

***Zinowiewia sebastianii* (Celastraceae), a new high-Andean species from the Colombian Eastern Cordillera**

***Zinowiewia sebastianii* (Celastraceae), una nueva especie altoandina de la Cordillera Oriental Colombiana**

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ABSTRACT

Zinowiewia sebastianii, a new species from high-Andean forests of the Eastern Cordillera at the department of Boyacá (Colombia) is described and illustrated, and its taxonomic affinities are discussed. Individuals of the new species are shrubs to 5 m tall, with interpetiolar, laciniate stipules, leaf blades with 8–11 pairs of lateral veins and entire, plane margin, 2-forked dichasia to 1 × 1 cm, axillary to the distal leaves, calyx, corolla and androecium pentamerous or tetramerous, and two-celled, one-seeded samaras 18–20 × 5–7 mm. Based on the low number of individuals of *Z. sebastianii* observed within an area of occupancy < 10 km², in severely fragmented forests, the species is proposed as Critically Endangered (CR), as it faces an extremely high risk of extinction in the wild.

Key words. Angiosperms, Critically endangered (CR) species, flora of Boyacá, flora of Colombia, Iguaque Flora and Fauna Sanctuary, neotropical plants.

RESUMEN

Zinowiewia sebastianii, una nueva especie del bosque altoandino de la Cordillera Oriental de Colombia, en el departamento de Boyacá (Colombia) es descrita e ilustrada, y sus afinidades taxonómicas son discutidas. Los individuos de la nueva especie son arbustos hasta de 5 m alto, con estípulas interpeciolares laciñadas, lámina foliar con 8-11 pares de venas laterales y margen plano, entero, dicásicos 2-ramificados hasta de 1 × 1 cm, formados en las axilas de las hojas distales, cáliz, corola y androceo pentámeros o tetrámeros, y sámaras biloculares, uniseminadas de 18-20 × 5-7 mm. Basados en el bajo número de individuos de *Z. sebastianii* observados dentro de un área de ocupación < 10 km², en bosques extremadamente fragmentados, proponemos que la nueva especie sea considerada en Peligro Crítico (CR), ya que enfrenta un alto riesgo de extinción en estado silvestre.

Palabras clave. Angiospermas, especies en peligro crítico (CR), flora de Boyacá, flora de Colombia, Santuario de Flora y Fauna de Iguaque, plantas neotropicales.

INTRODUCTION

The genus *Zinowiewia* (Celastraceae) comprises 17 species distributed from Mexico to Peru. Five species are known to occur in South America, primarily in the northern Andes, extending to the Sierra Nevada de Santa Marta (Colombia), and

the Cordillera del Norte (Venezuela). The species of *Zinowiewia* are noteworthy in having samaras with one apical wing (Fig. 1g, i, j, l), a trait found in the New World Celastraceae only in the genera *Plenckia*, from Bolivia, Brazil, and Paraguay, and *Rzendowskia* from Mexico (Simmons and Hedin 1999, Simmons 2004). Samaras

in the family appear to have evolved independently several times (Simmons *et al.* 2001, Simmons *et al.* 2012). Most of the species of *Zinowiewia* are large (> 20 m tall) trees sometimes with buttressed trunks, and have minute pentamerous flowers arranged in dichasial cymes (Figs. 1, 2; Turczaninow 1859, Lundell 1939a, Edwin and Ding Hou 1975, Ulloa-Ulloa and Jørgensen 1994, Simmons 2004, Barrie 2015). Despite *Z. concinna* has been reported as a secondary dominant tree in Mexico at about 2100 m in elevation (Vásquez and Givnish 1998), individuals in the remaining species from South America are rare and scattered, with very low densities in lowland to montane forests.

The Ecuadorian *Zinowiewia madsenii* reaches 2900 m in elevation (Ulloa-Ulloa and Jørgensen 1994). In Colombia, 14 records unequivocally assigned to the genus are known (Fig. 3), including the type specimen of *Z. sulphurea* Lundell, endemic to the department of Cauca (Western Cordillera), two collections from the Sierra Nevada de Santa Marta preliminarily assigned to *Z. integerrima* (Turcz.) Turcz., and 11 additional collections from the Central and the Eastern cordilleras, preliminarily identified as *Z. australis* Lundell (Sánchez 2000, González 2014) or as *Z. costaricensis* Lundell (Marín-Corba and Betancur 1997).

After a 30-year period following the morphology and phenology of the population from the department of Boyacá (Colombia), located between 2750 and 3000 m in elevation, the first author (FG) has consistently found a set of diagnostic characters that does not match those of any of the known species of the genus, including *Z. australis*. These characters are related primarily to the habit, the leaf venation, the order of branching of the inflorescence, the floral merosity, and the size and morphology

of the samara. Additionally, the population is located above 2750 m in elevation, isolated from the remaining South American species, which reach up to 2000 m at the nearest spots in Colombia (Fig. 3). The new species here described is the only South American taxon that reaches high-Andean *Quercus* forests.

MATERIAL AND METHODS

The terminology used for the descriptions follows primarily Jackson (1900) and Hickey and King (2000). The taxonomic schemes followed here for the species of *Zinowiewia* are primarily those presented by Ulloa-Ulloa and Jørgensen (1994) for the South American species, and Barrie (2015) for the Mesoamerican species currently recognized. The type specimens of all *Zinowiewia* species were consulted through Jstor (<https://plants.jstor.org/>). In addition, all specimens of *Zinowiewia* deposited at the Herbario Nacional Colombiano, Universidad Nacional de Colombia (COL), the Herbario de la Universidad de Antioquia (HUA), and the Herbario de la Universidad del Valle (CUVC) were examined.

RESULTS AND DISCUSSION

All specimens examined from the Eastern Cordillera at the department of Boyacá (Colombia) above 2750 m in elevation are shrubs 5 m tall (exceptionally small trees to 10 + meters), with two interpetiolar and lacinate stipules, leaf blades with 8–11 pairs of lateral veins and entire, plane margin (Fig. 1 a, b), 2-forked dichasia to 1×1 cm, axillary to the distal most leaves, flowers with calyx, corolla and androecium pentamerous or tetramerous (Figs. 1 a-k, 2a-d, f), and two-celled, one-seeded samaras $18–20 \times 5–7$ mm (Fig. 1m). This combination of traits does not occur in any of the species recognized by Turczaninow (1858, 1859), Lundell (1938, 1939 a, 1939 b, 1940, 1970, 1981, 1985,

1987), Steyermark (1988), Ulloa-Ulloa and Jørgensen (1994) or Barrie (2015). These morphological traits and the ecological and altitudinal isolation indicate that these specimens correspond to a new species that is described below.

***Zinowiewia sebastianii* F. González, sp. nov.** TYPE: Colombia. Boyacá: Villa de Leyva, zona de amortiguación Santuario de Flora y Fauna de Iguaque, cerca de la cabaña de información, 2900 m, 9 jun 2001 (fl, fr), F. González 3826 (holotype COL; isotypes FMB, HUA, MEDEL, NY, to be distributed) (Figs. 1, 2).

Species similar to *Z. australis*, from which it differs by the small stature (5 m tall, exceptionally more), laciniate stipules, membranaceous leaf blade with 8–11 lateral veins per side and margin not revolute, 2-forked dichasia (each 1 × 1 cm) axillary to the distal most leaves, tetrumerous and pentamerous flowers, dark red, erose, reddish sepal margins, latrorse anthers, and slightly veined samaras 18–20 × 5–7 mm, with two locules, one of which is sterile (versus large trees to 40 m tall, entire stipules, subchartaceous leaf blade with 4–6 lateral veins per side and margin revolute, 4 to 6-forked dichasia (each 3.5 × 2.5 cm) located on defoliate branches, exclusively pentamerous flowers, entire, light green sepal margins, extrorse anthers, and one-celled, markedly veined samaras 20–28 × 7.5–17 mm in *Z. australis*).

Shrub to 5 m tall (exceptionally more), stems initially green and smooth, then becoming light maroon and lenticellate with age; inner bark light maroon suffused with yellow lines. Branchlets glabrous. Leaves opposite; stipules two per leaf, located at the flanks of the petiole base, narrowly triangular, minute, to 0.9 × 0.4 mm, reddish to brown, margin laciniate, prematurely deciduous; petiole 4–8

mm long, shallowly canaliculate, purplish red adaxially, green abaxially, with a ring-like articulation near its base; leaf blade elliptic to narrowly elliptic, 8–10 × 2.5–3 cm, dark green above, light green below, membranaceous, central vein yellowish on both sides, lateral veins 8–11 per side, plane to prominulous on both sides, margin entire, plane, base attenuate, apex acuminate. Cymes dichasial, 2-forked, one per axil of the distal most leaves, reaching 1 × 1 mm when fully developed. Bracts narrowly triangular, to 1 × 1 mm, with reddish, laciniate margins; bracteoles irregularly triangular, 0.3–0.5 × 0.2–0.4 mm, with reddish, laciniate margins. Peduncle of the inflorescence 2.5–3.5 mm long, light green; pedicel of the main (first order) flower of the dichasium 1.3–1.5 mm long, higher order pedicels 0.8–1.2 mm long, both with a ring-like articulation near the base, light green. Floral buds light green, reaching 1.5 mm in diameter prior anthesis. Calyx, corolla and androecium pentamerous (ca. 75%) or tetramerous (ca. 25%) on the same individual (n=45). Calyx imbricate, quincuncial, sepals triangular, 0.3–0.4 × 0.4–0.5 mm, light green, margins erose, with short purplish red fringes, abaxial epidermis striate. Corolla imbricate, quincuncial, petals alternate to sepals, broadly ovate, 0.8–1.4 × 0.7–1.3 mm, light green to yellowish with the basal area slightly suffused of purplish red, patent during full anthesis, adaxial epidermis striate, margin smooth, entire, initially whitish but turning reddish by late anthesis. Stamens alternate to petals and placed peripheral to the nectary disk; filament 0.3–0.4 mm long; anthers globose, 0.4–0.5 long, 0.3–0.4 mm in diam., dithecal, tetrasporangiate, white, dorsifixed, latrorse dehiscent, epidermis striate; nectary disk fleshy, conspicuous, light green, tetra- or pentagonal, with numerous stomata. Gynoecium initially bicarpellate, bilocular, and with two ovules per locule, gradually elongating from a

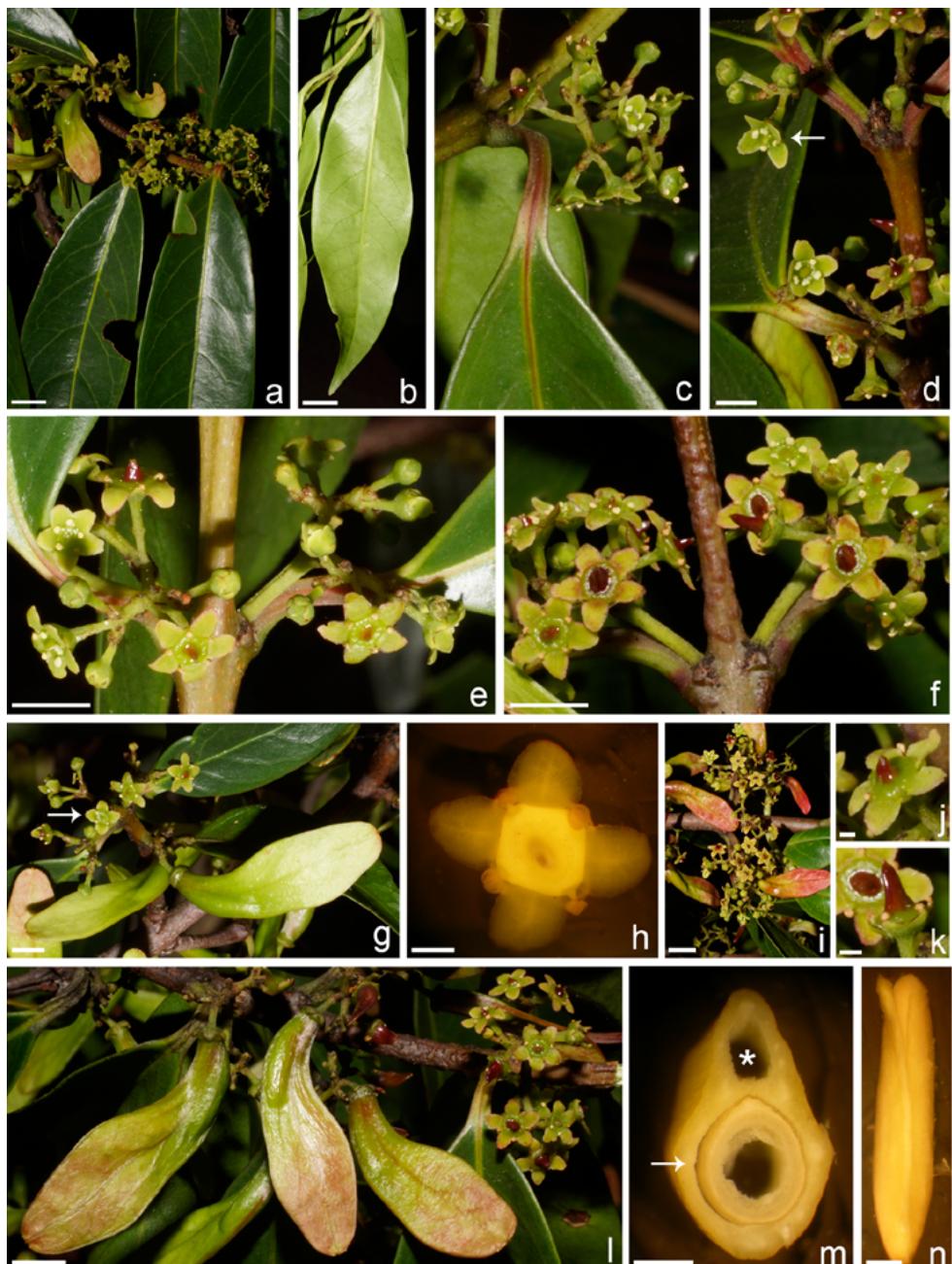


Figure 1. *Zinowiewia sebastianii* (González 4644). **a.** Apex of a flowering branchlet. **b.** detail of lower leaf surface. **c.** detail of petiole and dichasium. **d-g.** Fully developed dichasia; note tetramerous flowers (arrows) in **d** and **g**. **h.** Detail of a tetramerous flower. **i-k.** Late gynoecium elongation and samara formation. **l.** Samaras; note the 2-forked dichasia when fully developed and fruit set. **m.** Transverse section through the base of a samara showing the fertile, one-seeded locule (arrow) and the vestigial locule (asterisk). **n.** Seed. Scale bars: 5 mm in **a, b, i**; 2 mm in **c-g, l**; 500 µm in **h, j, k, m, n**.

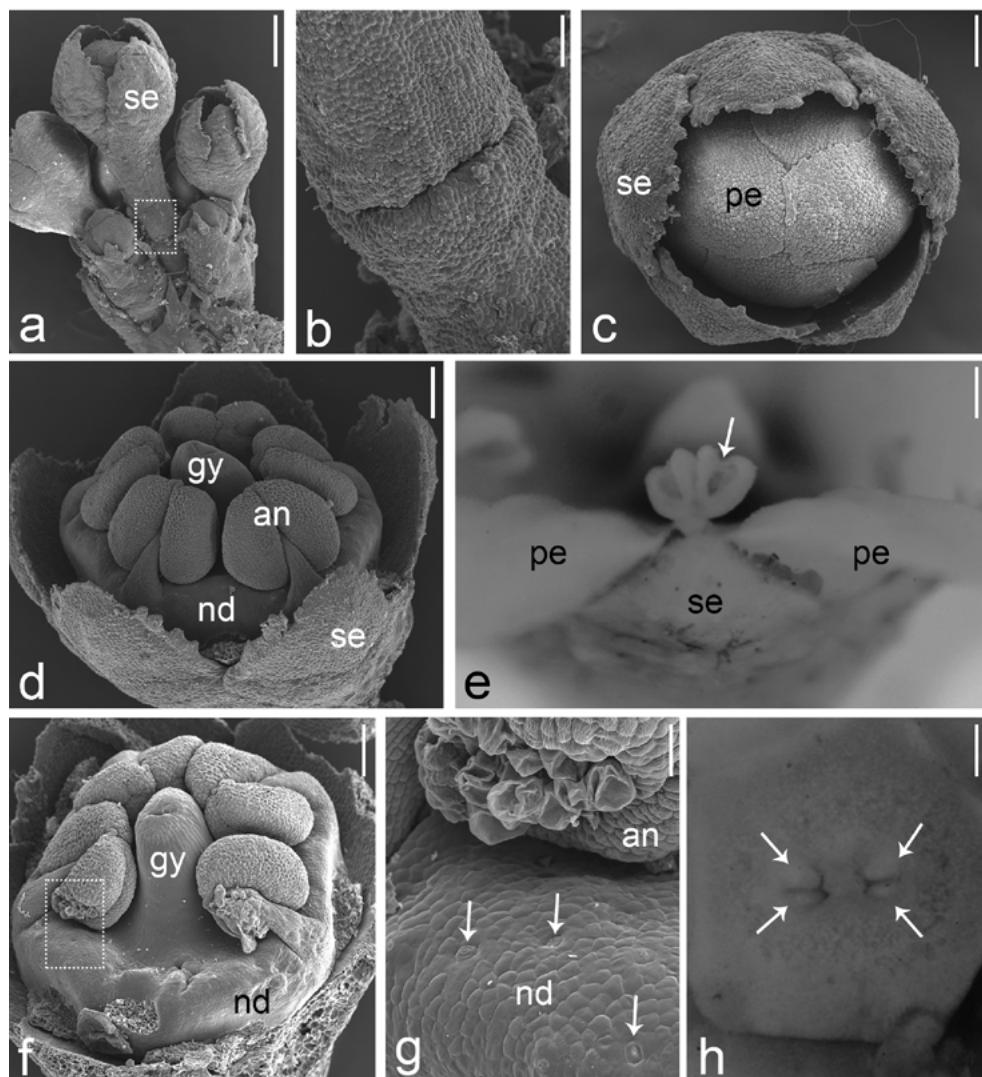


Figure 2. Microphotographs of *Zinowiewia sebastianii* (González 3826). **a.** Dichasium. **b.** Detail of **a** showing the suprabasal articulation of the terminal flower. **c.** Floral bud, top view. **d.** Flower at anthesis, petals removed. **e.** Detail of a latrorse anther. **f.** Flower during gynoecium elongation. **g.** Detail of anther dehiscence and stomata (arrows) on the stigmatic disk. **h.** Young bilocular ovary with two ovule initials (arrows) per locule. Abbreviations: an, anther; gy, gynoecium; nd, stigmatic disk; pe, petal; se, sepal. Scale bars: 500 µm in **a, e, f**; 100 µm in **b-d, h**; 20 µm in **g**.

yellowish green, completely submerged by the stigmatic disk, then turning asymmetric, conical, bright purplish-red, conspicuously exserted during anthesis, with one locule and three of the four ovules aborted; style

and stigma not differentiated except by the subapical epidermal cells that are heavily striate during elongation. Samaras obovoid, slightly curved, 16–19 × 5–6 mm, green when young, then turning purplish red, the

Table 1. Comparison between the new species and the remaining South American species of *Zinowiewia*.

	<i>Zinowiewia sebastianii</i> F. González, sp. nov.	<i>Z. australis</i> Lundell (based on protologue and Ulloa-Ulloa and Jørgensen 1994).	<i>Z. aywardii</i> Steyermark (based on protologue)	<i>Z. integriformis</i> Turcz. (based on protologue, Lundell 1939; and Barrie, 2015)	<i>Z. madsenii</i> C. Ulloa & P. Jørg. (based on protologue)	<i>Z. sulphurea</i> Lundell (based on protologue)
Habit	Shrubs to 5 m tall (exceptionally to 10+ m tall)	trees to 40 m tall	trees to 45 m tall	trees to 30 m tall	shrubs to trees to 15 m tall	trees to 20 m tall
Stipule margin	laciniate	entire	?	?	?	?
Leaf blade	membranaceous, margin plane	chartaceous, margin revolute	chartaceous, margin revolute	chartaceous, margin plane	chartaceous, margin revolute	chartaceous, margin revolute
Number of lateral veins on each side	8 to 11	4 to 8	(5–) 8 to 12	5 to 7	4 to 6	6 to 8
Branching, position and size of dichasia	2-forked, axillary to the distalmost leaves, to 1 × 1 cm	4 to 6-forked, mostly on defoliate branches, to 3.5 × 2.5 cm	5 to 6-forked, axillary to the distalmost leaves, to 2.5 × 4–6 cm	5 to 8-forked, axillary to the distalmost leaves, to 5.5 × 2.5 cm	1 to 2-forked, axillary to the distalmost leaves, to 1.3 × 1.3 cm	2 to 3-forked, to 1.3 × 1 cm
Length of dichasial peduncle	2.5–3.5 mm	3–8 mm	3–9 mm	5–30 mm	4–8 mm	3–4 mm
Calyx, corolla and androecium	merosity	4 or 5	5	5	5	5
Sepal margins	erose	entire	erose	entire	erose	erose
Samara	two-celled, one-seeded, 16–19 × 5–6 mm, higher order veins inconspicuous	one-celled, one-seeded, 7.5–17 mm, higher order veins prominent	one-celled, one-seeded, 20–28 × 7–8.5 mm, higher order veins prominent	one-celled, one-seeded, 14–20 × 7–9 mm, higher order veins prominent	one-celled, one-seeded, 20–25 × 7–8.5 mm, higher order veins prominent	one-celled ¹ , one-seeded, 14–19 × 4–7.5 mm, higher order veins prominent
Geographic distribution and elevation	Colombia (Boyacá), 2740–2950 m	N Venezuela (Aragua, DF, Vargas, Miranda Yaracuy), below 1000 m. Colombia (Norte de Santander), Cundinamarca, Quindío, Huila, below 2000 m. Ecuador, Peru, 250–1250 (–2000) m	NE Venezuela (Bolívar, Delta Amacuro), 300–1000 m	Mexico (Oaxaca, Puebla, Veracruz) and Mesoamerica, 400–2500 m. Probably in Colombia, Sierra Nevada de Santa Marta	Ecuador (Loja), 2990–3150 m	Colombia (Cauca), c. 2520 m

two main veins and margins suffused with purplish red, higher order veins obscure and inconspicuous, pseudomonomerous due to the extreme reduction of one of the two carpels, apex slightly emarginated and mucronulate. Seed one per fruit, oblong, 6–8 mm long, 0.9–1 mm diameter, straight to slightly curved.

Paratypes. COLOMBIA. Boyacá: Villa de Leyva, Santuario de Flora y Fauna de Iguaque, cabaña de Carrizal, 2740 m, 5°44' Norte, 73°28' Oeste, 25 mar 1993 (st), J. Betancur *et al.* 4009 (COL); Villa de Leyva, Santuario de Flora y Fauna de Iguaque, cabaña de Carrizal, 2740 m, 5°44' Norte, 73°28' Oeste, 26 mar 1993 (fl, fr), J. Betancur *et al.* 4059 (COL); Santuario de Flora y Fauna de Iguaque, borde de bosque altoandino, 2950 m, 27 ago 2016 (fl, fr), F. González 4644 (COL).

Etymology. The first author dedicates the new species to his son, Sebastián González, for all his love, support, patience, and for his help during field work.

Distribution, habitat, conservation status and phenology. So far, the new species has only been observed in high Andean forests of the Department of Boyacá (Colombia), between 2740 and 2950 m elevation. The few known individuals grow at the borders of *Quercus humboldtii* Bonpl. (Fagaceae) and *Weinmannia microphylla* Kunth (Cunoniaceae) forests. Other tree components of these forests include *Clusia alata* Planch. & Triana (Clusiaceae), *Drimys granadensis* L. f. (Winteraceae), *Hedyosmum crenatum* Occhioni (Chloranthaceae), *Meliosma* sp. (Sabiaceae), *Ocotea calophylla* Mez, *Prumnopitys montana* (Humb. & Bonpl. ex Willd.) de Laub. (Podocarpaceae), *Roupala monosperma* (Ruiz & Pav.) I.M. Johnston (Proteaceae), and *Schefflera paniculitomentosa* Cuatrec (Araliaceae),

among others. A detailed floristic study of the *Quercus* forest corresponding to the type locality of the new species was carried out by Marín-Corba and Betancur (1997). These authors confirmed the extremely low number of individuals, and the low density and frequency and dominance values of *Z. sebastianii*.

After extensive field work by various researchers during the last 60 years in the Natural Reserve where the new species grows, only a few individuals of *Zinowiewia sebastianii* have been observed in the region (six observed by the senior author in a 30 yr period), within an area of occupancy < 10 km², in severely fragmented forests. Altogether, these criteria render the new species as Critically Endangered (CR), as it faces an extremely high risk of extinction in the wild.

Zinowiewia sebastianii has been collected in flowers and fruits in March, June and August.

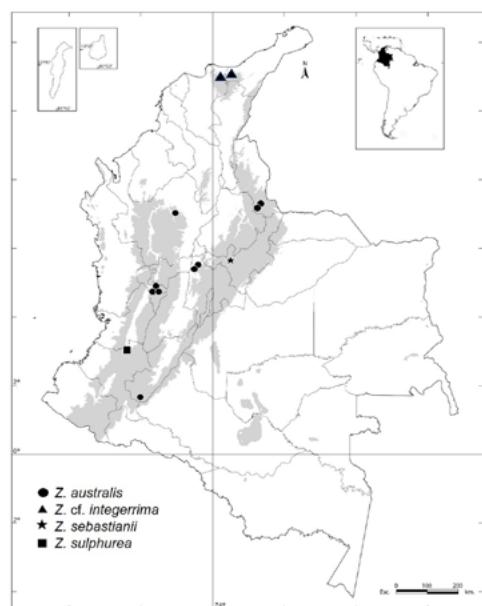


Figure 3. Map of distribution of the species of *Zinowiewia* in Colombia.

The fact that all the known collections bear flowers and fruits in these isolated shrubs suggests that the individuals are self-compatible, and that successful pollination occurs in a short period. The size and color of the flowers and the presence of a massive nectary disk suggests insect, likely bee or wasp, pollination.

General comments. The small stature of *Zinowiewia sebastianii* noticeably contrasts to the large size of most *Zinowiewia* species, some of which reach 30+ m tall (Table 1). The preliminary identification of the new species as part of *Z. australis*, a species described from the extra-Andean Cordillera del Norte (Venezuela), at about 1800 m of elevation (Lundell 1938), is due to superficial similarities in the leaf shape. However, these two species differ in a number of important diagnostic traits, mainly regarding the order of branching and the position of the dichasias (see above). After following the growth and phenology *in vivo* for thirty years, we have consistently noticed that the size of *Z. sebastianii* individuals barely exceed 5 m tall, and that dichasias are axillary to the distal leaves and set fruits after only two events of branching of the dichasium (Fig. 1a, g, i, l). In addition, the new species consistently forms tetramerous and pentamerous flowers on the same individual; approximately 25% of the flowers observed in the FG 4644 individual ($n=45$) were tetramerous (Fig. 1d, g, h). The allocation of tetramerous versus pentamerous flowers is random, as in some cases the tetramerous flowers corresponded to the main (first order) flower of the dichasium, whereas in other instances they corresponded to the higher order flowers. Tetramery encompasses the calyx, the corolla, the androecium, and the contour of the nectary disk (Fig. 1h). The exceptional formation of tetramerous flowers was mentioned to occur in the genus by Lundell (1939a).

Finally, we have found stipule-morphology differences between *Zinowiewia australis* and *Z. sebastianii*, and tentatively use these differences as further support to keep apart these two species (Table 1). Unfortunately, this trait has been overlooked in the remaining species, likely due to the small size and the deciduous stipules.

AUTHORS PARTICIPATION

FG carried out the field and microscopic observations, followed *in vivo* and described the new species, and provided the diagnostic traits to propose the new species. Both authors wrote the Introduction and the Discussion and additional taxonomic comments and comparison with the congeneric species.

CONFLICT OF INTEREST

The authors declare that they do not have any conflict of interest that could compromise the current research.

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LITERATURE CITED

- Barrie FR. 2015. *Zinowiewia*. In: Davidse G, Sousa Sánchez M, Knapp S, Chiang Cabrera F, editors. Flora Mesoamericana. Vol. 2(3). Saururaceae a Zygophyllaceae. Saint Louis: Missouri Botanical Garden. p. 222.
- Edwin G, Ding Hou. 1975. Celastraceae. In: Woodson Jr RE, Schery RW, editors. Flora of Panama. Ann. Missouri Bot. Gard. 62:45–56.

- González F. 2014. Villa de Leyva Florece. Guía Ilustrada de las Plantas de Villa de Leyva y alrededores. Bogotá: Panamericana Formas e Impresos.
- Hickey M, King C. 2000. The Cambridge illustrated glossary of botanical terms. Cambridge: Cambridge University Press.
- Jackson BD. 1900. A glossary of botanical terms. London: Duckworth & Co.
- Lundell CL. 1938. Studies in the American Celastraceae I. New species of *llicrotropis*, *Wimmeria* and *Zinowiewia*. Bull. Torrey Bot. Club 65:463–476.
- Lundell CL. 1939a. A revision of the genus *Zinowiewia*. Contr. Univ. Michigan Herb. 3:35–46, plates VIII-X.
- Lundell CL. 1939b. Studies of Mexican and Central American plants-VII. Lloydia 2:73–108.
- Lundell CL. 1940. Studies in the American Celastraceae-III. Notes on Mexican and Central American species. Bull. Torrey Bot. Club 67:616–620. doi: 10.2307/2481583.
- Lundell CL. 1970. Studies of American Plants-- II. Wrightia 4:129–152.
- Lundell CL. 1981. Studies of American Plants-- XX. Phytologia 48:131–136.
- Lundell CL. 1985. Mesoamerican Celastraceae- III. Phytologia 57:453–454.
- Lundell CL. 1987. Studies of American Plants-- XXII. Phytologia 63:73–78.
- Marín-Corba CA, J. Betancur J. 1997. Estudio florístico en un robledal del Santuario de Flora y Fauna de Iguaque (Boyacá, Colombia). Rev. Acad. Colomb. Cienc. 21:249–259.
- Sánchez LR. 2000. Revisión taxonómica de la familia Celastraceae para la flora de Colombia. [Tesis de Maestría en Ciencias]. [Bogotá]: Universidad Nacional de Colombia
- Simmons MP. 2004. Celastraceae. In: Kubitzki K, editor. The families and genera of vascular plants, Vol. 6. Berlin: Springer Verlag. p. 29–64.
- Simmons MP, Hedin JP. 1999. Relationships and morphological character change among genera of Celastraceae *sensu lato* (Including Hippocrateaceae). Ann. Missouri Bot. Gard. 86:723–757. doi: 10.2307/2666152.
- Simmons MP, Bacon CD, Cappa JJ, McKenna MJ. 2012. Phylogeny of Celastraceae subfamilies Cassinoideae and Tripterygioideae inferred from morphological characters and nuclear and plastid loci. Syst. Bot. 37:456–467.
- Simmons MP, Savolainen V, Clevinger CC, Archer RH, Davis JI. 2001. Phylogeny of the Celastraceae inferred from 26S nuclear ribosomal DNA, phytochrome B, *rbcL*, *atpB* and morphology. Molec. Phylogenetic Evol. 19(3):353–366. doi: 10.1006/mpev.2001.0937.
- Steyermark JA. 1988. Flora of the Venezuelan Guayana-V. Ann. Missouri Bot. Gard. 75:1058–1086.
- Turczaninow N. 1858. Animadversiones in secundam partem herbarii Turczaninowiani, nunc Universitatis Caesareae Charkowiensis. Bull. Soc. Imp. Nat. Moscou 31:379–476.
- Turczaninow N. 1859. Animadversiones ad secundam partem catalogi plantarum herbarii Universitatis Charkowiensis. Bull. Soc. Imp. Nat. Moscou 32:258–277.
- Ulloa-Ulloa C, Jørgensen PM. 1994. A new species of *Zinowiewia* (Celastraceae), and notes on the genus in Ecuador. Novon 4:183–186. doi: 10.2307/3391593.
- Vásquez JA, Givnish TJ. 1998. Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlán. J. Ecol. 86:999–1020. doi: 10.1046/j.1365-2745.1998.00325.x.

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