

SANGUISUGA, A NEW GENUS OF NEOTROPICAL CYTINACEAE AND SOUTH AMERICAN CONNECTION IN THE FAMILY

***Sanguisuga*, Un Género Nuevo Neotropical De Cytinaceae Y Una Conexión Sudamericana En La Familia**

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ABSTRACT

Sanguisuga caesarea, a new genus and species of Cytinaceae from Colombia and the first record of this family in South America, is described and illustrated. *Sanguisuga* is close to *Bdallophytum* but differs from it by exhibiting andromonoecia, with male flowers only at the base of the inflorescence, flowers zygomorphic, semiclosed, and dorsoventrally compressed. The tongue-shaped tepals are arched, curved inwards and include a ventral, sigmoid, nectar-secreting tepal. The elongated seeds are obpyriform with a length/width ratio of 1,5-1,8.

Key words. *Bdallophytum*, Colombia, Cytinaceae, parasitic plants, South America, taxonomy.

RESUMEN

Se describe e ilustra a *Sanguisuga caesarea*, un género nuevo y una especie nueva de Cytinaceae de Colombia y el primer registro de esta familia en Sudamérica. El género nuevo es afín a *Bdallophytum* pero se diferencia por presentar andromonoecia, con las flores masculinas en la base de la inflorescencia, flores zigomorfas comprimidas dorsiventralmente, semicerradas, con los tépalos arqueados e incurvos; tépalo inferior-medio sigmoide-lingüiforme y nectarífero y las semillas más alargadas, obpiriformes con una relación largo/ancho de 1,5-1,8.

Palabras clave. *Bdallophytum*, Colombia, Cytinaceae, plantas parásitas, Sudamérica, taxonomía.

INTRODUCTION

In the family Cytinaceae two genera, *Cytinus* L. and *Bdallophytum* Eichler, and a dozen species have so far been recognized. This small family of holoparasitic angiosperms, endophytes of roots, having flowers grouped in inflorescences and connate stamens, is considered in the current phylogenetic system as part of the order Malvales (Nickrent 2002, 2007, Nickrent *et al.* 2004,

Stevens 2011), and as a group independent of Rafflesiaceae s.l., a family that previously had been treated two genera (Harms 1935, Meijer 1993). Within Malvales, it is considered that the neotropical family Muntingiaceae (Bayer 2003), is the closest photosynthetic relative to Cytinaceae with which it shares some characteristics such as type of indumentum, pollen, position of ovary and placentar type (Nickrent 2007).

Cytinus includes at least 7-8 species parasitic on Cistaceae, Asteraceae and Rosaceae and is distributed mainly in the Mediterranean, South Africa and Madagascar (Burgoyne 2006, Vega *et al.* 2007, 2010 Grayum, Nickrent 2011). *Bdallophytum* known to have only three neotropical species, restricted to the region between Mexico and Costa Rica, with known records from Mexico, Guatemala, Nicaragua and Costa Rica (Eichler 1872, Kuijt 2001, Alvarado 2009 Grayum 2010). The species of this genus usually live associated with the roots of the genus *Bursera* Jacq. ex L. (Burseraceae). The genus *Bdallophytum*, (whose name derives from the Greek *bdell* = leech and *phyton* = plant) is characterized by a spicate inflorescence, flowers purple or purplish, campanulate or rotate perigone and seeds with an ornate testa, allowing one to easily separate it from the genus *Cytinus* that presents flowers grouped in aggregated racemes or glomeruli (or more rarely solitary flowers), tubular perigone of brighter colors (red, yellow or white) and smooth seeds (Solms-Lubach 1874, 1901, Bouman & Meijer 1994, Alvarado 2009).

A recent floristic study conducted in dry forests of northern Colombia, revealed the presence of a previously unknown parasitic plant in South America, which appeared associated with the roots of trees of the genus *Bursera* and presented upon preliminary analysis some similarities with the aforementioned genus in Cytinaceae, *Bdallophytum*. As a result of the study of these samples, there is disclosed herein a new genus of Cytinaceae, which presents some morphological innovations not previously documented in this family. In turn, this finding represents an extension of the distributional range for Cytinaceae of about 800 km further south and confirms a hypothetical South American connection in the origin and distribution of this family of parasitic plants (Nickrent 2007). The nearest known populations of Cytinaceae (Costa Rica), are about 2500 km distant in a straight line from those now located in northern Colombia (Fig. 7).

Materials and Methods

The material studied comes from the field work developed by the second author in the dry forests of Valledupar, in foothills of the Sierra Nevada de Santa Marta (Dept. of Cesar, in the Caribbean region of Colombia), where one can track the plant for recollecting fruiting specimens. The specimens were preserved in 70% ethyl alcohol, without crushing, being properly stored in the liquid sample collection (antotecas) of the COL and MA herbaria. Some sections of the plant, made with a scalpel blade, and these have been preserved as dry and mounted specimens with photos in the general herbaria of both institutions. The observations were made with a Nikon SMZ645 Binocular microscope and detailed photographs were taken with a Canon camera attached to it. Palynological samples (for optical microscopy) were prepared in the Palynology Laboratory of the Institute of Natural Sciences, National University of Colombia, following the acetolysis technique of Erdtman (1986) and for observing the micropreps we used a trinocular Zeiss microscope, model Axiostar Plus. A Canon Power Shot A70 was used with the 100X lens for photographs. All measurements were taken in microns (μ) with ocular micrometer. The palynological slide collection was deposited in the palynological collection of ICN of the

Universidad Nacional de Colombia. For scanning electron microscopy (SEM) samples were mounted on aluminum supports, coated with a 40-50 nm layer of gold and examined with a Hitachi S-3000N scanning electron microscope at 15 kV. For the description of palynomorphs we followed the terminology of Punt *et al.* (1994).

Descriptive terminology. For descriptive terminology was basically followed that recently used for this group (Alvarado 2009, Stevens 2011 and Nickrent 2007, 2011). However, we present here then some dimensions and morphological details of certain organs or structures of this plant, not listed as such in the literature. **Haustorial nodules:** In the roots parasitized by the endophyte are hemispherical or discoid protruberances, in mode of buds, with smooth surface (young) and generally less than the root diameter (Figs 1a, 3a). **Floriferous Nodules:** globose or conical structures, constituted by clusters of horny, linear or narrowly triangular scales. They occur along parasitized host roots and the shoots originate by tearing through the haustorial nodules (Figs 1a, 3b, d.) **Caudex or haustorial root stock:** it is a term used to refer to the scaly thickening accompanied by two or more floriferous nodules, which occasionally occur in the lattice, where two or more parasitized roots converge (Figs. 2a, 3a). **Perigone:** Used because for the petaloid perianth when not differentiated into calyx and corolla and apparently originated in a single whorl (calyx) of tepals (Figs. 1d, 1, 4f, g). **Coenocarp:** We use this name because it is a multiple fruit type, constituted by both the fleshy axis of inflorescence and individual ovaries, partially or completely encompassed in the axial tissue (Fig. 4).

RESULTS

Sanguisuga caesarea Fern. Alonso & H. Cuadros **gen. et sp. nov.** Fig. 1

TIPO: COLOMBIA. Departamento del Cesar. Estribaciones de la Sierra Nevada de Santa Marta, Mun. de Valleldupar, Corregimiento Rioseco, finca “Las Palomas”, 10° 40’ N, 73° 7’ E, 290 m, 6 Mar 2011, fl, H. Cuadros, D. Cortés & C. Delgado 6333 (holotype COL, isotypes COL, MA). **Figs. 1-6.**

New genus and new species, similar to genus *Bdallophytum* Eichler (Cytinaceae) but differs by being a andromonoecious plant with hermaphroditic flowers, male flowers only at the base of the inflorescence and lacking female flowers; with zygomorphic flowers, dorsiventrally compressed, semiclosed, with tepaloid perigone, 7-9(10) lacinated; tepals unequal, arched, curved inwards, with a ventral, sigmoid, tongue-shaped, nectar-secreting tepal; seeds obpyriform, with a length/width ratio of 1,5-1,8.

Description. Plant herbaceous, achlorophyllous, holoparasitic and andromonoecious (hermaphrodite and female flowers on the same individual); endophyte vegetative tissue (not visible) developed in shallow roots of plants of the genus *Bursera* L. (Burseraceae). Parasitized roots generally horizontally disposed and with a rhizomatous aspect, located about 8.12 cm depth, of several decimeters in length and 3-4.5 (6) mm thick, with shiny, crust, fragmented and peelable (Figs. 1a, 2a); with smooth nodose formations similar to buds (**haustorial nodules**) 2.5-3 mm in diameter, irregularly distributed along the parasitized roots; with **floriferous nodules** (Figs 1a, 3b, d) dispersed in roots, globose or conical, rigid and with an echinate aspect, consisting of groups of horny scales, linear or narrowly triangular, occasionally with several floriferous nodules grouped at the confluence of several roots (Figs. 2a, 3a), forming

a **caudex** or thickened **haustorial rootstock** (20-30 x 10 mm). **Young flowering stems** (Figs. 3b-c) emerging from the roots in the mode of an ovoid or clavate shoot, 2-5 x 2-2.5 cm, covered with scale-like leaves that are purple, subcoriaceous, rosette and imbricate, glandular-pubescent. **Floriferous stems** developed (Figs. 2,3b, d), spicate, fleshy, yellowish-white, 8-13 cm long and 2.0 to 2.8 cm thick at its distal third, partly overgrown with leaves and scale-like purple or purple-black floral **bracts** in the area distal, succulent, ovate or rhombic, acuminate, with irregularly serrated or subentire margin and with **indumentum** uniformly yellowish brown (when dry), glandular-pubescent, with clavate coarse hairs (Figs 1b, 3c, f.); spikes with 50-70 flowers, hermaphroditic ones in the middle and top and unisexual males at the base of the inflorescence (in the same axis); female flowers absent. **Hermaphroditic flowers** (Figs. 1a, 2a, c), helically arranged in several orthostiches with purple **bracts**, persistent, 4-5 x 3.5-4.5 mm, broadly ovate, glandular-pubescent, with indument characteristics as already described; **perigone** purple with a single whorl (not differentiated into calyx and corolla), thick, glossy, 4-5 mm x 6.0-7.5 mm wide at the distal part and c. 4.0 mm at the base; in the floral bud a flattened appearance; at anthesis subcampanulate, compressed and dorsiventrally oriented, irregularly 7-9 (10) segmented; tepals unequal and fused into a tube only in the basal $\frac{1}{4}$ and imbricately arranged; with 4-6 in the upper position, arched downward and 3-4 in the lower position, ascending (Figs 1c-d, 2c, 4e.); tepals thick, convex on the outer abaxial side, concave on the adaxial side, cucullate or cymbaform [boat-shaped] and of a linear-spatulate contour, incurved aspect (Figs. 1f, 2f-g) and oriented towards the axis of the flower (not adopting an erect or patent position at anthesis); with a lower median tepal, sigmoid (Fig. 1F2), linguliform in its distal half and provided with secretory glandular areas; tepals pubescent-sericeous finely velvety on the outside and glabrous on the inside. **Androecium** dorsiventrally compressed with a solid **staminal column** (Figs. 1g, h, l and 4), intimately fused to the style, c. 2 mm long, the top of the column with 6-8 (9) **stamens with sessile anthers**, purple at anthesis, upright and aligned parallel (with respect to the axis of the flower), covering $\frac{2}{3}$ of the staminal column and forming a partial upper (anterior) ring of c. 5 mm wide, with the stigmatic area located at rear position (lower) column (Figs. 1h, 2f-g) generally occupying the lower third or fourth of the staminal ring (from ca. 1.5 mm), the distal region of the column; very rarely, anthers forming a continuous ring and entirely surrounding the upper stigmatic area; **anthers** radially arched and extrorse (Fig. 4h-i) apparently monothechal but dithechal-like (because each pair of stamens is slightly clustered and contiguous); thecae 1.2 to 1.8 mm long with two pollen sacs; **connective** undifferentiated or projecting and the thecae with wide longitudinal dehiscence. **Pollen** (Fig. 6a-d), in monads, radioisometric, elliptical and oblate spheroidal-meridian view, slightly in perspective planoconvexos rectangular and polar, small, about 11-13 microns polar diameter and 12-14 equatorial diameter, (3)-4 colpate, colpi about 10 microns long, apocolpium small convex mesocolpium narrow, flat to convex, apertural membrane of finely granular appearance, exine of mesocolpium slightly foveolate. **Styles** fused (Fig. 1g, h, 4c, g) and **stigma** purple, commissural, discoid-capitate, oblong and irregularly lobed, 1.5 mm wide. **Ovary inferior**, globose, entirely encompassed in the inflorescence axis (Fig. 1c, l), unilocular, with parietal placentation intrusive placenta with 6-11 branches or folds, sometimes with a false bilocular appearance. Inflorescence axis forming bacciform individual fruits and **fruit** conerescent **multiple or coenocarp** (Fig. 5), fusiform or ovoid at maturity, salmon-pink, 70-90 mm x 30-40 mm in its middle, arranged on a **foot** of 25-35 x 15-20 mm, with scales and remains of the male flower perigones; surface of the coenocarp covered by slightly elevated mamelons, with a scar in the shape of an areola or circular "eye" in the center, or more frequently with the blackened remains of perigone and

bracts; bracts exposed only in the distal half (Fig. 5a-b); outer surface of the coenocarp with thick, brown glandular trichomes. Individual **fruits** fleshy (Fig. 5d), slightly curved at its distal part and fused into the encompassed inflorescence axis; the convex portion of each fruit ca. 7-9 x 6-8 mm in length and 2-3 mm high; old infructescences black with yellow-orange seeds. **Seeds** embedded in mucilage (Figs. 5e, 6e-g), testa white-yellowish (turns white when treated with alcohol), obpyriform or obovoid, with narrow projection or projections on both ends, 0.32 to 0.42 mm long and 0.18 to 0.25 mm in width, *neck* (micropylar projection) short, and *foot* or basal constriction very noticeable, gradually thinned, ca. 1 mm long; testa surface ramentaceous, coarsely tuberculate-reticulate. **Male flowers** (Fig. 1j, 4j-k) located in the lower 1/3 of the stem, loosely arranged, sometimes seemingly pseudo-verticillate, each also accompanied with reddish-purple bracts; perigone smaller, 3-4 mm high x 5.4 mm wide, consisting of 4-6 concave pieces and curved toward the axis of the flower, with 5-10 erect and aligned anthers, forming a continuous ring at the top of the staminal column, but without the presence of a stigma in the center.

Etymology. The generic name *Sanguisuga* means “leech” and comes from the Latin *sanguisuga*-*ae* (*sanguis-inis* = blood and *sugo-gis-gere* = suck), referring, for similitude, the status of this parasitic plant. The specific epithet name refers to the basin where the plant grows, the Cesar River Valley, in the Caribbean region of Colombia.

Geographic distribution and habitat. We know of collections of *S. caesarea* only from the Valledupar region in the center of the Department of Cesar, Colombia, in the foothills of the Sierra Nevada de Santa Marta at altitudes below 500 m (Fig. 7b). In the region the average annual temperature is 28.9° C, the relative humidity 67% and the annual rainfall only 1000 mm. It is located in preserved environments of the tropical dry forest where it grows associated with (as preliminary observations) the surface roots of *Bursera tomentosa* (Jacq.) Triana & Planch. (Burseraceae) in brown soils with clay-sandy texture, from the weathering of granite and sandstone of the hills in the area. *Sanguisuga* plants arise between litter found on the forest floor and also in the cracks in the rocky fragmented soil. In these formations the host plant is part of a relatively low forest canopy (10-12 m) in the company of other species of trees and shrubs such as: *Astronium graveolens* Jacq. (Anacardiaceae); *Aspidosperma polyneuron* Mull. Arg (Apocynaceae), *Tabebuia billbergii* (Bureau) K. Schum. (Bignoniaceae), *Pseudobombax septenatum* (Jacq.) Dugand (Bombacaceae), *Bursera graveolens* (Kunth) Triana & Planch., *Bursera simaruba* (L.) Sarg. (Burseraceae), *Acanthocereus tetragonus* (L.) Hummelinck, *Pereskia guamacho* FAC Weber and *Pilosocereus lanuginosus* (L.) Biles & GD Rowley (Cactaceae), *Hippocratea volubilis* L. (Celastraceae), *Piptadenia flava* (Spreng. ex. DC) Benth., *Platymiscium pinnatum* (Jacq.) Dugand (Fabaceae), *Bulnesia arborea* (Jacq.) Engl. (Zygophyllaceae), *Gyrocarpus L. americanus* (Hernandiaceae).

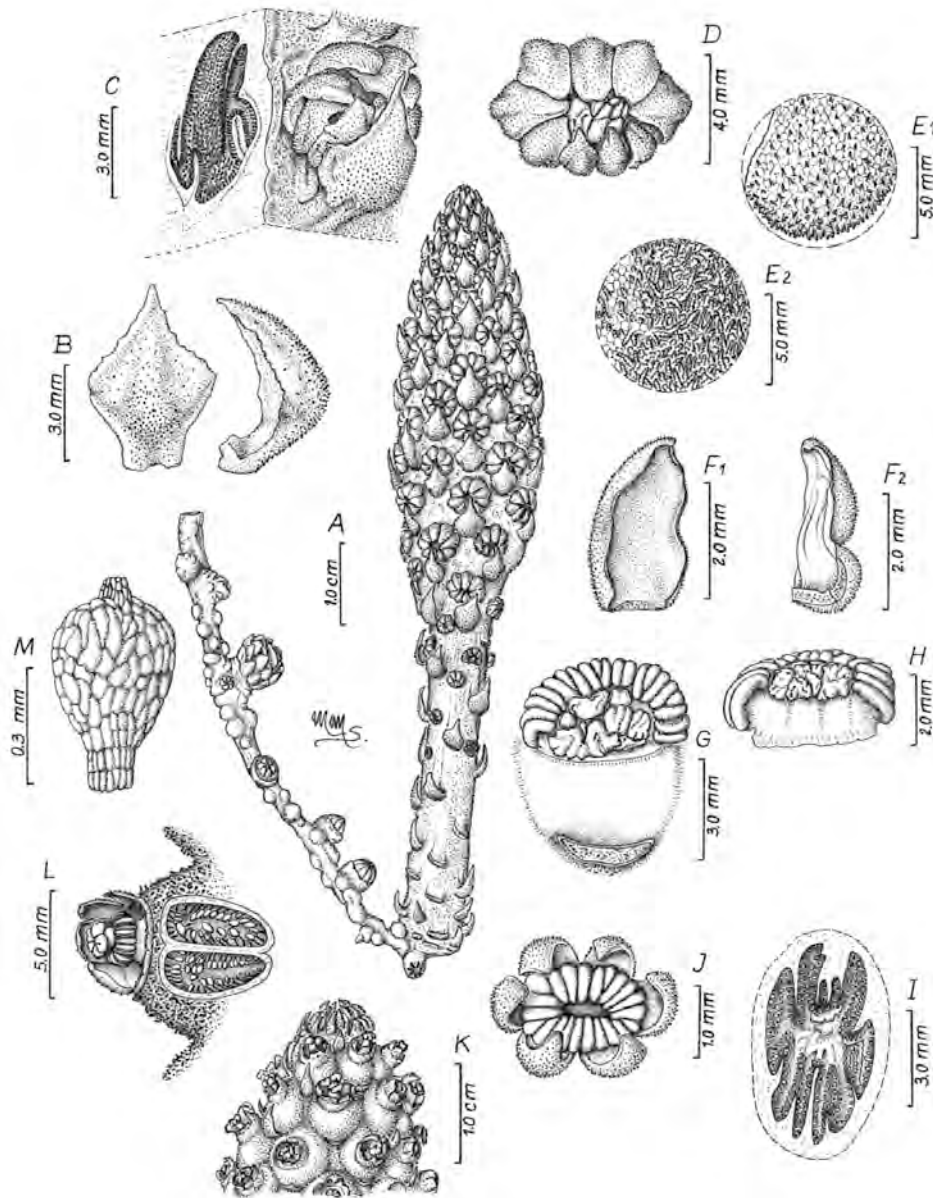


Figure 1. *Sanguisuga caesarea* Fern. Alonso & H. Cuadros.

A - Habit, floriferous axis and parasitized root with haustoriales nodules and floriferous nodules. **B** - Bracts in dorsal (front) and lateral view. **C** - Lateral view of the hermaphroditic flower and lateral cut of the inflorescence axis showing the intrusive placentas of the ovary. **D** - front view of the hermaphroditic flower. **E1** - Detail of the external pubescence of the floral bract. **E2** - Detail of the glandular pubescence of the surface of the inflorescence axis. **F1**- lateral view of the unspecialized tepal. **F2** - lateral view of the lower specialized (sigmoid and glanduliferous) tepal. **G** - Frontal view of the anthers at the end of the staminal column, stigma in the lower position and the position of the floral bract (sectioned). **H** - lateral view of the staminal column, the arch of anthers and stigmatic area **I** - Transverse section of the ovary, showing the intrusive placentas. **J** - Male flowers in frontal view. **K** - Upper part of the infructescence or cenocarp, with the free upper portion of the ovary and persistent residues of the perigone of each flower. **L** - Sagittal section of a flower showing: the disposition of the perigone, the bottom of the staminal column, partial ring of the anthers (upper portion), the stigma, the curved area of the fruit and the sagittal section of the ovary, showing the seeds. **M** - seed detail in dorsal view, showing processes or narrowing at both ends. (Drawing made from the type collection: A-J, in part from Cuadros 6333, and K-M, in part from the paratype Cuadros 6337).



Figure 2. *Sanguisuga caesarea* Fern. Alonso & H. Cuadros. Plant habit. **a-** floriferous axis accompanied by nodular roots of the host (*Bursera*), parasitized by the endophyte. **b-** Detail of the basal part of floriferous axis with scale-like leaves and male flowers. **c-** middle and upper zone of the inflorescence with hermaphroditic flowers, where the dorsiventral compression of the perigone is shown. **d** and **e** young floriferous axes emerging from the forest humic substrate. Scale = 1 cm. (Type material photographed in their habitat in Valledupar, Cesar. Photos: Hermes Cuadros and Denisse V. Cortés).

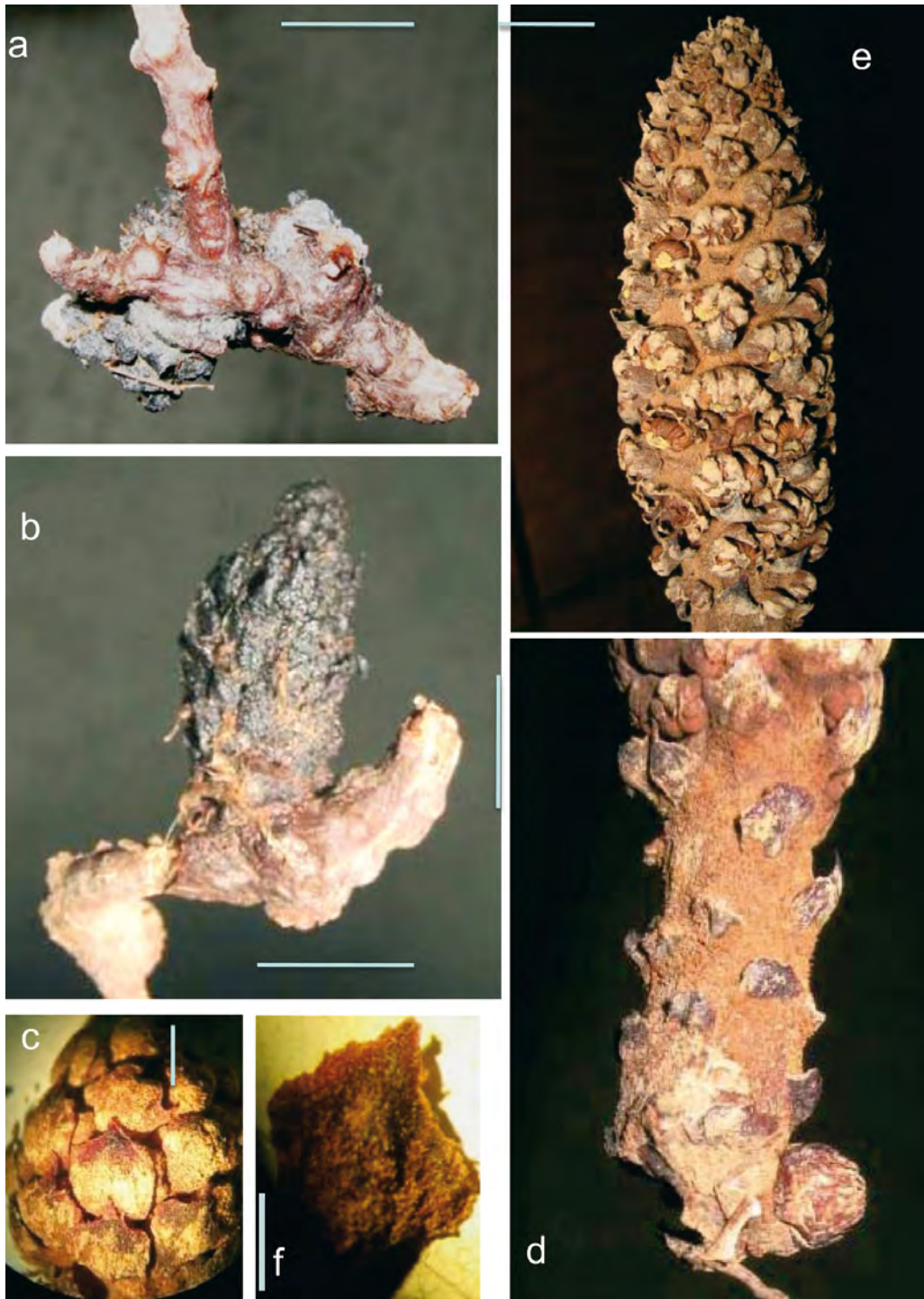


Figure 3. *Sanguisuga caesarea* Fern. Alonso & H. Cuadros. **a-** Caudex or haustorial rootstock, at the confluence of several nodular roots of the host (*Bursera*) parasitized by the endophyte. **b-** detail of the squamate floriferous node (in a dormant state), leaving a parasitized root. **c -** Top of a young floriferous axis (growing), with floral bracts covering the flower buds **d -** Base of the floriferous axis showing glandular indumentum, the scale-like leaves and a young floriferous nodule in the lower right. **e -** Inflorescence showing the arrangement of flowers and bracts **f. -** floral bract with irregularly dentate margin. Scales: a-d = 1cm; e-f= 2mm. (Photographs J.L. Fernandez, from the type material *Cuadros 6333*).

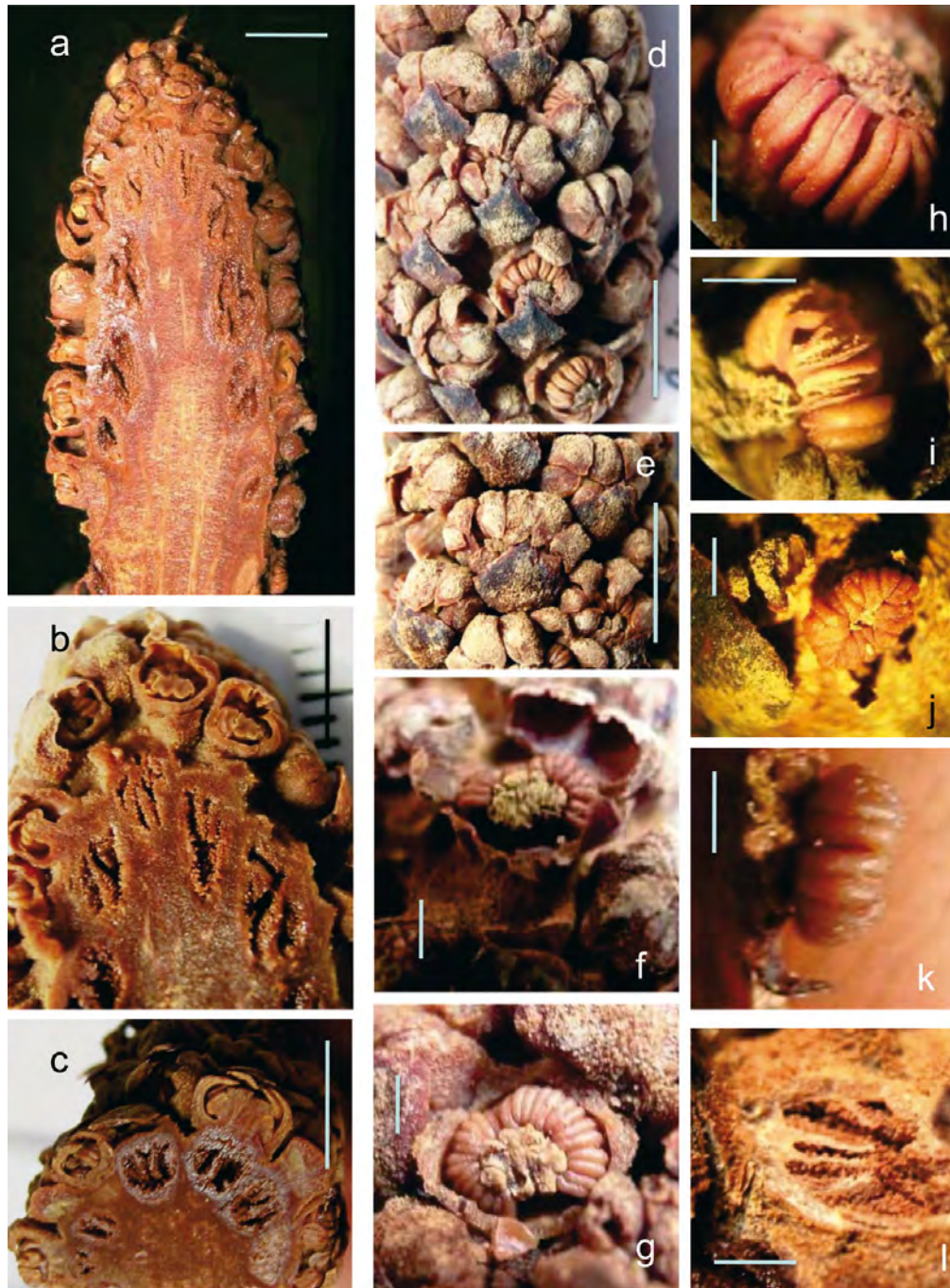


Figure 4. *Sanguisuga caesarea* Fern. Alonso & H. Cuadros. Morphology of inflorescences and flowers. **a, b**- Sagittal section of the floriferous axis showing the position of bracts perigone staminal column and ovary with intrusive placentas, included in the fleshy inflorescence axis. **c** - Section of the flower showing the arrangement of imbricate tepals, the ring of anthers and the capitate stigma. **d, e**- detail of the disposition of the bracts - dark-, and parts of the perigone of the flowers from the middle of the inflorescence. **f, g**- open flower front view, showing two incurved, cucullate tepals, removed – an the cross-section and other parts –cut-, the ring stamen and the capitate-lobed stigma. **h, i**- Detail of the anther ring (h) and longitudinal lines of dehiscence, showing pollen (i). **j, k**- male flower and bract, with complete anther ring and without stigma, after sectioning the tepals. **l**- Cross section of floriferous axis, showing the section of an ovary with intrusive placentas, septa and numerous young seeds. Scales: a-e = 1 cm, e-l = 2 mm. (Photographs JL Fernández, of the type material *Cuadros 6333*).



Figure 5. *Sanguisuga caesarea* Fern. Alonso & H. Cuadros. Infructescence morphology (cenocarpo), fruits and seeds.

a, b- Infructescence developing in its original position from the substrate, showing the different lobulations of carpels and blackening persistent remnants of bracts, perigone and staminal column. **c, d-** Mature infructescence, fleshy, in its natural position from the substrate, with polygonal surface and the more flattened mamelons of the individual fruits, at the start of dispersal of the tiny seeds (bottom). **e-** Detail of an areola or eye of the ripe fruit, with the remains of the staminal column (center) and the distal part of the floral bracts, blackened (bottom). **f-** Cross section of a single bacciform fruit, showing the placentas with mature seeds embedded in mucilage, the white-yellowish is from the effects of alcohol. Scales: a-d = 1 cm, e-f = 2 mm. (Photographs of paratype *Cuadros 6337* in their habitat: a-d; and fruit preserved in alcohol: -e. H. Photographs by H. Cuadros).

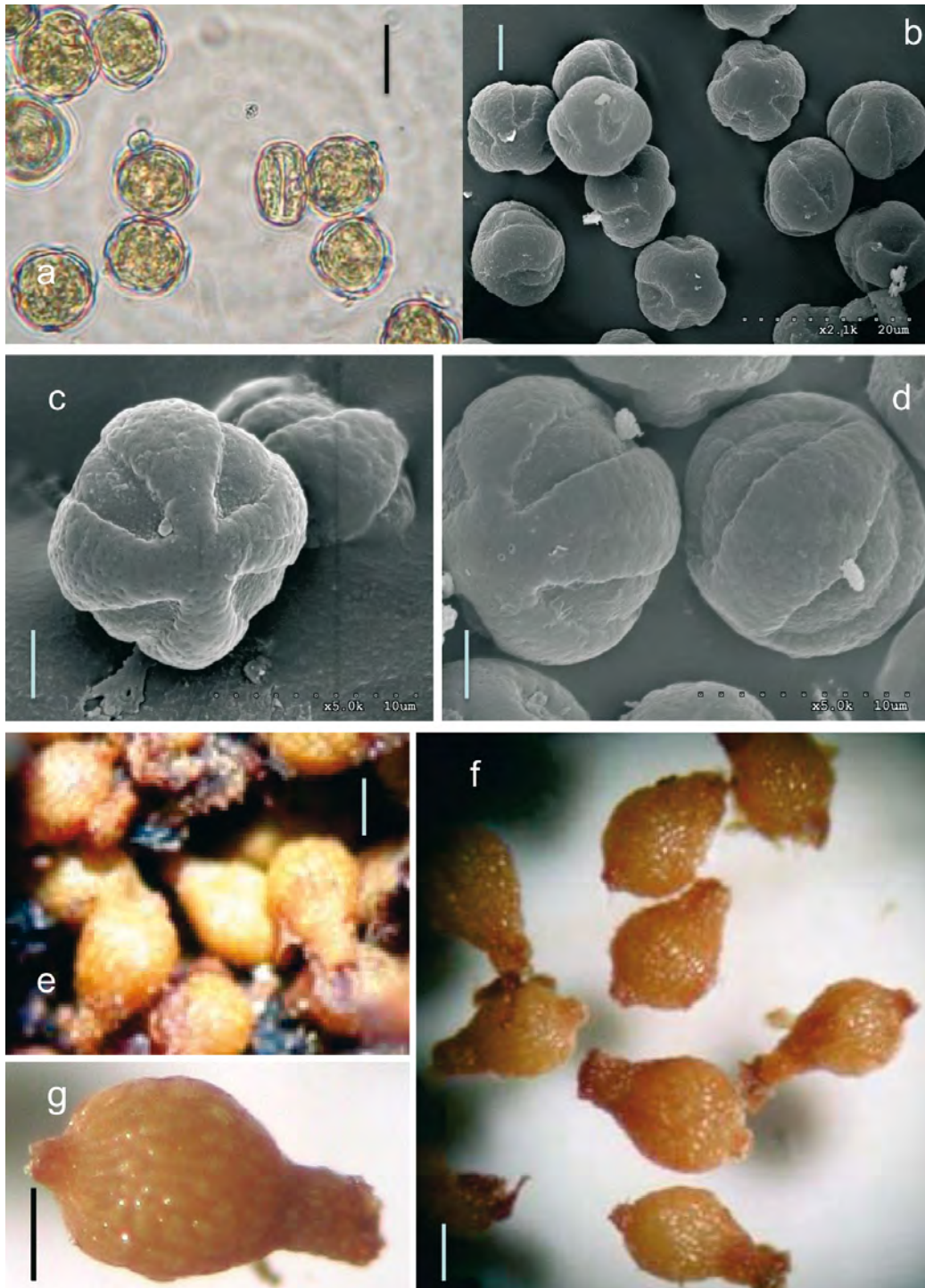


Figure 6. *Sanguisuga caesarea* Fern. Alonso & H. Cuadros.

a- Photograph of the pollen taken by the optical microscope. **b-d:** Photographs of the pollen taken by the scanning electron microscope Hitachi S-300N. **b-** Group of pollen grains showing different views. **c-** grain in polar view showing acolpia and four mesocolpia. **d-** grains in equatorial view showing apertural membranes and mesocolpium in its entirety. **e-g-** mature seeds, **e-** seeds accompanied by remnants of the placenta. **f, g-** Detail showing the seed's basal narrowing (foot) and apical (neck) and surface reticulated, ramentaceous testa. Scales: a = 10 micrometers, b = 5 micrometers; c-d = 3 micrometers.; e-g = 0.1 mm. (a-d: photograph of the holotype *Cuadros 6333*; e-g: photograph of the paratype *Cuadros 6337*, preserved in alcohol).

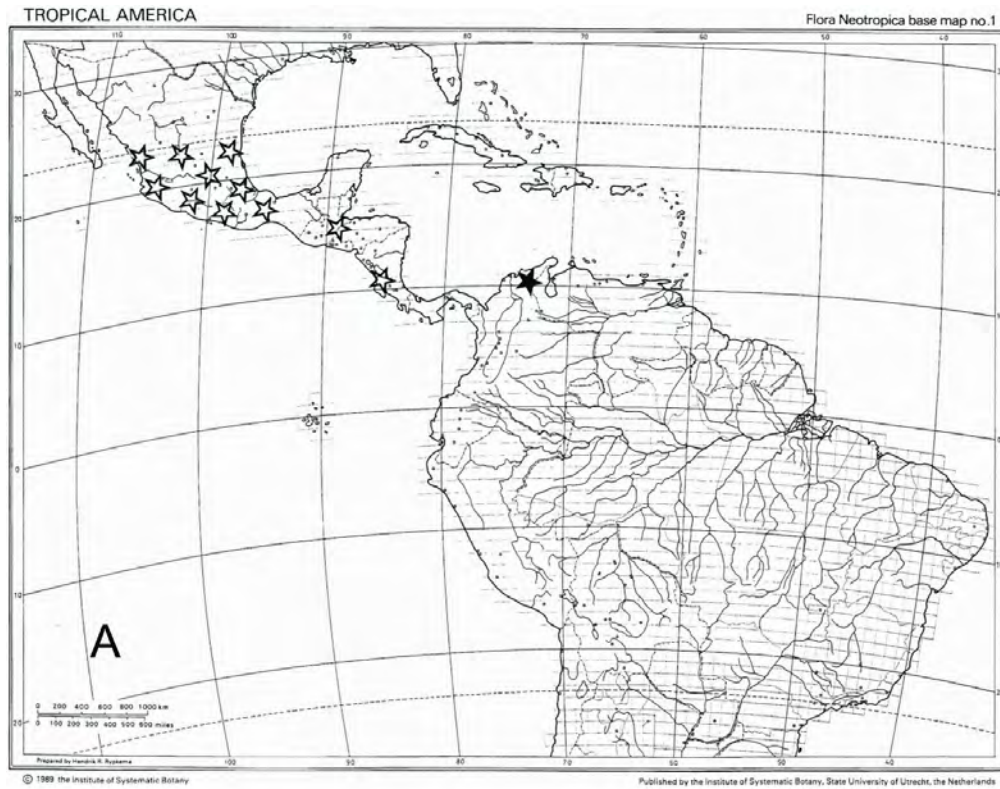


Figure A- 7. Distribution of the family Cytinaceae in the Neotropics. Genus *Bdallophytum*: white stars; genus *Sanguisuga*, black star. **B-** Locality of the type of *Sanguisuga caesarea* Fern. Alonso & H. Cuadros. Appearance of the tropical dry forest dominated by species of the genera *Aspidosperma*, *Astronium*, *Bulnesia*, *Gyrocarpus*, *Pereskia* and *Platymiscium*. Location: Cerro Las Palomas, Municipality Valledupar, Cesar, Colombia. (Photography H. Cuadros).

There is a recent technical environmental study of the El Cerrejon mining region (Guajira), which includes photographs of some plants in a remnant of the dry forest at Cerro Potreritos, Hato Grande, located at 250-300 m in the foothills of the Sierra Nevada de Santa Marta (Gualdrón 2011). One of them, identified as *Balanophoraceae* indet., associated with similar environments, and relatively close, appears to be the same plant as now described from Valledupar (El Cesar).

The nearest populations of plants in this family are of *Bdallophytum americanum* (R. Br) Eichler ex Solms. in northern Costa Rica, about 2500 km in a straight line (Fig. 7A). These plants are mainly associated with *Bursera*, but have also been reported as parasitizing plants of other families such as *Gyrocarpus* Jacq. (Hernandiaceae), *Cochlospermum* Kunth (Bixaceae), *Ficus* L. (Moraceae), and *Haematoxylum* L. (Fabaceae) (Gomez 1983, Kuijt 2001, Grayum 2010). The presence of *Sanguisuga* in the north of South America supports the hypothesis of the past existence of an ancestor of Cytinaceae in the Neotropics, and its morphological connection with the family Muntingiaceae, endemic to this floristic region (Nickrent & al. 2004, Nickrent 2007).

Phenology. The known records that are disclosed here correspond to observed flowering in July and September and fruiting in August-September. Apparently flowering starts after rains (April-June) succeeding the longest dry period and coincident with the presence of moisture in the topsoil. The fructification lasts until the new rainy season (September to December), when it is possible to observe simultaneously fruit dispersion with the new flowering stems.

DISCUSSION

Circumscription of *Sanguisuga* and its affinities with Cytinaceae. Within the family Cytinaceae in its current circumscription (Nickrent & al 2004, Nickrent 2007), *Sanguisuga* has obvious affinities in habit, inflorescence, androecium, pollen and seed with the mesoamerican genus *Bdallophytum* Eichler. However there are significant differences in the newly described taxon in other characters (which we now turn), that allows one to separate without difficulty *Bdallophytum*, such as: **a**) - Distribution of flower sexuality (andromonoecious plants). **b**) - zigomorfa and openness of perigone. **c**) - uniform color of the floral parts and flower scent and **d**) - specialized nectariferous tepal. Also it has slight differences in: **e**) - pollen type and **f**) - seed morphology, both of which are also discussed.

a - andromonoecious Plants . Although *Sanguisuga* is a polygamomonoecious species, as some *Bdallophytum* species - *B. oxylepis* (B.L. Rob.) Harms -, in the plant now described andromonoecy, a condition previously undescribed in the family, occurs. Along with numerous hermaphroditic flowers, there are only some male flowers at the base of the inflorescence (Figs. 1j, 4j-k). In these male flowers an (inferior) ovary is conspicuously absent in sagittal sections of flowers which are contiguous with the inflorescence axis. In contrast in *B.oxylepis* presents gynomonoecy, hermaphroditic flowers and only female unisexual flowers, with males absent. *Sanguisuga* male flowers present the anthers in the upper part of the staminal column in a continuous ring, and has an empty central depression that is occupied by the stigmatic disk in hermaphroditic flowers (Fig. 1j, 4j-k). In contrast, it has been observed that in the male flowers of the dioecious species *B. andrieuxii* Eichler a continuous disk of anthers is presented and also

2-4 additional ones occupy the depression occupying this central space of said ring (*Panero & al. 5762nd*, MA, MEXU). This provision is easily observable at the beginning of anthesis, whereas when the anthers are torn longitudinally the androecium distribution appears to be irregular, as referred to by Alvarado (2009) for this species. It should be noted that, unlike what is indicated in some recent works on the mere presence of unisexual or hermaphroditic flowers as exceptional characters in Cytinaceae (Meijer 1993, Takhtajan 1996, Nickrent *et al.* 2004, Nickrent 2007, Takhtajan 2009, Stevens 2011), it is found that indeed this family also does have hermaphroditic flowers, as already noted for *Bdallophytum oxylepis* (Alvarado 2009) and now for the genus *Sanguisuga* (this work).

b - Uniform Color of the floral parts and smell the flowers. In *Bdallophytum* flowers are presented with contrasting color on their sides: bracts and purple-vinaceous perigone, a white androecium and an off-white stigma. Moreover a markedly foul odor has been described in flowers which attracts scavenging insects (Alvarado 2009). In *Sanguisuga* there is little difference (Fig. 1b) in the color of the androecium and stigma with respect to the perigone, as they are all purple-vinaceous. Nor is there a particularly strong smell in the flowers of this plant and no insects were observed visiting flowers, so it is likely that these differences also have specific implications for a different floral biology in both genera (García-Franco & Rico-Gray 1997a; de Vega *et al.* 2009).

c - Zygomorphy and the perigone aperture. To date about flower symmetry, in *Bdallophytum* and in Cytinaceae in general, only actinomorphic flowers with tubular or campanulate perigones have been described, anthesis patent in its distal area, both in case of unisexual as in the hermaphrodites (Takhtajan 1996, Meijer 1993, Alvarado 2009). In the genus now described a markedly different situation is found, which we interpret as a major morphological innovation (with evolutionary implications) in the family, this being the presence of (slightly) zygomorphic flowers oriented dorsiventrally with perigone partially closed at anthesis, with parts that maintain the incurved pieces position and are convex in distal position (Figs. 1c-d, 2c, 4d-e). The perigone in *Sanguisuga* consists of 7-9 (10) lacinate tepals, succulent and basally fused into a short tube. The tepals, imbricate prior to flowering, are uneven, arched and are aligned or arranged in two series as “lips”, facing each other, some ascending and others descending, down the axis of the flower. We note however that in Alvarado (2009) a photograph of the inflorescence of *B. andreuxii* was published where male flowers are seen with campanulate-rotate with an incipient zygomorphic perigone appearance, although no reference is made to this feature in the publication.

d - Nectariferous tepal. The genus *Sanguisuga* shows a nectariferous structure that apparently does not correspond to any previously described in the family (Meijer 1993, Nickrent 2007). Between the tepals that are arranged in the “lower lip” of *Sanguisuga*, that are thick, and that occupy a central position, is a sigmoid-linguliform nectary on the inner side, which presents secreting glandular areas (Figs 1d, 1f2). These smooth glandular areas seem unrelated to the lines of trichomes or trichomatous convexities described in the inner perigone of some *Cytinus* species (Harms 1935, Burgoyne 2006, Nickrent, 2007). In *Cytinus* nectariferous glands are conspicuous, at the basis of the staminal column, which originate from thickened trichomes (Meijer 1993, Nickrent 2007, Takhtajan, 2009). *Bdallophytum* does not show specialized secretory tepals on the perigone nor have such nectariferous papillae at the base of the staminal column been

described (Meijer 1993, Alvarado 2009). However, in studies of reproductive biology in this genus (*B. americanum*) the secretion of nectar at the bottom of the perigone has been confirmed (García-Franco & Rico-Garay, 1997b) in both male and female flowers. The secretory zone apparently occurs in a manner continuous with the nectar disc at the junction of the perianth tube and the base of the staminal column and not as conspicuously differentiated papillae (*Cytinus*).

e - **Pollen.** The pollen of *Sanguisuga* is very small, less than 15 microns in its largest diameter, the equatorial (Fig. 6a-d) and disaggregated in monads as in *Bdallophytum*. Tetrads do not occur as in the austral species of *Cytinus* (sect. *Hypolepis* (Pers.) Bak. f.). Slight differences with pollen *Bdallophytum* are presented. The *Sanguisuga* pollen grain size (11-13 microns polar diameter and equatorial 12-14 microns) is slightly less than that referred to the genus *Bdallophytum*, 13-16 x 12-13 microns (Takhtajan *et al.*, 1985). This genus has prolate, more elongated pollen than *Sanguisuga*, which has oblate-spheroidal pollen. In turn *Sanguisuga* grains are much smaller (one third) as described in the other genus, *Cytinus* (Takhtajan *et al.* 1985, Stevens, 2011). The latest published information on pollen morphology of Cytinaceae is still incomplete (Meijer 1993 Nickrent *et al.* 2004, Alvarado 2009). However, there is a job that provides consistent information in this respect (Takhtajan *et al.* 1985), which was valued when considering the disintegration or dismemberment of Rafflesiaceae in the classical or traditional sense into different age groups (Takhtajan 1996). These families were then framed in different orders based on recent phylogenetic analysis (Nickrent *et al.* 2004).

f - **Seed.** *Sanguisuga* seeds are ornamented and generally similar to *Bdallophytum*. They are obpyriform (Fig. 6e-g), with a length / width ratio of 1.5-1.8, slightly different from those described in the genus *Bdallophytum* which are fusiform-globular and with a length / width ratio of 1.2-1.4. *Sanguisuga* seeds show a marked gradual thinning, basal, c. 1 mm in length, which distinguishes its seeds from those described in the genus *Bdallophytum* which are fusiform-globular with little thinning at the basal end or the hilum (Solms-Lubach 1874, Bouman & Meijer 1994, Alvarado 2009).

In short, if we compare the two neotropical Cytinaceae genera, we can see that in *Sanguisuga* flowers occur without marked odor, with uniform purple coloration on its parts and a perigone consisting of inconspicuously incurved tepals, characters we could easily associate with autogamous or semiautogamous flowers, not or hardly dependent on pollinators. However, the distribution “bilabiate” and some open parts of the perigone, the presence of nectariferous tepals in a ventral position, and the anteroposterior orientation of the androecium / stigma (Fig. 1g-h), meanwhile, seem to exhibit a condition morphologically derived or specialized, related to a specific pollinator in this new genus, probably some kind of small leaf litter insect. In *Bdallophytum*, flowers with little-specialized perigones occur, campanulate or rotate types, with patent lobes with contrasting colors with respect to androecium-stigma (white) and with a foul odor which attracts unspecialized insects such as of various kinds of carrion flies of the family Sarcophagidae as described in the literature (García-Franco & Rico-Gray 1997b; Alvarado 2009). This, taking the approaches considered in the analysis of Nickrent *et al.* (2004) and Nickrent (2007), we show *Bdallophytum* as a less specialized type of plant than *Sanguisuga*.

Paratypes. COLOMBIA. Departamento del Cesar. Estribaciones de la Sierra Nevada de Santa Marta, Mun. de Valledupar, Corregimiento Rioseco, Cerro Las Palomas, en la margen izquierda del río Badillo, 290-350 m, 10° 40' N, 73° 7' O, 17 sep 2011, fl, fr, *H. Cuadros et al.* 6337 (COL, MA).

Key to identifying the genera of Cytinaceae

- 1- Flowers with perigone clearly tubular, yellow, red or white; nectar glands with projections and recesses at the base of the staminal column; seed testa smooth *Cytinus*
1'- Flowers with a campanulate or rotate perigone, shortly tubular, purple or purplish, without protruding glands or nectar cavities at the base of the staminal column; seeds with ornamented testa..... 2
2- Plants dioecious or gynomonoeious (with hermaphroditic flowers and female flowers); flowers with a fetid odor, with actinomorphic perigone, rotate or campanulate-rotate, with tepals patent or recurved at anthesis, without lower tepal differentiated into a nectary, but nectar-secreting ring at the confluence of the perigone and staminal column *Bdallophytum*
2'- Plants andromonoecious (with hermaphroditic flowers and male flowers); flowers without a marked odor, with a zygomorphic perigone, campanulate but dorsiventrally compressed and semi-closed (tepals incurved at anthesis), with nectary present on the sigmoid tepal located in a center lower position of the flower..... *Sanguisuga*

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