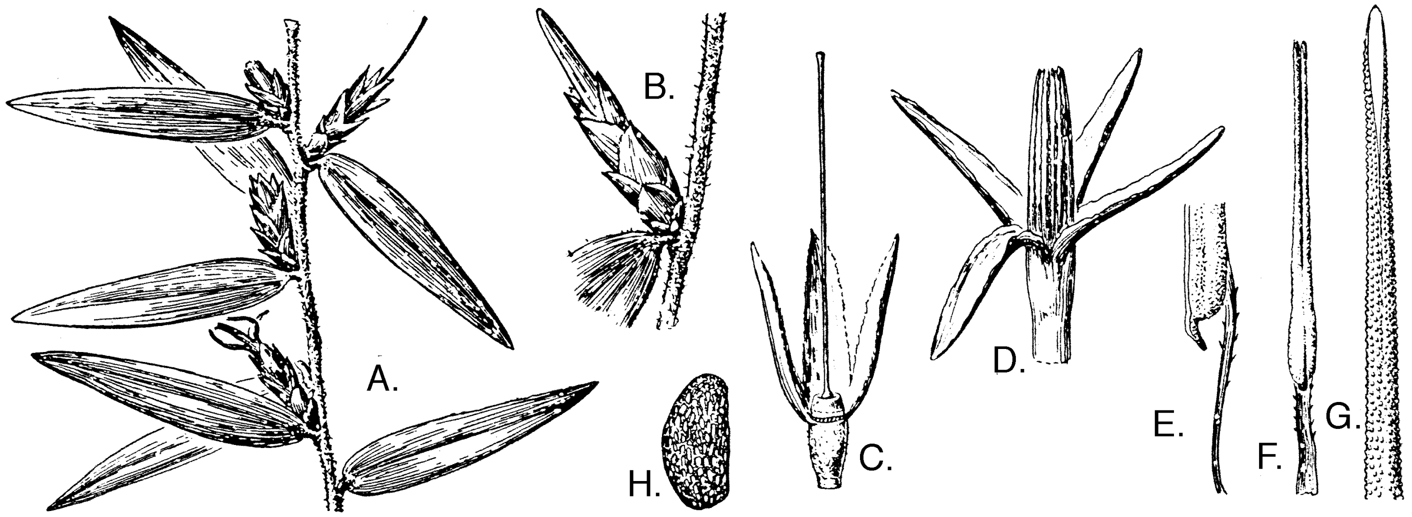


Fig. 23. Illustration of *Disterigma styphelioides.* **A.** Portion of a branch; **B.** Flower Bud; **C.** Calyx with one of the lobes removed showing nectariferous disk and style; **D.** Corolla and stamens; **E.** Lateral view of the base of the anther; **F.** Adaxial view of the stamen; **G.** Close-up of the anther tubule; **H.** Seed (*Killip 35222*, US) . Originally published as *Killipiella styphelioides.* Modified from J. Wash. Acad. Sciences 33(8): 244, fig. 1 (1943).

mm long, exserted. **Berry** white, more or less spherical, 4 mm diam., the persistent calyx lobes converging and overlapping, green; seed embryo color unknown.

Distribution and ecology. *Disterigma styphelioides* is endemic to the department of Chocó (Colombia), within or in the western limits of the Chocó biogeographic region (Map 14). This very rare species is only known from three collections, the most recent one from 1984. It grows in the lowland rainforest as well as in the transitional zone to the premontane forest, between 200-600 (-1000?) m. It has been recorded inside the forest or in pastureland with remnant vegetation. Flowering specimens have been found in April and May, and fruiting in May.

Etymology. This species was named after the genus *Styphelia* Smith (Ericaceae: Epacrideae) that it vegetatively resembles.

Specimens examined. COLOMBIA. Chocó: Bolívar-Quibdó road, about 37-40 km W of El Carmen, 671-1360 m, 21-22 May 1984 (fl, fr), *Luteyn et al. 10684* (COL); Medellín-Quibdó road, km 177-179, 450-500 m, 5 Apr 1979 (fl), *Luteyn & Lebrón-Luteyn 7217* (COL).

Disterigma styphelioides is distinguished because of its relatively long and narrow leaves with parallel secondary veins adaxially; its solitary flowers with numerous overlapping bracts; its calyx aestivation imbricate with the sinuses obscured by the overlapping bases of the lobes at anthesis; its long, white, and tubular corollas with the lobes so deep and reflexed as to expose the stamens half of their length; its staminal filaments are either distinct or connate; its conspicuous papillae on both thecae and tubules; and its fruit white with the persistent calyx lobes converging and overlapping in to a cone. For a discussion about the morphological similarities of this species with others see Table 14 under *D. pseudokillipiella*.

Killipiella styphelioides is the type species of *Killipiella*, a genus synonymized by Luteyn (1996) into *Disterigma*; however, the combination for *D. styphelioides* has not been provided until now. When Smith (1943) described this species he could not find any affinities between it and any other known Vaccinieae. Although he did not doubt its position within the inferior-ovaried Vaccinieae (Vacciniaceae according to his concept) he noted the superficial resemblance of *K. styphelioides* with some Epacridaceae (now Epacrideae, superior ovary taxa mostly from Australia); its leaves were similar to the leaves of some *Styphelia* and its flowers had the general aspect of those of *Styphelia* and *Epacris* (Fig. 24). Without doubt, Smith was taken by the unusual appearance of this neotropical plant, especially because other similarly looking *Disterigma* were not discovered until much later. Smith suggested *Disterigma* as the possible closest relative of *Killipiella* but he failed to recognize many shared characters between them and that he then regarded as restricted to the new genus (i.e., conspicuous pulvinate nectary, foveolate seeds, papillae on both thecae and tubules, anthers with basal appendages). In his description, Smith did not mention the presence of an apical pair of differentiated bracteoles in *K. styphelioides*, the key character of *Disterigma*, neither did he mention that staminal filaments of this species are either distinct or connate. Although Smith (1943) pointed out that most of the ovules in *K. styphelioides* were aborted and only 1-3 seeds were developed, the fruits I have studied had numerous fully developed seeds. Other differences with the original description provided by Smith are found in the inflorecences. Smith interpreted the solitary flowers of *K. styphelioides* as “consisting of a short rachis bearing several imbricate bracts and a terminal flower ... being the actual pedicel reduced to an inconspicuous length”. Smith saw the solitary flowers as a

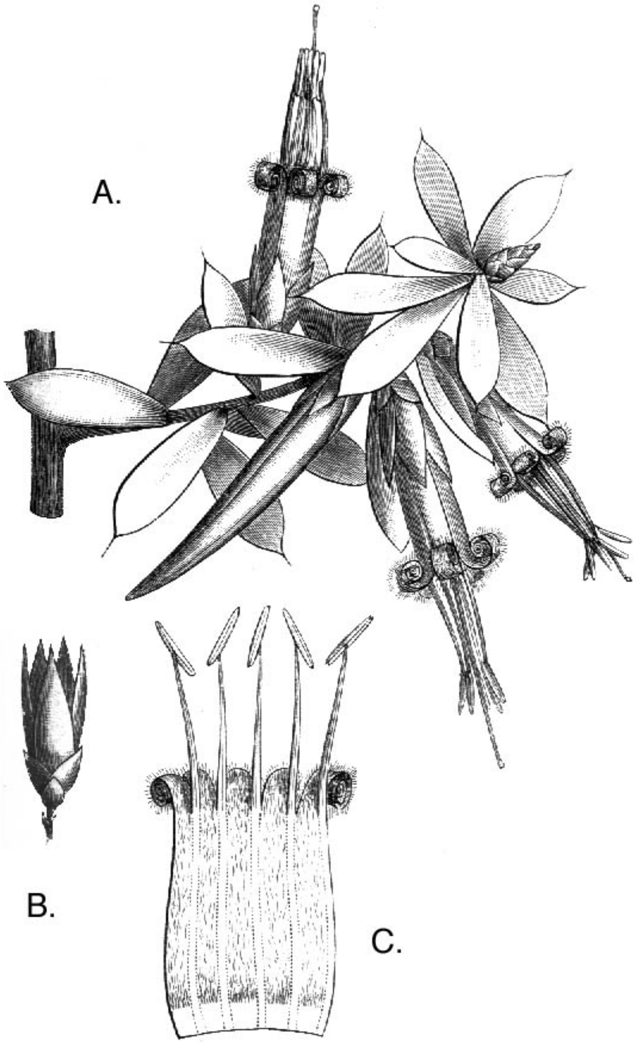


Fig. 24. Illustration of *Styphelia viridis.* **A.** Portion of a branch with open flowers and a floral bud; **B.** Calyx; **C.** Open corolla exposing the stamens. Modified from Prantl. Die Natürlichen Pflanzenfamilien 4(1), fig. 46 (1891).

reduction of a racemose inflorescence; although this transformation by reduction applies to the inflorescences of other Ericaceae, I have found no evidence of such a process taking place in any species of *Disterigma* (see introductory chapter). Therefore the flowers of *D. styphelioides* are truly axillary and are subtended by a short pedicel that is obscured by the numerous imbricate bracts and bracteoles.

30. Disterigma synanthum Pedraza, **sp. nov.** Type. Colombia. Valle del Cauca; old road Cali-Buenaventura, km 36-38, Finca las Elisas, 1320-1500 m, 10 Mar 1979 (fl), *Luteyn & Lebrón-Luteyn 7001* (holotype: COL; isotypes: COL, NY).

(Fig. 25)

Species nova foliis ovatis vel ellipticis, in apice acutis vel subacutis, obscure apiculatis, inflorescentia 2-3-flora, unifasciculata, axillari, interdum floribus solitariis, bracteis 6-9, bracteolis apicalibus 1, calycem 2.6 mm superantibus, cordiformibus, saepe lobis latis superimponentibus ad apicem divisis, pustulatis, longitudinaliter striatis, floribus 4-meris, calyce pustulato, aestivatione valvata, lobis calycis minoribus quam dimidio longitudinis limbi, sinubus rotundis, corolla alba, anguste urceolata pustulata, adaxialiter ad lobos et fauces superiores glabrata, filamentis geniculatis, antheris lateraliter connatis, bacca alba distincta.

Epiphytic or terrestrial **shrubs**, erect, 0.5–3 m tall. Young branchlets ridged, more or less smooth, puberulous, the hairs eglandular, brown or white, the mature branches indumentum similar but glabrate. **Leaves** 1–3 per cm, spirally arranged, diffuse; petiole 1.6–4 mm long, glabrate, the hairs eglandular; lamina ovate or elliptic, 2–3.8 x 1–2 cm, basally obtuse, marginally entire, apically ciliolate with eglandular hairs, apically acute and obscurely apiculate or sometimes subacute and obscurely apiculate, adaxially glabrate with inconspicuous eglandular hairs, abaxially glabrate with eglandular and glandular hairs, the venation 3-nerved on both sides, the midvein adaxially impressed and abaxially raised. **Inflorescence** axillary, of 2–3-flowered fascicles and sometimes solitary flowers; bracts 6–9, chartaceous, obovate, occasionally ovate or cordiform, 3.5–8.5 x 2.5–6 mm, marginally ciliolate with minute eglandular and glandular hairs at apex, apically obtuse or sometimes cleft, abaxially glabrous or glabrate with inconspicuous eglandular hairs; pedicel 0.7–1 mm long, much reduced and hidden by overlapping bracts, glabrous; differentiated apical bracteoles 1, originated by the fusion of the bracteoles by one of their ends, chartaceous, extending beyond calyx 2.6 mm (covering 100% of calyx), cordiform with the lobes broad and overlapping or rarely well apart, 6.5–8.8 x 4.5–5.5 mm (since the lobes often overlap the width given is for each lobe), marginally ciliolate with minute eglandular and glandular hairs, apically cleft, the surface pustulate and longitudinally striate, abaxially glabrous or glabrate with inconspicuous eglandular hairs, adaxially glabrous. **Flowers** 4-merous. Calyx aestivation valvate, campanulate, 4–5.5 mm long, pustulate; tube terete, 1.5–2.7 mm long, abaxially glabrous or glabrate with inconspicuous eglandular hairs; limb 2.5–2.8 mm long, abaxially and adaxially glabrous; lobes triangular, 0.7–1 x 1.5–2 mm, marginally eciliate, apically acute; sinuses rounded (U-shaped). Corolla white (fide collectoris), thin-fleshy, bistratose, narrowly urceolate, 8–8.8 mm long, 2 mm diam. (in dry), 1.6 mm wide at throat (in dry), pustulate, abaxially puberulous with glandular hairs, adaxially glabrate at the lobes and upper throat; lobes 1.3–1.5 x 1–1.1 mm, apically acute, adaxially rugose. Stamens 8, 7.5–8 mm long, exserted; filaments distinct, geniculate, broader at base, 3.8–4.2 mm long, abaxially glabrous, adaxially pilulose (distally); anthers loosely connate by the thecae, papillae only on thecae; thecae 1.6–2.2 mm long, basally

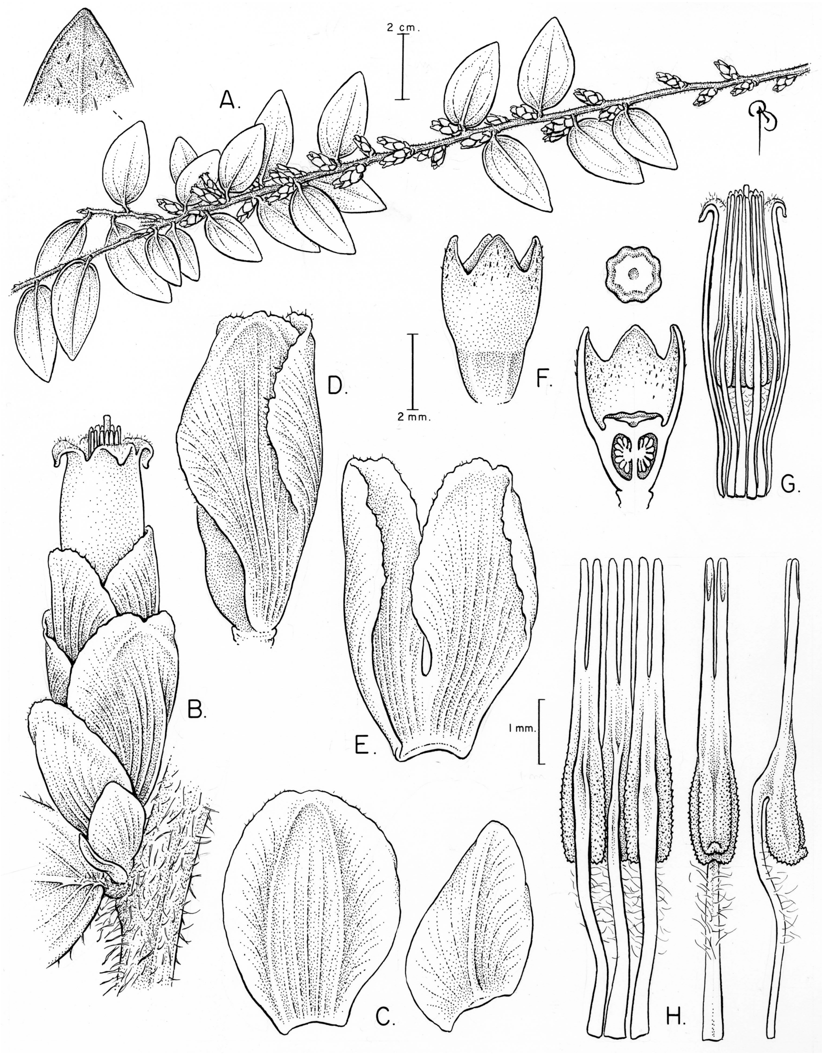


Fig. 25. Illustration of *Disterigma synanthum*. **A.** Branch showing few-flowered fascicles and solitary flowers, and with a detail of leaf apex; **B.** Flower with conspicuous multiple bracts; **C.** Bracts; **D.** Differentiated apical bracteole extending beyond the calyx; **E.** Heart-shaped differentiated apical bracteole, the surface pustulate and longitudinally striate; **F.** External view and longitudinal section of the calyx and inferior ovary, with a detail of the nectariferous disk; **G.** Longitudinal section of the corolla; **H.** Abaxial, adaxial, and lateral views of the stamens (*Hilty SX-24,* US).

appendaged; tubules 2, 2.8–3 mm long, fused at base for 0.7–1 mm of their length, dehiscing introrsely by longitudinal slits, 0.9–1 mm long. Ovary 4-locular; style 8.5 mm long, exserted. **Berry** white (fide collectoris), the persistent calyx lobes erect or spreading; seed embryo color unknown.

Distribution and ecology. *Disterigma synanthum* is endemic to the department of Valle del Cauca (Colombia), in the Chocó biogeographic region (Map 14). This very rare species is only known from two collections, the most recent one from 1972. It grows between 1000-1500 m, in the premontane cloud forest. It has been recorded growing both inside the forest as well as in pastureland with remnant vegetation. Flowering specimens have been found in March and September, and fruiting specimens in September (fide collectoris).

Etymology. This species is named after its unusually connate anthers.

Specimens examined. COLOMBIA. Valle del Cauca: Mun. Buenaventura, bajo Anchicayá, 300 m, 19 Oct 1989 (fl), *Gentry et al. 68271* (COL); Alto Yunda, Río Anchicaya, 1000 m, Sep 1972 (fl), *Hilty SX-24* (MO, US).

Disterigma synanthum is one of the three species of *Disterigma* that bear only one bracteole; more characteristically, the bracteole extends ca. 2.6 mm beyond the calyx. It is also the only species in the genus with loosely connate anthers; with the bracteole cordifom, cleft, and both pustulate and longitudinally striate; and with the calyx and corolla pustulate. Other distinctive characters of *D. synanthum* are its short calyx lobes less than half the limb length, its rounded sinuses, its corollas adaxially glabrate at the lobes and upper throat, and its geniculate filaments. The elliptic-ovate leaves of *D. synanthum, D. verruculatum,* and an undescribed new species from Cauca [*Lozano & Ruíz 7085*], are very similar between each other. Nevertheless, *D. synanthum* can be easily differentiated by the unique floral characters just mentioned, and because it is 4-merous instead of 5-merous like *D. verruculatum* and the undescribed new species.

31. Disterigma utleyorum Wilbur & Luteyn, Brittonia 29(3): 259. 1977. Type. Costa Rica. Heredia: Colonia Virgen del Socorro, 900 m, 2 Aug 1976 (fl, fr), *Wilbur 21706* (holotype, DUKE; isotypes, B, BM, CAS, CR n.v., DUKE, F n.v., GH n.v., K n.v., LL n.v., MICH, MO, NY (3x), fragment NY, PMA, TEX, US, WIS n.v.). The sheets F, GH, K, LL, and WIS were not found. (Fig. 10 G)

Epiphytic **shrubs**. Young branchlets ridged, more or less smooth, puberulous, the hairs minute, eglandular or glandular, white, the mature branches glabrate, the hairs inconspicuous, eglandular, white. **Leaves** 2–4 per cm, spirally arranged, diffuse; petiole 1–3 mm long, glabrate, the hairs minute, eglandular or glandular; lamina succulent and drying wrinkled, obovate or rarely suborbicular, 1.3–3 x 0.9–2.1 cm, basally attenuate, marginally entire, slightly revolute, apically ciliolate with minute eglandular hairs (especially in young leaves), apically obtuse (to almost subtruncate) and mucronate, adaxially and abaxially glabrate with inconspicuous eglandular and glandular hairs (especially in young leaves), the venation 3- or 5-nerved on both sides, the midvein adaxially and abaxially raised. Axillary **solitary flowers**; bracts 3–4, chartaceous, ovate or suborbicular, 0.5–1.5 x 1–2.3 mm, marginally ciliolate with eglandular and glandular hairs, apically obtuse or acute, abaxially glabrate with minute eglandular hairs; pedicel 0–0.8 mm long, much reduced and hidden by overlapping bracts, glabrous; differentiated apical bracteoles fused by their ends and forming 1 ring-shaped bracteole, chartaceous, enveloping the base of calyx tube or entire calyx tube, covering 26–41% of calyx, annular, 1.2–2 mm long, marginally ciliolate with minute eglandular and glandular hairs, apically flat and with two opposite indentations of variable depth (corresponding to the fused bracteole ends), the surface smooth, abaxially puberulous with minute eglandular hairs, adaxially glabrous. **Flowers** 4-merous. Calyx aestivation valvate, campanulate, 4.4–6 mm long; tube terete, 2–3.4 mm long, abaxially puberulous with minute eglandular and glandular hairs; limb 2.4–2.8 mm long, abaxially puberulous with minute eglandular and glandular hairs, adaxially glabrous; lobes triangular, 1–1.6 x 1.1–1.5 mm, marginally ciliolate with eglandular hairs, apically acute or rarely acuminate; sinuses rounded (U-shaped). Corolla white, thin-fleshy, not bistratose, campanulate, 7.5–9 mm long, 5 mm diam., 4.7 mm wide at throat, abaxially glabrate with inconspicuous eglandular and glandular hairs, adaxially glabrous; lobes 2.6–3 x 3–4 mm, apically acute, adaxially smooth. Stamens 8, 4.2–5.4 mm long, included; filaments distinct, straight, elliptic, 2.2–2.5 mm long, abaxially glabrous or glabrate, adaxially glabrate; anthers distinct, papillae small, only on thecae; thecae 1.8–2.1 mm long, with or without basal appendages; tubules 1, 1.4–2.2 mm long, dehiscing apically by a terminal pore, 0.3 mm long. Ovary 4-locular; style 5–6.3 mm long, included. **Berry** white, more or less spherical, 6 mm diam., the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seed embryo color unknown.

Distribution and ecology. Although *Disterigma utleyorum* is distributed from Costa Rica to northern Ecuador (Map 13), it is only known from patchy and scarce collections, perhaps because it is an epiphytic plant hard to spot, that usually grows high in the tree canopy; most of the collections come from fallen trees. This species grows between 300-1100 m, in the transition from the lowland rainforest to the premontane forest. It has been recorded growing both inside the forest as well as in pastureland with remnant vegetation. Flowering specimens have been found February, April, May, August, October-December, and fruiting specimens in March, August, October, and December.

Almost all herbarium collections mention that ants are found on *Disterigma utleyorum* or that the plant actually grows in ant nests (e.g., *Dodson 7414, P. Pedraza* & *C. Pedraza 981*). Ants from the subfamilies Dolichoderinae (*Azteca* sp.) and Formicinae (*P. Pedraza* & *C. Pedraza 982*, kindly identified by Roberto Keller) were found in Ecuador in a nest surrounding almost all the root system of *D. utleyorum*; however, it is not known from which of these two ant species the nest was. Similarly, Luteyn & Wilbur (1977) have collected this species with its root system confined to “a moist ball of earth and vegetable debris ... capped by a dense mat-forming acrocarpus moss”, the nest of a kind of biting ant.

Etymology. This species is named in honor of John and Kathy Utley who collected the first specimens seen by the authors.

Specimens examined. COSTA RICA. Heredia: vicinity of Colonia Virgen del Socorro, 2-4 km E of Cariblanco on the finca or Carlos Molina, 900 m, 10 Aug 1975 (fl, fr), *J. Utley & K. Utley 2830* (DUKE, NY).

PANAMA. Coclé: S of Aserradero El Copé, 8 km N of El Copé, 830-860 m, 9 Apr 1977 (fl), *Dressler 5635* (NY). **Veraguas:** 5 miles W of Santa Fé on road past Escuela Agrícola Alto Piedra, 800-1200 m, s.d. (st), *Liesner 942* (MO n.v., NY).

COLOMBIA. Nariño: Altaquer, 1000 m, s.d. (fr), *Foster 2114* (NY).

ECUADOR. Carchi: al N del Chical, trocha que de Piedras Blancas conduce a El Pailón-Gualpi-San Marcos-Tobar Donoso, 1050 m, 17 Dec 2003 (fl, fr), *P. Pedraza & C. Pedraza 981* (AAU, COL, MO, NY, PMA, QCA, QCNE). **Esmeraldas:** cantón Quininde, Montañas de Mache, Estación Biológica Bilsa, 400-600 m, 18 Nov 1994 (fl), *Bass & Pitman 272* (MO), 500 m, 12 Feb 1996 (fl), *Clark 2125* (MO, NY); cantón Quininde, NE de las Golondrinas, sitio La Bella Jungla, Cooperativa Unidos Venceremos, 300 m, 8 Oct 1993 (fr), *W. Palacios 11468* (MO, NY). **Imbabura:** cantón Ibarra, parroquia Lita, comunidad San Francisco, next to Río Verde, 900-1100 m, 24 Mar 2003 (fr), *Clark et al. 7504* (NY). **Los Ríos:** Hacienda Clementina, Cerro Samama, trail between Destacamento Pita and Limón, 400-600 m, 8 Oct 1998 (fl, fr), *Ståhl et al.5045* (NY, QCA). **Pichincha:** Cooperativa Santa Marta #2, along Río Verde, 2 km SE of Santo Domingo de los Colorados, 530 m, 5 Feb 1979 (fl), *Dodson 7414* (NY, SEL); Río Chiguilpe, 7 km S of Santo Domingo and 6 km E on side road off Quevedo-Santo Domingo road, 450 m, 24 May 1976 (fl), *Dodson et al. 6061* (NY, SEL).

Disterigma utleyorum is easily distinguished by its unique differentiated apical bracteoles fused by their both ends and forming one ring-shaped bracteole (Fig. 10 G); the ring bracteole, is apically flat except for two opposite indentations that correspond to the fused ends of the original pieces. This species is also unique in having only one tubule per anther, which dehisces apically by a pore. Also characteristic of *D. utleyorum* are the leaves succulent (drying wrinkled), obovate or rarely suborbicular, with the apex mucronate and obtuse to almost subtruncate; the rounded calyx sinuses; the white, campanulate, and adaxially glabrous corollas; and the white fruits. Although very different from any other *Disterigma*, it is possible to associate the leaves of *D. utleyorum* with the obovate forms of *D. hiatum*; however *D. hiatum* can be easily told apart from *D. utleyorum* because its leaves are not succulent, and therefore do not dry wrinkled, and also because its apex is apiculate and not distinctively mucronate like in *D. utleyorum*.

32. 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. 26)

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

Terrestrial **shrubs**, scandent or erect, 0.5–1.5 m tall. Young branchlets not ridged, with papilliform outgrowths, puberulous, the hairs eglandular, brown, the mature branches similar but the indumentum sometimes glabrate. **Leaves** 1–3 per cm, spirally arranged, rarely appearing distichous, diffuse; petiole 2.8–3.2 mm long, puberulous, the hairs eglandular; lamina ovate or elliptic, 1.6–5 x 0.9–2.8 cm, basally cuneate, marginally entire, sometimes slightly revolute, apically ciliolate with eglandular hairs, apically acuminate or cuspidate, somewhat glaucescent underneath, adaxially glabrate with eglandular hairs, abaxially glabrate with inconspicuous glandular hairs, the venation adaxially 7-nerved with the midvein impressed, abaxially hyphodromous with the midvein raised. **Inflorescence** axillary, of 2–4-flowered fascicles or the flowers appearing solitary due to asynchrony of floral bud development; bracts brown (even in floral buds), 4–5, scarious, ovate, obovate, or suborbicular (some are asymmetrical), 1.5–5 x 1.5–4.6 mm, marginally ciliolate with eglandular hairs, apically obtuse, abaxially glabrate with eglandular hairs (especially apically); pedicel 0.5–1 mm long, much reduced and hidden by overlapping bracts, glabrous; differentiated apical bracteoles brown, 2, distinct, scarious, extending beyond calyx 2.5–3.8 mm (covering 100% of calyx), elliptic or suborbicular (some asymmetrical), (4–)5–6.7 x (3–)4–6 mm, marginally ciliolate with eglandular hairs, apically obtuse and usually splitting, the surface finely pustulate, abaxially glabrate with eglandular hairs, adaxially glabrate with minute eglandular hairs distally. **Flowers** 5-merous (one 4-merous corolla seen). Calyx aestivation valvate, cylindric (rarely drying campanulate), 2.2–3 mm long; tube terete, (1.1–)1.3–2 mm long, abaxially glabrous; limb 0.9–1.1 mm long, abaxially puberulous with eglandular hairs (apically), adaxially glabrous; lobes triangular, 0.3–0.7 x 0.3–0.7 mm, marginally eciliate, apically acute; sinuses rounded (U-shaped). Corolla pale pink or white, thin-fleshy, bistratose, tubular, 7.1–9.1 mm long, 2.4–6.1 mm diam. (2.0–2.5 mm in dry), 2.3–6.6 mm wide at throat (1.5–2.0 mm in dry), abaxially glabrate with eglandular hairs, adaxially glabrous; lobes 1.2–1.8 x 0.8–1.9 mm, apically acute, adaxially slightly rugose. Stamens 10, 5–5.9 mm long, included; filaments distinct, straight, broader at base, 3.8–4.2 mm long, abaxially glabrate, adaxially puberulous (distally); anthers distinct, papillae only on thecae; thecae 1.3–1.7 mm long, without basal appendages; tubules 2, distinct, 1.1–1.5 mm long, dehiscing introrsely by longitudinal slits, 0.8–1.1 mm long almost reaching the base of tubules. Ovary 5-locular; style 6.8 mm long, included. **Berry** translucent white, more or less spherical, 7 mm diam. (mature?), the persistent calyx lobes erect or spreading, becoming succulent (at least at base), same color as mature berry; seeds with a mucilaginous coat, the embryo white.

Distribution and ecology. *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 (Map 14).

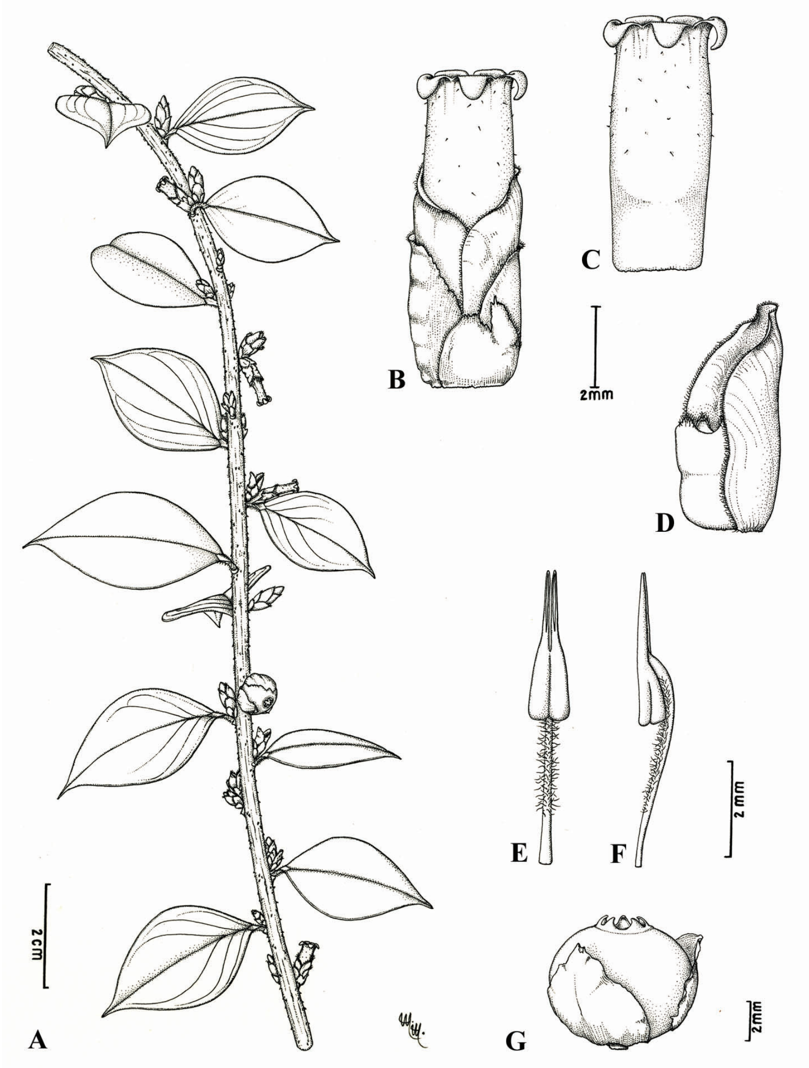


Fig. 26. Illustration of *Disterigma verruculatum*. **A.** Branch. **B.** Flower with bracts and bracteoles. **C.** Corolla. **D.** Calyx with one bracteole removed. **E.** Stamen, adaxial view.**F.** Stamen, lateral view. **G.** Mature fruit with persistent bracteoles (*P. Pedraza 1138*, COL).

Etymology. Named after the papilliform warts on the stems.

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 besides the stem outgrowths, *D. verruculatum* can also be easily differentiated by its acuminate or cuspidate leaves (vs. acute to obtuse 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), and berries that are always translucent white (vs. purple, violet, rarely white in southern Ecuador).

EXCLUDED TAXA

Five species of *Disterigma* s.l. have been excluded from *Disterigma* s.s. because they do not share the morphological and molecular synapomorphies of the genus (Pedraza-Peñalosa, in press; see phylogeny). In one way or the other, they could be associated with the many exceptions and extreme morphologies of *Thibaudia* or *Vaccinium*. However, transferring the species to *Thibaudia* or *Vaccinium* would be solely based on homoplasious characters, it will increase the disorder within these polyphyletic groups, and ultimately will not contribute to the better understanding of the phylogenetic relationships of neotropical Ericaceae. Because of that, and with the goal of not introducing further nomenclatural confusion, no transfers for *Disterigma bracteatum, D. pentandrum, D. rimbachii, D. trimerum,* and *D. ulei* are proposed at this moment. Although the relationships of these excluded species with the rest of the tribe are not completely understood, the morphological, molecular, and total evidence analyses support the close relationship between *D. bracteatum, D. pentandrum,* and *D. rimbachii*, which form well supported and diagnosable novel clade. As for the relationship of *D. trimerum* within the MesoAmerican blueberries and of *D. ulei* within Andean blueberries, the panorama is less clear. All available specimens from these five species were studied and identified, and a neotype is here proposed for *Disterigma ulei.*

1. *Disterigma bracteatum* Luteyn, SIDA 21(3): 1279. 2005, Type. Ecuador. Azuay: Jesús María-Molleturo-Cuenca road, 22.3-25.2 km E of coastal highway at Jesús María, 975-1160 m, 23 Nov 1998 (fl, fr), *Luteyn & Mogollón 15401* (holotype, NY; isotypes: AAU, COL, G, K, MO, QCA, QCNE, US).

2. *Disterigma pentandrum* S. F. Blake, J. Washington Acad. Sci. 16: 364. 1926. Type. Ecuador. Chimborazo: vicinity of Huigra, Hacienda de Licay, 3 Sep 1918 (fl), *Rose 22512* (holotype, US; isotypes, GH, NY). Photo NY neg. 9895 ex NY, photo NY neg. 11932 ex GH.

3. *Disterigma rimbachii* (A. C. Sm.) Luteyn, Fl. Ecuador 54: 258. 1996. *Ceratostema rimbachii* A. C. Smith, Phytologia 1: 130. 1935. *Pellegrinia rimbachii* (A. C. Sm.) Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 289. 1935. *Plutarchia rimbachii* (A. C. Sm.) A. C. Sm., Bull. Torrey Bot. Club 63: 311. 1936. Type. Ecuador. Tungurahua: E slope of Mount Tungurahua, 2000 m, Feb 1934 (fl), *Rimbach 188* (holotype, F; isotypes, NY, S). Photo NY neg. 9659 and12504, photo F neg. 52527.

    Sphyrospermum venustum A. C. Sm., J. Washington Acad. Sci. 46(4): 113. 1956. Type. Ecuador. Bolívar: between Chimborazo and Guaranda, 3000 m, 20 Sep 1954 (fl), *Rauh & Hirsch 388* (holotype, US). Photo NY neg. 11125 ex US.

4. *Disterigma trimerum* Wilbur & Luteyn, Brittonia 29(3): 258. 1977. Type. Panamá. Chiriquí: approaching to Cerro Horqueta, from 6.6 km NNE of Boquete, 1500-1800 m, 5 Jan 1975 (fl), *Wilbur & Luteyn 19321* (holotype, DUKE; isotypes, CAS, DUKE, F, GH, MICH, MO, NY (x4), fragment NY ex DUKE, PMA, US).

5. *Disterigma ulei* Sleumer. Bot. Jahrb. Syst. 71: 397. 1941. Type. Perú. Loreto: Cerro de Escalero, 1200 m, Nov 1902, Ule 6448 (holotype, B†. photo neg s.n. ex B† at NY). Neotype, here designated, Perú. Cajamarca:

Prov. Chota, ruta Querocoto-La Granja, 1 km from Paraguay, 2300 m, 10 Aug 1994, *Leiva et al. 1439* (neotype, F; isoneotype, NY).

6. *Metagonia prostrata* Nutt., see Luteyn, 1996, pag. 323 [=*Vaccinium crenatum* (G. Don) Sleumer].

INVALID AND UNPUBLISHED TAXA

Some herbarium specimens have been annotated with names that were never formally published. All these names are included here for clarification, because they can still be seen in the mentioned specimens and have been occasionally erroneously referred in databases and nomenclature catalogues as valid or published names.

1. *Disterigma imbricata* Rusby

Unpublished name on the label of *Tate 364* (NY), currently *Disterigma pernettyoides*.

2. *Disterigma macrocalyx* A. Gómez

Unpublished name on the label of *W. Vargas 1148* (HUA), currently *Disterigma noyesiae*; and on *W. Vargas 1147* (HUA), sterile, and currently *Disterigma* sp.

3. *Disterigma bocatorensis* Wilbur

Unpublished name on the label of *Churchill 5527* (MO), currently *Disterigma humboldtii*.

4. Disterigma uniflorum Luteyn

Unpublished name on the label of *Dudley 13496* (NA). The flowering material is a typical *Disterigma ovatum*; the accompanying leaf material has some sort of virus. I believe the large and separate piece of wood is not *Disterigma*, and most probably it is a mixed collection.

5. Vaccinium acuminatum var. *sprangelioides*

Unpublished name on the label of *Linden 914* (BM, CGE, F, NY, OXF, P), currently *Disterigma empetrifolium*.

6. Vaccinium campanulatum [author illegible]

Unpublished name on the label of *Spruce 5138* (BM, CGE, E, F, G, GH, K, L, NY, OXF, P, US), type of *Disterigma codonanthum*.

7. Vaccinium gnidioides Willdenow

Unpublished name on the label of *Humboldt & Bonpland s.n.* (B-W 7351-1), type of *Vaccinium penaeoides*.

8. Vaccinium serpillifolium

Unpublished name on the label of *Ruiz & Pavón s.n.* (from a photograph at B, the specimen possibly from BC), type collection of *Gaylussacia microphylla*.

Appendix 1. Alphabetical list of taxa sampled in the analysis of nrITS, *ndhF*, and morphological data of neotropical Vaccinieae. ABG= Atlanta Botanical Garden, NYBG= New York Botanical Garden, WFU TBA= Wake Forest University by Dr. Kron, TBA= New York Botanical Garden by Pedraza, RBGK= Royal Botanic Garden Kew, RBGE= Royal Botanic Garden Edinburgh, ACAD= Acadia University, Col_glabrous= specimen from Colombia with corolla adaxially glabrous, Col_glabrate= specimen from Colombia with corolla adaxially glabrate. *inedit species.

Taxon	**Distribution**	**Voucher**	**nrITS GenBank Acc. No.**	***ndhF* GenBank Acc. No.**
Anthopterus wardii Ball	Panama-Colombia	NY/Luteyn 15191	AF382656	AY331921
Cavendishia bracteata (Ruiz & Pav.) Hoer.	Mexico-Bolivia	NY/Luteyn 14223	AY331867	AY331922
Cavendishia capitulata Donn. Sm.	Costa Rica-Colombia	WFU/EAP 10	AY331868	AY331923
Cavendishia complectens Hemsl.	Nicaragua-Peru	ABG 91-1336	AF382657	AY419723
Cavendishia grandifolia Hoer.	Ecuador	NY/Luteyn 8023	AY331869	AY331924
Cavendishia martii (Meisn.) A. C. Sm.	Peru-Bolivia	NY/Luteyn 15443	AF382658	AY331925
Ceratostema lanigerum (Sleumer) Luteyn	Ecuador	NY/Luteyn 14216	AY331870	AY331926
Ceratostema rauhii Luteyn	Peru	NY/Rauh 68468	AY331871	AY331927
Ceratostema reginaldii (Sleumer) Luteyn	Ecuador	NY/Luteyn 14159	AY331872	AY331928
Ceratostema silvicola A. C. Sm.	Ecuador	NY/ABG 90-1101	AY331873	AY331929
Demosthenesia pearcii (Britton) A. C. Sm.	Peru-Bolivia	NY/Luteyn 15435	AF382663	AY331930
Disterigma acuminatum (H. B. K.) Nied.	Colombia-Peru	NY/P.Pedraza 1098	**TBA**	**TBA**
Disterigma acuminatum/Galeras	Colombia	NY/N.R.Salinas 245	**TBA**	**TBA**
Disterigma agathosmoides (Wedd.) Nied.	Panama-Ecuador	NY/Luteyn 15190, P.Pedraza 1001	**TBA**	**TBA**
Disterigma alaternoides (H. B. K.) Nied.	Colombia-Bolivia	NY/Luteyn 15074	**TBA**	**TBA**
Disterigma sp. nov. “appendiculatum”	Colombia	NY/P.Pedraza 1113	**TBA**	**TBA**
Disterigma sp. nov. “baguense”	Peru	NY/Barbour 4102		
Disterigma balslevii Luteyn	Ecuador	NY/P.Pedraza 998	**TBA**	**TBA**
Disterigma bracteatum Luteyn	Ecuador	NY/P.Pedraza 1016	**TBA**	**TBA**
Disterigma sp. nov. “campanulatum”	Ecuador	NY/Luteyn 8454		
Disterigma campii A. C. Sm.	Ecuador	NY/Luteyn 15056, P.Pedraza 1237	**TBA**	**TBA**

Taxon	Distribution	Voucher	nrITS GenBank Acc. No.	*ndhF* GenBank Acc. No.
Disterigma sp. nov "chocoanum"	Colombia	NY/P.Pedraza 1121	**TBA**	**TBA**
Disterigma codonanthum S. F. Blake	Colombia-Peru	NY/Luteyn 15117, P.Pedraza 1041	**TBA**	**TBA**
Disterigma cryptocalyx A. C. Sm.	Colombia-Ecuador	NY/Luteyn 14993 P.Pedraza 1071	**TBA**	**TBA**
Disterigma dendrophilum (Benth.) Nied.	Colombia-Ecuador	NY/P.Pedraza 1012		
Disterigma dumontii Luteyn	Colombia-Ecuador	NY/Luteyn 15177, P.Pedraza 1005	**TBA**	**TBA**
Disterigma empetrifolium (H. B. K.) Drude	Colombia-Bolivia	NY/C.Pedraza 7	**TBA**	**TBA**
Disterigma hammelii Wilbur & Luteyn	Panama	NY/Hammel 7390		
Disterigma sp. nov. "hiatum"	Colombia	NY/P.Pedraza 1112	**TBA**	**TBA**
Disterigma humboldtii (Klotzsch) Nied./ Colombia1	Mexico-Peru	NY/Pedraza 1075	**TBA**	**TBA**
Disterigma humboldtii/ Colombia2	Mexico-Peru	NY/Pedraza 1069	**TBA**	**TBA**
Disterigma humboldtii/Ecuador	Mexico-Peru	NY/Pedraza 959	**TBA**	**TBA**
Disterigma humboldtii/Panama	Mexico-Peru	NY/Luteyn 15571	**TBA**	**TBA**
Disterigma humboldtii/Peru	Mexico-Peru	NY/Pedraza 1614	**TBA**	**TBA**
Disterigma leucanthum A. C. Sm.	Ecuador	E/Cubey 2	**TBA**	**TBA**
Disterigma micranthum A. C. Sm.	Ecuador	NY/P.Pedraza 1229	**TBA**	**TBA**
Disterigma noyesiae Luteyn/Ecuador	Colombia-Ecuador	NY/P.Pedraza 989	**TBA**	**TBA**
Disterigma noyesiae/Colombia	Colombia-Ecuador	NY/P.Pedraza 1155	**TBA**	**TBA**
Disterigma sp. nov. "ollacheum"	Peru	NY/P.Pedraza 1528	**TBA**	**TBA**
Disterigma ovatum (Rusby) S. F Blake	Peru	NY/Luteyn 15457	**TBA**	**TBA**
Disterigma pallidum A. C. Sm.	Bolivia	NY/P.Pedraza 1506	AF382674	**TBA**
Disterigma panamense Standl.	Panama	NY/Luteyn 14797	**TBA**	**TBA**
Disterigma pentandrum S. F. Blake	Ecuador-Peru	NY/Luteyn 15085, P.Pedraza 1201	**TBA**	**TBA**
Disterigma pernettyoides (Griseb. Ex Wedd.) Nied.	Peru-Bolivia	NY/Luteyn 15441, P.Pedraza 1508	AF382675	**TBA**
Disterigma pseudokillipiella Luteyn	Colombia-Ecuador	NY/P.Pedraza 1143	**TBA**	**TBA**

Taxon	Distribution	Voucher	nrITS GenBank Acc. No.	*ndhF* GenBank Acc. No.
Disterigma rimbachii (A. C. Sm.) Luteyn	Ecuador	NY/P.Pedraza 1018	**TBA**	**TBA**
Disterigma staphelioides (Planch. Ex Wedd.) Nied.	Colombia, Venezuela, Guyana, Brazil?	NY/P.Pedraza 1062	**TBA**	**TBA**
Disterigma stereophyllum (A. C. Sm.) Luteyn	Colombia-Ecuador	NY/Luteyn 15206	**TBA**	**TBA**
Disterigma sp. nov. "synanthum"	Colombia	NY/Luteyn 7001		
Disterigma trimerum Wilbur & Luteyn	Panama	NY/Luteyn 15568	**TBA**	**TBA**
Disterigma ulei Sleumer	Peru-Bolivia	NY/P.Pedraza 1515	**TBA**	**TBA**
Disterigma utleyorum Wilbur & Luteyn	Costa Rica-Ecuador	NY/P.Pedraza 981	**TBA**	**TBA**
Disterigma sp. nov. "verruculatum"	Colombia	NY/P.Pedraza 1138	**TBA**	**TBA**
Macleania coccoloboides A. C. Sm.	Ecuador	NY/Luteyn 15852A	AF382680	AY331938
Macleania cordifolia Benth.	Ecuador	NYBG 887/96	AY331877	AY331939
Macleania floribunda W. J. Hooker	Ecuador-Peru		WFU TBA	WFU TBA
Macleania insignis M. Martens & Galeotti	Mexico-Costa Rica	RBGK 1969-19236	AF382681	AY331940
Psammisia dolichopoda A. C. Sm.	Panama-Ecuador	NY/Luteyn 15006	AF382690	AF419730
Psammisia ecuadorensis Hoer.	Ecuador	NY/Luteyn 15033	AF382691	AY331942
Psammisia sodiroi Hoer.	Colombia-Ecuador	NY/Luteyn 8021	AY331878	AY331943
Psammisia ulbrichiana Hoer.	Colombia-Peru	NY/Luteyn 15170	AY331879	AY331944
Satyria allenii A. C. Sm.	Panama	NY/Luteyn 15292	AF382692	AY331945
Satyria boliviana Luteyn	Bolivia	NY/Luteyn 15481	AF382693	AY331946
Satyria cerander (Dunal) A. C. Sm.	French Guiana/ Brazil	NY/Mori 25279	AY331880	AY331947
Satyria grandifolia Hoer.	Colombia-Peru	NY/Luteyn 15204	AF382694	AY331948
Satyria leucostoma Sleumer	Ecuador-Peru	NY/Luteyn 15051	AF382695	AY331949
Satyria meiantha J. D. Smith	Costa Rica	NY/Luteyn 15236	AF382696	AY331950
Satyria polyantha A. C. Sm.	Peru	WFU/EAP 83	AY331881	AY331952
Satyria sp. nov.	Panama	WFU/EAP 9	AY331882	AY331953
Satyria vargasii A. C. Sm.	Peru	WFU/EAP 75	AY331883	AY331954
Satyria ventricosa Luteyn	Panama	NY/Luteyn 15293	AY331884	AY331955

Taxon	Distribution	Voucher	nrITS GenBank Acc. No.	*ndhF* GenBank Acc. No.
Satyria warszewiczii Klotzsch	Mexico-Panama	RBGE 781009	AF382698	AY331956
Sphyrospermum boekei Luteyn	Colombia-Ecuador	NY/P.Pedraza 975	AF382701	**TBA**
Sphyrospermum buxifolium Poeppig & Endl.	Nicaragua-Bolivia, Guianas	NY/P.Pedraza 1022	**TBA**	**TBA**
Sphyrospermum ellipticum Sleumer	Ecuador	NYBG	AY331885	**TBA**
Sphyrospermum sodiroi (Hoer.) A. C. Sm.	Ecuador	NY/P.Pedraza 960	**TBA**	**TBA**
Symphysia racemosa (Vahl) Stearn	Antilles except Trinidad	ACAD/Vander Kloet 2277274	AF382705	AF419733
Themistoclesia costaricensis Lutyen & Wilbur	Costa Rica-Colombia	NY/Luteyn 14996	AF382706	AY331961
Themistoclesia epiphytica A. C. Sm.	Colombia-Ecuador	NY/Luteyn 15213	AF382707	AY331962
Thibaudia costaricensis Hoer.	Costa Rica-Panama	WFU/EAP 16	AY331887	AY331963
Thibaudia densiflora (Herzog) A. C. Sm.	Bolivia	NY/Luteyn 15459	AF382708	AY331964
Thibaudia diphylla Dunal	Peru	WFU/Moretz M001	AY331888	AY331965
Thibaudia floribunda Kunth	Colombia-Peru	NY/Luteyn 15090	AF382702	AY331966
Thibaudia inflata Luteyn	Ecuador	NY/Luteyn 15029	AY331889	AY331967
Thibaudia macrocalyx Remy	Bolivia	NY/Luteyn 15444	AF382711	AY331969
Thibaudia martiniana A. C. Sm.	Ecuador	NY/Luteyn 15028	AY331891	AY331970
Thibaudia pachyantha A. C. Sm.	Colombia-Ecuador	NY/Luteyn 15189	AF382712	AY331971
Thibaudia tomentosa Hoer.	Peru	NY/Luteyn 15502	AY331892	AY331973
Vaccinium poasanum J. D. Smith	Guatemala-Panama	ACAD/Vander Kloet 131686	AF382736	AF419762
Indeterminate sp. nov.	Peru	NY/Luteyn 15645	**TBA**	**TBA**

Appendix 2. Morphological character matrix for 47 species (53 terminals) of neotropical Vaccinieae. Polymorphism key, A= 0 & 1; B= 1 & 2; C= 0 & 2; D= 2 & 3.

	0 5 10 15 20 25 30 35 40 45 50 54
Anthopterus revolutus	100002001010100------200100202100-0002111000000010?000?
Anthopterus wardii	112002001010100------200100202110-001--1100000001010000
Cavendishia capitulata	1A0002111001010------203001010010-01021101000000101000?
Cavendishia grandifolia	1A2002111001010------203001010000-01021101000000101000?
Disterigma acuminatum	11B00100000100102121010010010B000-000210-00010001000000
Disterigma acuminatum/Galeras	012001000001001021210101100102000-00021100001000101000?
Disterigma agathosmoides	0010010000010010211001001001020010000211000000001000000
Disterigma alaternoides	11A00000001001021200100100010C0011000211000010001010000
Disterigma appendiculatum	1120010000010010222002101100220010001--10000000010?1?0?
Disterigma balslevii	111001000001001021C10100100012000-000201000010001000000
Disterigma bracteatum	11A001000001000------210100012000-10020100000000101000?
Disterigma campii	010001000001001021200100100111000-00021100001000020000?
Disterigma chocoanum	0100010000010010212001001001000011000111000000001000000
Disterigma codonanthum	1A1001000001001021210100100101000-0002A1000010000200000
Disterigma cryptocalyx	01B001000001001023200100100102000-000211000000001000000
Disterigma dumontii	01A00100000A001020D00100100201000-000011000000000200000
Disterigma empetrifolium	1AB00100000A00102120010010010200 0-0002A1000010001000000
Disterigma hiatum	1101000000010010212002010000120011000211000010002000000
Disterigma humboldtii/Colombia2	01100100100000102120010010010200100002110000000010?0?0?
Disterigma humboldtii/Colombia1	111001000001001021200100100100000-0002110000000010?0?0?
Disterigma humboldtii/Ecuador	01B00100100A001022200100100100000-000211000000001000000
Disterigma humboldtii/Panama	A1100100000100102120010010010000100002110000000010?0?0?

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Disterigma humboldtii/Peru          01100100000100102120010010010000100002110000100010?0?0?
Disterigma leucanthum               11A001000000001021301110110122001000021100000000101????
Disterigma micranthum               0110010000010010212001001001020000-000211000010001000000
Disterigma noyesiae/Colombia        0110010000010010232001001001100000-0002110000000010?0?0?
Disterigma noyesiae/Ecuador         0110010000010010232001001001020000-000211000010001000000
Disterigma ollacheum                110101000000001021D00200100102000-000211000010001010000
Disterigma ovatum                   110101000001001021D002001000020010000211000000000101000 1
                                     0   5    10  15   20   25  30   35   40  45  50  54
                                    |    |    |   |    |    |   |    |    |   |   |    |
Disterigma pallidum                 01AA01000001001101500101100010000-000211000010001010000
Disterigma panamense                00101100000100102120011010000C0010000211000010001000000
Disterigma pentandrum               11A001000001000------210100012000-10020100000000101000?
Disterigma pernettyoides            101001000000001021200100100001000-000201000010001000000
Disterigma pseudokillipiella        10B011000001001021210100100002001000021100000000 1000000
Disterigma rimbachii                110001000001000------200000112000-100201000000001010001
Disterigma staphelioides            01B001000001001021100100100012000-000211000000001010000
Disterigma stereophyllum            1110110000010010212101101201220010000111000000001001100
Disterigma trimerum                 110001001000000------001000013000-000200-0000000101000?
Disterigma ulei                     110001000001000------100100002000-000210-00010001010001
Disterigma utleyorum                110001000001001111400100100011000-000011000001-0020000?
Disterigma verruculatum             112000000001001023201201000010000-000211000000001000000
Macleania floribunda                11A000001000100------2000002100012001--0-00011-1101000?
Macleania insignis                  11A000001000100------2000002300013001--0-00011-1100000?
Satyria cerander                    112002001000100------200000010010-001--0-110100011?000?
Satyria warszewiczii                11B002001000100------200000010010-001--0-1101000111000?
Sphyrospermum boekei                111001001110100------102000013000-0002110001-000101001?
Sphyrospermum buxifolium            110001001110100------102100012000-1002110001-0001010011
Sphyrospermum ellipticum            110001001110100------102100012000-1002110001-0001000011
Sphyrospermum sodiroi               111001001110100------200000012010-0102110101-00010?0?1?
Themistoclesia epiphytica           112002001010100------200000130000-210210-0000000101001?
Thibaudia pachyantha                11B002001000100------200000030000-0002110000101010?0?0?
Thibaudia parvifolia                110001001000100------200000000000-001--100000000101000?
Indeterminate sp. nov.              01A10100000A100------300100004000-100210-00000000210000
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Appendix 3. Numerical list of taxa. The list of taxa also comprise putative hybrids between species of *Disterigma* and the species from *Disterigma s.l.* that are excluded from *Disterigma* s.s., which are in *italics.* All the examined herbarium specimens of the excluded species are here also listed because their identification is difficult and because they are rare in nature and/or endemic.

1. Disterigma acuminatum (Kunth in Humb., Bonpl. & Kunth) Nied.
2. Disterigma agathosmoides (Wedd.) Nied.
3. Disterigma alaternoides (Kunth in Humb., Bonpl. & Kunth) Nied.

3a. Disterigma alaternoides x Disterigma noyesiae

4. Disterigma appendiculatum Pedraza
5. Disterigma baguense Pedraza
6. Disterigma balslevii Luteyn

6a. Disterigma balslevii x Disterigma acuminatum

7. Disterigma campanulatum Pedraza
8. Disterigma campii A. C. Sm.
9. Disterigma chocoanum Pedraza
10. Disterigma codonanthum S. F. Blake
11. Disterigma cryptocalyx A. C. Sm.
12. Disterigma dendrophilum (Benth.) Nied.
13. Disterigma dumontii Luteyn
14. Disterigma empetrifolium (Kunth in Humb., Bonpl. & Kunth) Drude
15. Disterigma hammelii Wilbur & Luteyn
16. Disterigma hiatum Pedraza
17. Disterigma humboldtii (Klotzsch) Nied.
18. Disterigma leucanthum A. C. Sm.
19. Disterigma micranthum A. C. Sm.
20. Disterigma noyesiae Luteyn
21. Disterigma ollacheum Pedraza

22. Disterigma ovatum (Rusby) S. F. Blake
23. Disterigma pallidum A. C. Sm.
24. Disterigma panamense Standl.
25. Disterigma pernettyoides (Griseb. ex Wedd.) Nied.
26. Disterigma pseudokillipiella Luteyn
27. Disterigma staphelioides (Planch. ex Wedd.) Nied.

27a. Disterigma staphelioides x Disterigma humboldtii

28. Disterigma stereophyllum (A. C. Sm.) Luteyn
29. Disterigma styphelioides (A. C. Sm.) Pedraza
30. Disterigma synanthum Pedraza
31. Disterigma utleyorum Wilbur & Luteyn
32. Disterigma verruculatum Pedraza
33. *Disterigma bracteatum* Luteyn
34. *Disterigma pentandrum* S. F. Blake
35. *Disterigma rimbachii* (A. C. Sm.) Luteyn
36. *Disterigma trimerum* Wilbur & Luteyn
37. *Disterigma ulei* Sleumer

Appendix 4. List of exsiccatae.

Acevedo, P., 1375(3).
Ackerman, M. (et al.), 351(25).
Acleto, C., 145(1); 359, 395(14).
Acosta, M. (et al.), 33, 266(3).
Acosta-Solis, M., 5465(34); 5658(12); 5815(17); 6220, 6251(35); 6779(34); 7642 (10); 8170, 8755, 8771, 10555(14); 14182(3); 14799(35).
Agudelo, C. A., 2931(28).
Aguilar, R. (et al.), 1157(36); 3891(17).
Albert de Escobar, L. (et al.), 1453(14); 1562(3); 2523(2); 2848(1); 2872(3); 2961 (10); 2964(14).
Alexander, M., 8, 38(14).
Allen, P. H., 4845, 4986, 5694(17).
Almeda, F. (et al.), 2165, 2210, 2229, 2361, 2774, 2882, 2972, 3100(17); 3444 (24); 3628, 4569(17); 6122(15); 6225(2); 6260(36).
Alston, A. H. G., 6866, 7177(3).
Alvarez, A. (et al.), 1391(14).
Alverson, W. S., 2988(17).
Amaya, M., 305(28).
Anderson, W. R., 13420(17).
André, E. F., 2975 p.p.(1, 12, 27); K1334(34); 885, 2975(12); 3230(14); 3399(28); 4576(3).
Angel, R. (et al.), 2(14).
Angulo, L., 227 p.p.(17).
Anthony, H. E. (et al.), 395(14).
Antonio, T., 1630(17); 5074(36).
Apú, B., 88(17).
Aranda, J. (et al.), 1492(2); 2721, 3126(17).
Arbeláez S. G. (et al.), 679(14).
Archibald, J. C., 4049(14).
Argent, G. C. G (et al.), C12880, C12881(18); 428(8); 527(20); 528(12); 2342(11).
Arias, J. C., 113(13); 116(28).
Arsene, F. (et al.), 406(14).
Asplund, E., 7353(35); 7918(14); 8239(12); 8266(35); 8477, 8770(14); 9871(20); 9943(14); 17165(12); 17289(20); 17533, 17857(14).
Aulestia, C. (et al.), 1089(2).
Aymard, G. (et al.), 2919, 5241(3).
Badcock, W. J., 121(23).
Báez, S., 65(1).
Baker, R., SM6(17).
Baldeón, S. (et al.), 3256(3).
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