# UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

## POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE CIENCIAS

SISTEMÁTICA

**SISTEMÁTICA Y DISTRIBUCIÓN DEL GÉNERO *Spigelia* L. (LOGANIACEAE) EN NORTEAMÉRICA, CENTROAMÉRICA Y EL CARIBE.**

# TESIS

QUE PARA OPTAR POR EL GRADO DE:

**DOCTORA EN CIENCIAS BIOLÓGICAS**

PRESENTA:

**CARLA SOFÍA ISLAS HERNÁNDEZ**

**TUTOR PRINCIPAL DE TESIS: DR. LEONARDO OSVALDO ALVARADO CÁRDENAS**
**FACULTAD DE CIENCIAS, UNAM**
**COMITÉ TUTOR: DRA. HELGA OCHOTERENA BOOTH**
**INSTITUTO DE BIOLOGÍA, UNAM**
**DR. JOSE LUIS VILLASEÑOR RÍOS**
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CIUDAD UNIVERSITARIA, CD.MX 2022

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UNAM POSGRADO

POSGRADO CIENCIAS BIOLÓGICAS

COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE CIENCIAS
DIVISIÓN ACADÉMICA DE INVESTIGACIÓN Y POSGRADO
OFICIO FCIE/DAIP/525/2022

ASUNTO: Oficio de Jurado

**M. en C. Ivonne Ramírez Wence**
**Directora General de Administración Escolar, UNAM**
**P r e s e n t e**

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **15 de agosto de 2022** se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la estudiante **ISLAS HERNÁNDEZ CARLA SOFÍA** con número de cuenta **306270318** con la tesis titulada: **"Sistemática y distribución del género *Spigelia* L. (Loganiaceae) en Norteamérica, Centroamérica y El Caribe"**, realizada bajo la dirección del (la) **DR. LEONARDO OSVALDO ALVARADO CÁRDENAS:**

| | |
|---|---|
| Presidente: | **DRA. MARÍA HILDA FLORES OLVERA** |
| Vocal: | **DR. EDUARDO RUÍZ SÁNCHEZ** |
| Vocal: | **DRA. SUSANA VALENCIA AVALOS** |
| Vocal: | **DRA. ÁNGELA PATRICIA CUERVO ROBAYO** |
| Secretario: | **DR. JOSÉ LUIS VILLASEÑOR RÍOS** |

Sin otro particular, me es grato enviarle un cordial saludo.

**A T E N T A M E N T E**
**"POR MI RAZA HABLARÁ EL ESPÍRITU"**
Ciudad Universitaria, Cd. Mx., a 21 de octubre de 2022

**COORDINADOR DEL PROGRAMA**

POSGRADO EN CIENCIAS BIOLÓGICAS COORDINACIÓN

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS
Unidad de Posgrado, Edificio D, 1° Piso. Circuito de Posgrados, Ciudad Universitaria
Alcaldía Coyoacán. C. P. 04510 CDMX Tel. (+5255)5623 7002 http://pcbiol.posgrado.unam.mx/

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A mi papá, te extraño.

**INDICE**

# RESUMEN

*Spigelia* L. es un género neotropical distribuido desde Estados Unidos de América hasta Argentina. Aunque su distribución es continua en el continente, la diversidad presenta una separación espacial marcada, con un grupo en Norteamérica/Centroamérica/El Caribe (NA) y otro en Sudamérica (SA), cada uno de ellos con un importante centro de diversificación, México en NA y Brasil en SA.

A pesar de ser un grupo con una importante diversidad, su conocimiento sistemático no ha sido recopilado ni actualizado en los últimos 10 años, por lo que el número de especies, así como el conocimiento sobre su distribución, varía dependiendo de la publicación que se consulte. Además de esto, un gran número de las especies distribuidas en la región de NA no se han recolectado en años recientes, conocidas solo del ejemplar tipo o distribuidas en zonas de alto impacto antropogénico, por lo que sus poblaciones se encuentran altamente amenazadas, algunas de ellas en peligro de extinción o extintas.

Debido a esto, el trabajo tiene como objetivo la elaboración de un tratamiento sistemático actualizado de las especies de *Spigelia*, incluyendo información novedosa sobre los caracteres vegetativos, florales, palinológicos y carpológicos, así como de su distribución y riqueza en la región de NA. Como resultado de la investigación bibliográfica y de material de herbario, se encontraron 29 especies distribuidas en NA, con más de la mitad de ellas endémicas a este territorio. Durante la elaboración del tratamiento taxonómico para las especies de NA, se observó una importante variación en los caracteres carpológicos, los cuales se analizaron de manera independiente para evaluar su importancia en la separación de especies dentro del grupo. Paralelamente, se realizaron modelos de distribución potencial de las especies del género a partir de la información ambiental, con la finalidad de conocer las áreas de mayor riqueza, tanto conocida como potencial que nos permitan definir zonas potenciales de distribución y que puedan ser importantes en el diseño de estrategias de conservación para las especies amenazadas.

*Spigelia* L. is a neotropical genus with a continuous distribution from the United States of America to Argentina. Nevertheless, due to the diversity of the genus, it can be distinguished into two spatial groups, the first belonging to North America/Central America/Caribbean (NA) and the second in South America (SA). Both groups have an important diversification center: Mexico in NA and Brazil in SA.

Despite being a group with substantial diversity, there is a noteworthy lack of research concerning its systematics, which hasn't been updated in the last 10 years. Therefore, the number of species, as well as data on their distribution, varies depending on the paper consulted. In addition, a considerable number of species found in the NA region have not been collected in recent years, and in consequence, they are only known from the type specimen or their distribution within areas of high anthropogenic impact. For this reason, many of their populations are highly vulnerable to the danger of extinction, or extinct.

In view of this, the present thesis aims to provide an updated systematic treatment of *Spigelia*, including novel information on vegetative, floral, palynological and carpological characters, as well as their distribution and richness in the NA region. As a result of bibliographic research and herbarium material, 29 species were found distributed in NA, with more than half of them endemic to this region.

During the taxonomic treatment of NA species, it was observed that there is an evident variation in carpological characters, which were analyzed independently to assess their importance in the delimitation of species within the group. Simultaneously, potential distribution models were generated from environmental information of the genus's species to obtain the areas of greatest known and potential richness. The aforementioned information may be important for devising conservation strategies, especially for the threatened species.

# INTRODUCCIÓN

*Spigelia* L. es un género neotropical perteneciente a la familia Loganiaceae, con cerca de 90 especies distribuidas desde el sureste de los Estados Unidos hasta el centro de Sudamérica y El Caribe (Hutchinson, 1973; Gould, 1997), y una especie introducida en el Viejo Mundo (*Spigelia anthelmia*). Sus especies presentan flores vistosas, de colores rojos a blancos y algunas de ellas se cultivan o son utilizadas dentro de la medicina tradicional, gracias a sus metabolitos secundarios (Bravo, 1971). El género presenta una morfología contrastante con el resto de los géneros de la familia, tanto en caracteres vegetativos, florales, palinológicos como carpológicos, por lo que su posición dentro o con respecto a la familia Loganiaceae ha cambiado a lo largo de los años (Hutchinson, 1973; Thorne, 1983; Cronquist, 1981; Gould, 1997; Backlund *et al.,* 2000; Fernández-Casas, 2001). Filogenias recientes, basadas en marcadores moleculares de cloroplasto y núcleo, ubican al género *Spigelia* dentro de su propia tribu monogenérica, Spigelieae y como grupo hermano de Strychneae y Loganieae (Backlund *et al.,* 2000; Frasier, 2008; Gibbons *et al.,* 2013; Yang *et al.*, 2016).

Las relaciones entre las especies de *Spigelia* se han estudiado escasamente, tanto morfológica como molecularmente. Las filogenias propuestas para el género únicamente han incluido 15 de las cerca de 90 especies distribuidas en el continente y se han utilizado uno (Popovkin *et al.*, 2011) o dos marcadores (Gould, 1997), lo cual puede generar hipótesis filogenéticas incongruentes (Rokas & Carroll, 2005), debido a que la historia de los genes muchas veces es diferente a la de las especies (Copetti *et al.,* 2017; Shen *et al.*, 2017). La mayoría de los trabajos filogenéticos se han enfocado a resolver su ubicación dentro de la familia Loganiaceae (Frasier, 2008; Gibbons *et al.,* 2013; Yang *et al.*, 2016), y no en las relaciones infragenéricas.

Con base en caracteres morfológicos, el género se ha dividido en nueve secciones (Progel, 1868; Bravo, 1971). Ya que se encuentra basada en pocos caracteres, de los cuales podrían estar sujetos a evolución por convergencia, esta clasificación puede resultar artificial (Gould, 1997; Islas-Hernández *et al.*, 2017b). Además de no haber sido analizados bajo un marco filogenético y que las filogenias hechas para el grupo no los recuperan como grupos monofiléticos. Algunos de estos caracteres generan problemas al ser aplicados a la división de secciones, como es caso del largo y la forma de la corola y la posición de las estructuras reproductivas, ya que se ha visto que se encuentran correlacionados con la interacción con polinizadores en otros grupos de plantas (Grant & Grant, 1965). Por otra parte, los análisis moleculares nunca han incluido caracteres morfológicos para la obtención de las hipótesis filogenéticas. En consecuencia, el conocimiento detallado de la morfología nos permitirá tener caracteres con importancia taxonómica que ayuden a entender las relaciones intragenéricas.

En conjunto con el conocimiento sistemático del grupo, el análisis de la distribución será fundamental para ubicar las áreas de mayor riqueza de especies y entender los patrones de distribución (Liede-Schumann *et al.*, 2014). Actualmente no se conoce ningún trabajo en este aspecto para el grupo y las áreas de distribución de muchas especies se han reducido drásticamente en los últimos años (Islas-Hernández *et al.,* 2017a, 2017b). Las diferentes herramientas de modelado de nicho han resultado de enorme ayuda para evaluar patrones de riqueza de especies, basadas en datos de localidades conocidas de colecciones biológicas (Escalante *et al.*, 2009; Alvarado-Cárdenas *et al.*, 2017). El análisis geográfico de las especies de Norteamérica nos permitirá entender los patrones de distribución y riqueza de las especies, así como las variables abióticas que influyen predominantemente en dicha distribución.

Considerando la riqueza de especies de *Spigelia* en la región comprendida por Norteamérica, Centroamérica y El Caribe (NA) y su disyunción geográfica del núcleo de diversidad de Sudamérica (SA), este trabajo se enfocará en la elaboración de un tratamiento taxonómico para las especies distribuidas en la región de NA (Gould, 1997; Popovkin *et al.*, 2011). Se incluye una descripción detallada de la morfología del género y especies, a partir de las cuales se pretende conocer la utilidad taxonómica de las estructuras vegetativas, florales, polínicas y carpológicas, para la separación de grupos de especies que nos permitan en un futuro corroborar o ajustar la taxonomía del grupo con relación a las propuestas de considerar diferentes secciones (Progel, 1868) y de hipótesis filogenéticas previas (Gould, 1997; Popovkin *et al.*, 2011). Adicionalmente, se aplicarán herramientas de sistemas de información geográfica y modelado de nicho para complementar el conocimiento sobre la distribución de las especies, así como identificar sus centros de riqueza en la región de NA.

# OBJETIVOS

**Objetivo general**

Contribuir al conocimiento morfológico y geográfico del género *Spigelia* en Norteamérica, Centroamérica y El Caribe (NA).

**Objetivos particulares**

- Generar un tratamiento sistemático del género *Spigelia* en Norteamérica, Centroamérica y el Caribe.

- Describir y evaluar la variabilidad taxonómica de las estructuras carpológicas y seminales del género en México.

- Analizar la distribución conocida y potencial de las especies de *Spigelia* en Norteamérica, Centroamérica y el Caribe y determinar sus centros de mayor riqueza de especies.

# RESULTADOS

El trabajo de investigación se divide en tres capítulos enfocados a cumplir con el objetivo principal y objetivos particulares. Cada uno de los capítulos se realizó de tal manera que responden las preguntas planteadas a partir de los objetivos particulares.

El capítulo uno es un tratamiento sistemático de *Spigelia* a lo largo de su distribución en NA, incluyendo información sobre la historia taxonómica del género desde su publicación original hasta el presente. Se incluye, claves de identificación, imágenes de caracteres florales y carpológicos, así como mapas de distribución en la región de NA. Este capitulo será sometido para su publicación en Acta Botánica Mexicana. Como parte de los análisis del capítulo, se generaron dos artículos adicionales: la publicación de una especie nueva para la ciencia y el de algunas problemáticas taxonómicas dentro del género. Dichas publicaciones se incluyen al final del trabajo como anexos.

El segundo capítulo se enfoca en la descripción detallada y la utilidad taxonómica de las estructuras carpológicas y seminales del grupo en México. La información de este trabajo complementa las descripciones del capítulo uno y, con la implementación de los análisis estadísticos, nos ayuda a esclarecer cuáles de los caracteres carpológicos son útiles en la separación de especies, los cuales pueden ser incluidos en los análisis filogenéticos futuros. Este capítulo se publicó en Systematic Botany (47(1): 278-292) y fue aprobado por el CT como el artículo de requisito, para cumplir con los requerimientos del posgrado.

El tercer capítulo se enfoca en el análisis de la distribución de las especies del género *Spigelia*, con el objetivo de conocer la distribución y riqueza potencial del género en NA. Este capítulo será organizado de acuerdo con las normas editoriales de Plant Diversity y será sometido para su publicación.

A continuación, se presentan los manuscritos de los tres capítulos con información novedosa sobre el género *Spigelia* en la región de NA.

# CAPÍTULO UNO

## Synthesis of the genus *Spigelia* L. (Loganiaceae) in North America, Central America, and the Caribbean.

C. Sofia Islas-Hernández[1*] & Leonardo O. Alvarado-Cárdenas[1]

**Abstract**

*Spigelia* is a neotropical genus with about 90 species distributed from the United States to Argentina. The diversity of the genus presents a spatial separation with a group in North-Central America/Caribbean (NA) and another in South America (SA), each with an important center of diversification. However, the systematic knowledge of the group has not been updated in the last 10 years, so the objective of this work is to generate a taxonomic revision for the genus distributed in the NA region. The work was carried out through the search for bibliographic information to obtain the taxonomic history, as well as the review of herborized material, from which diagnostic descriptions and distribution maps were made. Twenty-nine species distributed in the NA region were found, which represents about 30% of the diversity of the genus, distributed in the tropical and subtropical zones. In the NA region, Mesoamerica is one of the regions in which plant diversity is concentrated, which classifies it as a hotspot. The work includes novel information on the morphology of the group, such as descriptions of the pollen and carpological characters, an identification keys for regions in NA and distribution maps in the study area.

Keywords: Diversity, morphology, diagnosis, distribution, conservation.

**Introduction**

The genus *Spigelia* L. is endemic of America, with the greatest diversity in the tropics (Gould, 1997). Around 90 species are recognized, distributed from the southeastern United States to the northern part of Argentina (Bravo, 1971; Gould, 1997; Stevens, 2001; Fernández-Casas & Huft, 2009; BFG, 2015). *Spigelia* species can be distinguished from the other genera of Loganiaceae on the continent (*Mitreola* and *Strychnos*), by its herbaceous or small shrubs habit, with leaves opposite or sometimes pseudowhorled under the inflorescence, with interpeciolar stipules, inflorescences in scorpioid cymes, with sessile or subsessile flowers, bilocular capsule, with a persistent metastyle (basal portion of the style) and loculicidal, septicidal and circumcisile dehiscence at the same time, which allows the dispersion of the seeds (Hernrickson, 1996; Alvarado-Cárdenas, 2007; Fernández-Casas, 2009).

*Spigelia* has two main centers of diversity on the continent, Brazil, and Mexico (BFG, 2015; Islas-Hernández *et al.*, 2017a, 2017b, Islas-Hernández & Alvarado-Cárdenas, 2020). This distribution, despite being continuous throughout the continent, presents an important separation in the components of its diversity, with a group in North / Central America / the Caribbean (NA) and another group in South America (SA). There are 22 species exclusive to NA, 55 exclusives to SA and seven shared species, two of them widely distributed from Mexico to Argentina (Bravo, 1971; Gould, 1997; Fernández-Casas & Huft, 2009; BFG, 2015). However, the systematic knowledge of the group is limited or outdated in regional taxonomic treatments (Bravo, 1971; Gibson, 1969; Alvarado-Cárdenas, 2007; Fernández-Casas, 2003b, 2009; Fernández-Casas & Huft, 2009; Islas-Hernández & Alvarado-Cárdenas, 2017, 2018), which do not include the species published in the last ten years, as well as new distribution records. The aim of this work is to generate a taxonomic review of the *Spigelia* species, distributed in North America, Central America, and the Caribbean (NA). Likewise, novel information on the morphology of the group, a detailed description of the genus, a key for the identification of the species and diagnostic descriptions of the species is presented. Information on its distribution by country and maps of its known distribution in the study area are also included.

**Material and methods**

The research work was carried out by searching bibliographic information, to know the number of published and accepted species that are distributed in the North America, Central America, and the Caribbean (NA) area. Subsequently, a review of national herbaria (CICY, ENCB, FCME, FEZA, HGOM, HUAA, HUAP, HUMO, IBUG, IEB, IMSS, INEGI, MEXU, OAX, QMEX, SERO, UAMIZ, and XAL), as well as international herbaria (QCNE, MO, NY, TEX, and US) and virtual collections (Jstore, NYBG and Tropicos), was made to obtain information on morphological characters for the taxonomic treatment and detailed description of the characters, as well as geographic information on their known distribution.

The taxonomic treatment includes the synonymy of the species, with a diagnosis, as well as taxonomic keys for all species distributed in NA, divided by its distribution in USA, Mexico, and Central America/The Caribbean. The morphological information obtained from the herbarium specimens allowed us to have the measurements and details of the structures for diagnoses, integrating information on structures that had not been previously described and with taxonomic importance to separate between species. Vegetative, reproductive and dispersal characters are described, based on previous works on the genus (Gould, 1997, 1999; Alvarado-Cárdenas, 2007; Fernández-Casas & Huft, 2009; Alvarado Cárdenas & Jiménez, 2015; Islas-Hernández *et al.*, 2017a, 2017b; Islas-Hernández & Alvarado-Cárdenas, 2017, 2018, 2020) and observations of fresh material and herbarium specimens. The images of the species were obtained from specimens from different herbaria and photographs from the Naturalista (iNaturalista) database.

Acetolysis was performed on the pollen grains of species with available structures to obtain the characters included in the morphological data matrix. The processed samples were photographed in the SEM to have detailed descriptions of the micromorphological structures of the pollen. To know in detail some floral structures, to complement the genus description, anatomical sections were made to flowers of *Spigelia humboldtiana* and *S. splendens*, of which material was preserved in alcohol 70%. The flowers were fixed in Glyco-Fixx for two weeks and dehydrated in a series of ethanol (Johansen, 1940) to be embedded in paraffin and sectioned longitudinally and transversely into 12 µm thick segments on a

Leica rotary microtome. The sections were stained by the quadruple technique of Johansen (1940) and the safranin-fast green technique. They were later mounted on synthetic resin and photographed under a Leica microscope with a digital camera.

With all the vegetative, floral, palynological and carpological data emptied into a morphological data matrix, separating each of the important structures, and with the help of the monographaR package (Reginato, 2016), on the R platform (RC Team, 2013), we obtained the diagnoses included in the taxonomic treatment. We followed the species concept of Templeton (1989) to contrast among the similar taxa. This concept has some of the advantages of pluralistic approaches, and we consider it appropriate for the description of the taxa.

The geographic information of the herbarium specimens was processed through ArcMap to obtain the distribution maps included in the taxonomic treatment. In addition, the known distribution of the species was analyzed through the GeoCAT program (Bachman *et al.*, 2011). This program allows the generation of risk categories based on the criteria of the IUCN (Foden & Young, 2016), based on the Extension of Occurrence (EOO) and the Occupation Area (AOO).

**Results**

Of the nearly 90 species of the genus *Spigelia*, 29 are reported distributed in North America, Central America, and The Caribbean (Table 1). The genus is homogeneously distributed throughout the NA region, but with an important variation in the number of species present per country (Fig. 1-A). Mexico has the greatest diversity with 23 species, followed by the United States of America and Guatemala with 6 species, and Costa Rica with 5 species (Fig. 1-B).

To obtain the vegetative, floral, and carpological characters, about 3,500 specimens sheltered in 23 herbaria were reviewed, including 21 types directly and 15 in virtual collections.

The information derived from the observation and measurement of the specimens allowed us to obtain a much more complete and detailed description of the genus *Spigelia*, covering the vegetative, reproductive, palynological, carpological and seminal structures. These structures were described for each of the 29 species from which diagnoses, that include 9 vegetative characters and 14 reproductive characters, were generated.

**Morphological attributes of *Spigelia***

*Primary body*

The species of the genus *Spigelia* present cylindrical or quadrangular stems, with opposite decussate leaves, with entire margins. In some species pseudowhorled leaves under the inflorescence are observed (Fig. 2), that is, the internode of the leaves under the inflorescence is shortened, giving the appearance of having four leaves in the same node. The lamina varies in shape, from elliptical, obovate, ovate, oblong, linear, to lanceolate. The texture can be membranous to leathery, glabrous, or pubescent. According to the classification of Hickey and Wolf (1975), the venation is eucamptodrome pinnate, similar in all species. The stipules are present in the nodes and vary in shape from linear to deltate, in the least of the cases they are not present, when present they are membranous, interpeciolar, sometimes ciliated.

*Inflorescences*

The inflorescences, according to Weberling's (1989) classification, are drepanium-type cincinnus (Fig. 3) since the flowers develop alternately on both sides of the main axis or monochasium. These can have a terminal or axillary position on the steam, with the presence of bracts and bracteoles.

*Flowers*

The flowers, both in the family and in the genus, are pentamers; the calyx is gamosepalous with deeply divided lobes, generally lanceolate, green, or green with purple apex. The corolla is gamopetalous, infundibuliform, hypocrateriform, tubular or rarely urceolate, with white, red or combine colors or purple stripes. The stamens are 5, filamentose, sometimes sessile, or subsessile, attached to the corolla tube, exerted, or included, anthers basifixed or dorsifixed, ovate-sagittate, with longitudinal dehiscence. The ovary is superior, with two syncarpous carpels, the number of ovules ranges from 2 to 16, with an axillary placentation, the style is cylindrical, articulated near the base, the length of the style and its articulation may vary depending on the species. The stigma can be capitate or terete, in some species with abundant trichomes (Fig. 4), these have been reported for the secondary presentation of pollen, described in some species (Erbar & Leins, 1999).

*Pollen*

The pollen grains are distributed in monads or tetrads, the shape is sub-spheroidal, occasionally oblate or prolate (Kremp, 1968), with tricolpate openings, sometimes tetracolpate, colpi occasionally with margo, exine 2-6 µm thick, with varied ornamentation.

*Fruit*

The fruits are bilobed globose capsules, the pericarp is thin, smooth, or papillose, the color ranges from green to brown, with loculicidal, septicidal and circumscisile dehiscence at the same time, which allows the dispersion of the seeds. The lower part of the articulation of the style remains in the fruit forming the metastyle. After dehiscence, the base of the fruit called carpoatlas remains on the peduncle (Fernández-Casas, 2003a), which consists of a hardened disk with a central perforation, in some cases it usually shows remains of a septal membrane, that separated the two locules, as well as a transverse ridge, two projections in the middle of the carpoatlas that reflect the septicidal dehiscence of the carpels, present only in some species with difference in size. The disc can be flat or concave, and varies in shape depending on the species, ranging from oblong to elliptical or rhombic (Ash *et al.*, 1999).

*Seeds*

The seeds range from 4 to 32 per capsule. The testa has a sulcate, reticulated, rough, scaly or foveolate ornamentation, with verrucate or smooth in the depressions. The seeds mainly have a pyramidal shape, where it is easy to distinguish a highly ornamented dorsal face and a ventral one where the hilum is in a depression, in some cases they become compressed (Fernández-Casas, 2003a; Islas-Hernández *et al.*, 2022).

**Taxonomic treatment of *Spigelia*** L.

***SPIGELIA*** L., Sp. Pl. 1: 149-150. 1753.

**Type: *Spigelia anthelmia*** L.

**Synonyms:** *Anthelmenthia* P. Browne (1756, p. 156). − *Spigelia* P. Browne (1756, p.367). − *Arapabaca* Adans. (1763, p.519). − *Montira* Aubl. (1775, p. 637). − *Heinzelmannia* Neck. ex Endl. (1790, p. 371-372). − *Canala* Pohl (1831, p. 62-63). − *Coelostylis* Torr. & A. Gray in Endl., (1839, p. 33). − *Pseudospigelia* W. Klett (1923, p. 134).

**Description**

Annual or perennial herbs or small shrubs. Cylindrical or quadrangular stems, linear or sometimes branched. Stipules deltate, lanceolate or reduced to a fringe. Leaves membranous, opposite, sometimes pseudowhorled under the inflorescence, simple, sessile, or short petiolate, venation camptodromous, glabrous or pilose. Inflorescences scorpioid or monochasium cymes, axillary or terminal. Flowers sessile or shortly pedicellate, bracteate. Calyx 5-lobed, sepals deltate, lanceolate, linear, or ovate, green, or green with purple apex or margin. Corolla gamopetalous, pentamerous, hypocrateriform, tubular, campanulate or infundibuliform, elongated tube, sometimes contracted at the insertion of the filaments, 5-lobulate, petals lanceolate, ovate or deltate, exceeding the calyx, white, purple, red, green, or yellow. Stamens 5, epipetalous, inserts below, above or in the middle of the corolla tube, exerted or included, filamentose, sometimes sessile o subsessile, anthers basifixed or dorsifixed, ovate-sagittate or sagittate. Pollen in monads or tetrads, subspheroidal, occasionally oblate or prolate, tri- or tetracolpate. Ovary superior, globose or ovoid, numerous ovules; style 1, glabrous or pubescent, articulated in the lower half; stigma 1, capitate or terete, glabrous, or pubescent. Fruits capsules, globose, ovoid or bilobed, smooth, papillose, verrucose or hirsute, dehiscence septicidal, loculicidal and finally circumscissile at the base, metastyle present, sometimes deciduous, fruit base persistent in a disk called carpoatlas. Seeds elliptical, semispherical, ovate, or compressed, with the testa verrucose, tuberculate, or ribbed.

**Taxonomic history**

The genus *Spigelia* was published by Linnaeus (1753) in Species Plantarum including one species (*Spigelia anthelmia* L.), classified within Pentandria Monogynia. Before the publication of Species Plantarum and after it was taken as a start of the botanical nomenclature, the genus had been described under the different names mentioned in the synonymy (Stokes, 1812; Henrickson, 1996; Gould, 1997; Bernardi, 2000; Fernández-Casas, 2001).

Due to its great morphological variation in vegetative, floral and palynological characters, its position within the family has changed over the years with respect to the rest of the genera (Cronquist, 1981; Hutchinson, 1973; Thorne, 1983; Gould, 1997; Backlund *et al.* 2000; Fernández-Casas, 2001; Frasier, 2008; Gibbons *et al.*, 2013; Yang *et al.*, 2016). Martius (1826) published the monotypic family Spigeliaceae, at the same time that he described the family Loganiaceae. Meisner (1840) circumscribes Spigeliaceae within the Loganiaceae as the tribe Spigelieae, to which later A. De Candolle adds the genera *Mitreola* L., *Mitrasacme* Labill. and *Polypremum* L., previously included in the Rubiaceae family (Gould, 1997).

Hutchinson (1973) considered that the genus *Spigelia*, together with the genera *Mitreola* and *Mitrasacme*, should be taken as an independent family, as Martius had previously published, which separated by the valvar corolla, completely united carpels, non-verticillate leaves, interpetiolar stipules, and non-winged seeds. However, this classification changed again with Leeuwenberg & Leenhouts (1980), who agree with that established by Meisner and A. De Candolle, maintaining the tribe Spigeliae with the same genera mentioned by them. Struwe *et al.* (1994) carried out cladistic work based on morphology, embryology, anatomy and phytochemistry. Their results show the tribe as paraphyletic and as a sister to Strychneae tribe.

More recent phylogenies, based on the chloroplast markers *rps*16 and *pet*D, have included several species of *Spigelia*, with some representatives from South America. In these works, the species are grouped as a clade within the Loganiaceae, conforming the monogeneric tribe Spigelieae and as a sister group to the Strychneae and Loganieae tribes, this last one including the genera *Mitreola* and *Mitrasacme* (Frasier, 2008, Popovkin *et al.*, 2011; Yang *et al.*, 2016). In APG IV (2016), classification that is followed in this work, the genus remains within the Loganiaceae family, in its monogeneric tribe Spigelieae with about 90 species reported for the American continent (Stevens, 2001). However, the relationships within the group have not yet been resolved and the proposed sections have been rejected because they are based on few morphological characters (Islas-Hernández *et al.*, 2022), some of which are associated with evolution by convergence (Gould, 1997).

The use and increase of characters, together with the vegetative and floral ones, may allow in the future to have a better separation of monophyletic sections. Within the genus *Spigelia*, the use of carpological morphology has been of great help in the separation of groups that present an important correlation with floral and pollen characters, as well as with their distribution (Islas-Hernández *et al.*, 2022).

**Dichotomous key of the *Spigelia* species distributed in United States of America**

1a. Leaves pseudowhorled under the inflorescence ....................................2

1b. Leaves opposite under the inflorescence ................................... 4

2a. Leaves sessile ....................................*Spigelia* loganioides (Torr. & A. Gray in Endl.) A. DC.

2b. Leaves petiolated ................................... 3

3a. Inflorescence terminal, scorpioid cyme; carpoatlas rhombic; seeds with testa rugose ……………………………… *Spigelia* anthelmia L.

3b. Inflorescence axillary, monochasium cyme; carpoatlas elliptic; seeds with testa foveolada....................................*Spigelia* texana (Torr. & A. Gray) A. DC.

4a. Stipule deltate; metastyle smaller than the capsule ......................................*Spigelia* hedyotidea A. DC.

4b. Stipule linear; metastyle longer than the capsule ................................... 5

5a. Inflorescence monochasium cyme, pedicelate; sepals green; stamens included; carpoatlas rhombic.................................... *Spigelia* gentianoides Chapm. ex A. DC.

5b. Inflorescence scorpioid cyme, sessile; sepals green with purple apex; stamen exert; carpoatlas elliptic ................................... *Spigelia* marilandica (L.) L.

**Dichotomous key of the *Spigelia* species distributed in Mexico**

1a. Flowers with corollas up to 4.5 cm long.................................... 2

1b. Flowers with corollas more than 4.5 cm long....................................15

2a. Stem cylindrical ................................... 3

2b. Stem quadrangular....................................6

3a. Stipules linear; stamens exert from the corolla tube......................................*Spigelia* trispicata H. Hurley ex K.R. Gould

3b. Stipules deltate; stamens included in the corolla tube ................................... 4

4a. Corolla hypocrateriform ....................................*Spigelia* dolichostachya Fern. Casas

4b. Corolla infundibuliform or tubular.....................................5

5a. Leaves petiolate; corolla infundibuliform, 1-1.5 cm long, tube and lobes white with purple lines; capsules pubescent at the apex ....................................*Spigelia* anthelmia L.

5b. Leaves sessile; corolla tubular, 3-4 cm long, tube and lobes red; capsule completely glabrous… ................................*Spigelia* splendens H. Wendl. ex Hook.

6a. Leaves opposite under the inflorescence ................................... 7

6b. Leaves pseudowhorled under the inflorescence ....................................10

7a. Inflorescences terminal....................................8

7b. Inflorescences axillary ....................................9

8a. Leaves petiolate, lamina elliptic, chartaceous ..........................................*Spigelia* elbakyanieae S. Islas & L.O. Alvarado

8b. Leaves sessile, lamina oblong, membranaceous .......................................*Spigelia* queretarensis Fern. Casas

9a. Corolla infundibuliform, lobes lanceolate; stamens filamentose; stigma capitate; carpoatlas oblong ....................................*Spigelia* hedyotidea A. DC.

9b. Corolla campanulate, lobes ovate; stamens sessile; stigma terete; carpoatlas quadrangular ....................................*Spigelia* polystachya Klotzsch ex Progel

10a. Corollas with tube and lobes red.................................... *Spigelia* mexicana A. DC.

10b. Corollas with tube and lobes white or white whit purple sections ..................................... 11

11a. Corolla campanulate ................................... *Spigelia* pygmaea D.N. Gibson

11b. Corolla infundibuliform ....................................12

12a. Stem pubescent; inflorescence monochasium cyme with 1-2 flowers ...................................... *Spigelia* texana (Torr. & A. Gray) A. DC.

12b. Stem glabrous or glabrescent; inflorescence scorpioid cyme with 3 or more flowers ...................................... 13

13a. Leaves sessile; stigma capitate ....................................*Spigelia* xochiquetzalliana S. Islas, Lozada-Pérez & L.O. Alvarado

13b. Leaves petiolate; stigma terete.................................... 14

14a. Stem without lignification; leaves succulent; inflorescences terminal; capsules glabrous ...................................... *Spigelia* carnosa Standl. & Steyerm.

14b. Stem with lignification; leaves membranaceous; inflorescences axillary; capsules pubescents ................................... *Spigelia* coelostylioides K.R. Gould

15a. Inflorescence monochasium cyme.....................................16

15b. Inflorescence scorpioid cyme..................................... 18

16a. Corolla hypocrateriform; sepals green with purple apex; stamens insert above half the tube of the corolla ....................................*Spigelia* ayotzinapensis S. Islas, L.O. Alvarado & R. Bustamante

16b. Corolla infundibuliform; sepals green; stamens insert half the tube of the corolla ...................................... 17

17a. Corolla with tube and lobes white with purple margin; capsule pubescent; carpoatlas elliptic; pollen with 4 apertures....................................*Spigelia* guerrerensis L.O. Alvarado & J. Jiménez Ram.

17b. Corolla with tube and lobes purple; capsule glabrous; carpoatlas oblong; pollen with 3 apertures ....................................*Spigelia* scabrella Benth.

18a. Stipule deltate ................................... 19

18b. Stipule absent or linear .....................................21

19a. Leaves pseudowhorled under the inflorescence; stamens included ……………………………… *Spigelia* humboldtiana Cham. & Schltdl.
19b. Leaves opposite under the inflorescence, stamens exert .................................. 20
20a. Stem pubescent; leaves sessile; corolla tubular red with lobes yellow ……………………………… *Spigelia* chiapensis K.R. Gould
20b. Stem glabrous; leaves petiolate; corolla hypocrateriform pink with lobes pink with white margin .................................. *Spigelia* colimensis Fern. Casas
21a. Stipule absent; corolla with tube white; stamens included ……………………………… *Spigelia* mocinoi S. Islas & L.O. Alvarado
21b. Stipule linear; corolla with tube red; stamens exert.................................... 22
22a. Corolla hypocrateriform, lobes red; stigma capitate......................................*Spigelia* longiflora M. Martens & Galeotti
22b. Corolla infundibuliform, lobes yellow; stigma terete .....................................*Spigelia* speciosa Kunth.

**Dichotomous key of the *Spigelia* species distributed in Central America and the Caribbean**

1a. Leaves pseudowhorled under the inflorescence ....................................2
1b. Leaves opposite under the inflorescence .................................. 4
2a. Inflorescence monochasium cyme .................................. *Spigelia* sphagnicola C. Wright.
2b. Inflorescence scorpioid cyme.................................... 3
3a. Corolla hypocrateriform; stigma capitate; metastyle smaller than the capsule; carpoatlas elliptic ....................................*Spigelia* ambigua C. Wright.
3b. Corolla campanulate; stigma terete; metastyle absent; carpoatlas quadrangular ……………………………… *Spigelia* polystachya Klotzsch ex Progel
4a. Steam cylindrical .................................. 5
4b. Steam quadrangular....................................6
5a. Leaves petiolate; corolla infundibuliform; carpoatlas rhombic ……………………………… *Spigelia* anthelmia L.
5b. Leaves sessile; corolla tubular; carpoatlas elliptic .......................................*Spigelia* splendens H. Wendl. ex Hook.
6a. Corolla with tube and lobes completely white ................................... 7
6b. Corolla with tube white and lobes purple, pink or with purple lines ……………………………… 8
7a. Leaves succulent; corolla infundibuliform; stigma terete; carpoatlas elliptic ……………………………… *Spigelia* carnosa Standl. & Steyerm.
7b. Leaves membranaceous, corolla campanulate; stigma capitate; carpoatlas oblong ……………………………… *Spigelia* pygmaea D.N. Gibson

8a. Corolla more than 4 cm long; stigma capitate........................................*Spigelia* humboldtiana Cham. & Schltdl.
8b. Corolla less than 2 cm long; stigma terete.................................... 9
9a. Leaves membranaceous to subcoriaceous; corolla with lobes white with purple margin, ovate; carpoatlas oblong....................................*Spigelia* coelostylioides K.R. Gould
9b. Leaves chartaceous; corolla with lobes pink or purple, lanceolate; carpoatlas rhombic ………………………………… *Spigelia* hamelioides Kunth

***Spigelia ambigua*** C. Wright., Fl. Cub. (Sauvalle) 116 (1870).

TYPE: CUBA: En lagunitas de poca profundidad, jurisdicción Pinar del Río, *C. Wright 3595* (lectotype: US112904!, lectotype designated by Macedo & Buril (2021, p. 2) isolectotypes: GH72226!, NY277648!,).

= *Spigelia blainii* Millsp., Publ. Field Columb. Mus., Bot. Ser. 1: 432 (1900). TYPE: CUBA: Isla de Piños. *J. Blain 51* (holotype: F0062128F!).

= *Spigelia nana* Alain., Mem. Soc. Cub. Hist. Nat. Felipe Poey 22: 116 (1955). TYPE: CUBA. *E.P. Killip 43875* (isotype: US00112918!).

**Description**

Herbs not branched, stem quadrangular, glabrous, without lignification. Leaves opposite under the inflorescence, sessile, lamina ovate, membranaceous, 2 cm long. Stipules present, deltate. Inflorescence terminal, scorpioid cyme, 6-7 flowers, sessile (Fig. 5-A). Sepals green, ovate. Corolla hypocrateriform, 1.2 cm long, tube and lobes white with purple margin, lobes lanceolate. Stamens included. Pollen not observed. Stigma capitate, style not seen. Capsules glabrous, 3 mm diameter; metastyle present, smaller than de capsule; carpoatlas elliptic (Fig. 5-B), transverse ridge absent. Seeds not seen.

**Distribution and habitat**

Endemic species of Cuba (Fig. 6). It grows in Savannas on white sands, of almost pure quartz (Fernández-Casas, 1998). From sea level to 50 m elevation.

**Conservation status**

Critically endangered (CR). The species distributes in coastal areas in Cuba (AOO: 403.34 $km^2$), is known from only five specimens preserved in consulted herbaria and has not been collected in the last 70 years.

**Taxonomic remarks**

*Spigelia ambigua* was originally described as *S. humilis* Bentham. However, this taxon was segregate into four species due to its morphological and geographical variability

(Fernández-Casas, 1998), leaving *S. ambigua* as an endemic species of Cuba, unlike the other three taxa, all of them distributed in the Amazon region. *Spigelia ambigua* can be distinguished from *S. humilis* by being monopodial herbs (*vs.* shrubs), membranous leaves (*vs.* fleshy leaves), and flowers in scorpioid cymes (*vs.* solitary flowers).

**Specimens examined**

CUBA**.** Isla de La Juventud: San Francisco de las Piedras, *E.P. Killip 45200* (US); Santa Fe, *A.A. Taylor 200* (US), *E.P. Killip 43875* (US). Pinar del Río: Pinar del Río, *C. Wright 2561* (NY), C. *Wright 3595* (US).

***Spigelia anthelmia*** L., Sp. Pl. 1: 149 (1753).

TYPE: BRAZIL: Brasilia: Habitat in Cajenna, sin fecha, *Anon. s.n.* (lectotype: LINN-HL210-2!, lectotype designated by Leeuwenberg (1961, p.461-465)).

≡ *Spigelia anthelmia* var. *nervosa* (Steud.) Progel, Fl. Bras. (Martius) 6(1): 262 (1868).

= *Spigelia anthelmia* var. *obliquinervia* A. DC., Prodr. [A. P. de Candolle] 9: 7 (1845). TYPE: In Carabaeis, ex. gr. Jamaica: Tabago, *Anon. s.n.* (holotype: GDC, G00132026!).

= *Spigelia anthelmia* var. *peruviana* A. DC., Prodr. [A. P. de Candolle] 9: 7 (1845). TYPE**:** Peru, *H. Ruiz et J.A. Pavón s.n.* (holotype: GDC132037!).

= *Spigelia killipii* Ewan. Caldasia 4: 302 (1947). TYPE**:** Colombia: Chocó: forest near junction of Río Condoto and Río San Juan, *E.P. Killip 35101* (holotype: US1771863!).

= *Spigelia multispica* Steud., Flora 26: 764 (1843). TYPE**:** Surinam: Para District. *W.R. Hostmann & H. Kappler 851 a* (holotype: P00507680!; isotype: K000573349!, MO694152!).

= *Spigelia multispica* var. *discolor* Progel, Fl. Bras. (Martius) 6(1): 263 (1868). TYPE: French Guiana, *P.A. Poiteau s.n.* (holotype: P; isotype: K000573348!).

= *Spigelia nervosa* Steud., Flora 26: 764 (1843). TYPE**:** Surinam: in subhumidis umbrosis. *W.R. Hostmann & H. Kappler 505* (holotype: P; isotype: BM, K, MO).

= *Spigelia stipularis* Progel, Fl. Bras. (Martius) 6(1): 262 (1868). TYPE: Colombia, *J.W.K. Moritz 426* (holotype: B).

**Description**

Herbs branched, stem cylindrical, glabrous, without lignification. Leaves pseudowhorled under the inflorescence, petiolate, lamina ovate-lanceolate, membranaceous, 4-20 cm long. Stipules present, deltate. Inflorescence terminal, scorpioid cyme, 6-20 flowers, pedicelate (Fig. 5-C). Sepals green, lanceolate. Corolla infundibuliform, 1-1.5 cm long, tube and lobes white with purple lines, lobes deltate. Stamens insert above half the tube of the corolla, included, filament present. Pollen suboblate, with medium polar area, 3 simple apertures, without margo on the colpi. Stigma terete, style pubescent. Capsules pubescent at the apex, 4.5 mm diameter; metastyle present, smaller than de capsule; carpoatlas rhombic (Fig. 5-D), transverse ridge absent. Seeds 16, ovate, testa rugose with triangular projections (Fig. 5-E).

**Distribution and habitat**

Species distributed in the Bahamas, Belize (Fernández-Casas & Huft, 2009), Cuba (Fernández-Casas, 2009), Costa Rica, Dominica, Dominican Republic, El Salvador, Guatemala, Honduras (Fernández-Casas & Huft, 2009), Jamaica, Mexico, Nicaragua, Panama, and United States of America (Fig. 6). Outside the study area is distributed in Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guiana, Peru, Suriname, and Venezuela (Fernández-Casas & Huft, 2009). This species is also introduced in Asia (Liang, *et al.*, 2019) and Africa (Leeuwenberg, 1961). It inhabits in thorn forest, mountain mesophilic forest, deciduous tropical forest, humid tropical forest, sub-deciduous tropical forest, and grasslands. It can be found from sea level to 1000 m elevation.

**Conservation status**

Least concern (LC). This species is widely distributed from Florida in the United States to Panama. (AOO: 242,500.00 $km^2$). Populations are not affected by anthropogenic activities, nor by changes in land use, collecting in recent years even on roadsides. Due to this the species is not considered threatened.

**Taxonomic remarks**

*Spigelia anthelmia* together with *S. humboldtiana*, are the most widely distributed species in the American continent. It can be distinguished from the latter by its lanceolate leaves, numerous terminal inflorescences, minutely ciliate calyx lobes, and papillose apex of the fruits. Specimens of *S. anthelmia* have been misidentified in herbaria as *S. polystachya* Klotzsch ex Progel, probably because of their similarity in the lanceolate shape of the leaves. However, *S. anthelmia* can be distinguished by being herbs up to 1 m tall (*vs.* plants less than 15 cm), with flowers greater than 1 cm long (*vs.* flowers less than 3 mm long) and apically papillose fruits (*vs.* completely glabrous fruits).

**Specimens examined**

UNITED STATES OF AMERICA. Florida: Monroe, D.S. Correll 40299 (TEX).

MEXICO. Campeche: Calakmul, D. Álvarez 1591 (MEXU, XAL), D. Álvarez 1931 (MEXU), D. Álvarez 2175 (MEXU), D. Álvarez 2283 (MEXU), D. Álvarez 250 (MEXU), D. Álvarez 399 (MEXU), D. Álvarez 6052 (MEXU), D. Álvarez 7681 (MEXU), E. Madris 117 (MEXU), E. Madris 133 (MEXU), E. Madris 157 (MEXU), E. Martínez 27835 (MEXU), E. Martínez 27978 (MEXU), E. Martínez 28119 (MEXU), E. Martínez 28716 (MEXU), E. Martínez 28752 (MEXU), E. Martínez 29144 (MEXU), E. Martínez 29198 (MEXU), E. Martínez 29310 (MEXU), E. Martínez 29643 (MEXU, TEX), E. Martínez 30023 (MEXU), E. Martínez 31791 (MEXU), E. Martínez 35935 (IBUG, MEXU), E.M. Lira 157 (CICY), G. Bacab 134 (MEXU), J. Calónico 21531 (MEXU), P. Acevedo-Rodriguez. 12227 (CICY, US); Campeche, A. Puch 1240 (XAL), B. Fausty 121 (CICY), B. Fausty 201 (CICY), B. Fausty 581 (CICY), C. Chan 7535 (MEXU), C. Gutiérrez 5891 (CICY, XAL), C. Gutiérrez 5909 (CICY), C. Gutiérrez 7475 (MEXU, UAMIZ), C. Gutiérrez 7865 (CICY, MEXU, UAMIZ), C. Gutiérrez 8627 (CICY), C. Pavón 37 (MEXU), J.L. Tapia 1216 (CICY, MEXU, XAL); Carmen, C. Chan 4930 (CICY), E. Cabrera 14137 (MEXU), P. Zamora 5642 (MEXU, TEX); Champotón, A. Puch s.n. (CICY), C. Gutiérrez 4468 (TEX, UAMIZ), C. Gutiérrez 4591 (CICY, TEX, UAMIZ, XAL), E. Góngoora 1044 (XAL), P. Zamora 4680 (CICY, TEX, XAL), P. Zamora 4710 (CICY, TEX); Ciudad del Carmen, E. Cabrera 14137 (IEB), G. Carnevali 5845 (CICY, XAL), P. Zamora 5642 (XAL); Escárcega, C. Chan 3897 (CICY); Hecelchakan, Q.Q. Cabrera 49 (MEXU); Hopelchén, C. Gutiérrez 4905 (UAMIZ), D. Álvarez 10196 (MEXU), D. Álvarez 8629 (MEXU), E. Cabrera 11760 (MEXU, TEX), E. Martínez 28604 (MEXU), E.

Martínez 28654 (MEXU), E. Martínez 37808 (MEXU), E. Martínez 38180 (MEXU), P. Alvaro 363 (MEXU, TEX), S. Villegas s.n. (MEXU); Palenque, E. Cabrera 1975 (MEXU); Tenabo, P. Zamora 5804 (MEXU). Chiapas: Acapetahua, E. Matuda 16686 (MEXU); Amatenango del Valle, O. Téllez 7225 (INEGI, MEXU); Catazajá, C. Gutiérrez 6037 (XAL); Chiapa de Corzo, D.E. Breedlove 51578 (ENCB); Chicoasen, E. Martínez 31207 (MEXU); Jiquipilas, O. Farrera 733 (MEXU); Ocosingo, E. Martínez 10265 (MEXU), E. Martínez 8889 (MEXU), E. Martínez 9585 (MEXU), G. Aguilar 1610 (MEXU), G. Aguilar 3958 (MEXU), G. Aguilar 5044 (MEXU); Palenque, C. Cowan 3282 (MEXU), C.P. Cowan 3282 (CICY), D.E. Breedlove 26651 (MEXU), E. Cabrera 12404 (MEXU), R. Hernández 1244 (ENCB, MEXU); Salto de Agua, D.E. Breedlove 55259 (ENCB); Tuxtla Gutiérrez, E. Palacios 878 (FCME); Villa Comaltitlan, R. Hernández 1244 (MEXU). Guerrero: Chilpancingo de los Bravo, W. Schwabe s.n. (MEXU). Oaxaca: Asunción Ixaltepec, L.I. López 51 (MEXU), S.H. Salas 4656 (MEXU, SERO); San Juan Bautista Tuxtepec, G. Martínez 1364 (FCME, MEXU, OAX, XAL); Tuxtepec, G. Martínez 1364 (TEX), G. Martínez 259 (US), L.M. García R. s.n. (OAX). Puebla: Hueytamalco, F. Ventura 17871 (OAX). Querétaro: Jalpan de Serra, B. Servín 1369 (IEB, QMEX). Quintana Roo: Bacalar, L. Wolfgang 3207 (MEXU); Benito Juárez, E. Cabrera 79 (CICY); Felipe Carrillo Puerto, E. Cabrera 6293 (MEXU), I. Olmsted 57 (MEXU), O. Téllez 2815 (MEXU); José María Morelos, D. Álvarez 10517 (MEXU), D. Álvarez 10621 (MEXU), D. Álvarez 10971 (MEXU), D. Álvarez 11176 (MEXU), D. Álvarez 11533 (MEXU), D. Álvarez 8249 (MEXU), D. Álvarez 8469 (MEXU), D. Álvarez 9417 (MEXU), E. Martínez 37726 (MEXU), E. Martínez 38130 (MEXU); Lázaro Cárdenas, A.M. Chan 137 (CICY, XAL); Othón P. Blanco, C. Chan 4345 (CICY, MEXU), E. Cabrera 2134 (CICY, MEXU), E. Ucan 1341 (CICY, XAL), G. Carnevali 5591 (CICY, XAL), M. Narváez 432 (CICY, XAL), O. Téllez 1983 (MEXU), O. Téllez 3594 (MEXU), P. Herrera 20 (MEXU), S. Torres 233 (CICY). San Luis Potosí: Cárdenas, J. Rzedowski 24562 (ENCB); Ciudad del Maíz, L. González s.n. (ENCB); Tamasopo, J. Rzedowski 10667 (ENCB); Tamazuchale, J. Rzedowski 11011 (ENCB); Xilitla, J. Rzedowski 10600 (ENCB). Tabasco: Carmen, E. Cabrera 15085 (MEXU); Centro, R. Hernández 1869 (MEXU); Paraíso, E. Cabrera 14732 (IEB, MEXU); Teapa, H. Cáliz de Dios 9648 (OAX), J. Calónico 21155 (MEXU), T.B. Croat 65337 (MEXU); Villahermosa, A. Ramírez 26 (MEXU), A.M. Hanan 1122 (MEXU), J.L. Dominguez 236 (XAL),

R. Guerrero 233 (XAL). Veracruz: Actopan, G. Castillo 18371 (MEXU, XAL); Alto Lucero, F. Vazquez 698 (XAL); Catemaco, L. González 1502 (ENCB), L. Paray 1937 (ENCB), R.C. Trigos 85 (HUAP); Dos Ríos, F. Ventura 11801 (IEB, MEXU, XAL), F. Ventura 8872 (IEB, MEXU, XAL); Jacomulco, G. Castillo 8551 (XAL); Jalcomulco, G. Castillo 3314 (XAL); Poteapan, M.C. González 176 (XAL); San Andrés Tuxtla, L. González s.n. (ENCB); Sontecomapan, R. Cedillo 64 (HUAP); Tlacotalpan, T.P. Ramamoorthy 1746 (INEGI, MEXU). Yucatán: Chankom, C. Chan 3841 (CICY); Chemax, E. Cabrera 8887 (MEXU); Chikindzonot, C. Chan 3472 (CICY, MEXU); Maxcanú, C. Chan 6961 (CICY, MEXU, UAMIZ); Mérida, M. Juan-Qui 1 (CICY, MEXU); Muna, C. Chan 3994 (CICY, MEXU), E. Cabrera 11705 (MEXU, TEX); Oxkutzacak, F. May 136 (CICY, XAL), G. Carnevali 7115 (CICY), O.L. Sanabria s.n. (CICY, XAL); Oxkutzcab, G. Carnevali 7115 (MEXU); Tekax, D. Álvarez 9396 (MEXU); Tizimín, J.L Tapia M 1653 (CICY), J.L. Tapia 1653 (MEXU, TEX, XAL); Valladolid, C. Vargas 127 (CICY), E. Cabrera 11524 (MEXU), E. Cabrera 88887 (CICY), Valladolid, E. Cabrera 79 (MEXU), E. Cabrera 9314 (MEXU), G. Campos-Ríos 1084 (CICY); Yaxcabá, J.S. Flores 10231 (CICY).

GUATEMALA. Petén: Tikal, R. Tún 1055 (US). Honduras. Atlántida: El Cayo, P.H. Gentle 9356 (TEX). El Paraíso: Yuscarán, H. Pfeifer 1533 (US). Isla de la Bahía: Barbereta, C. Nelson 8401 (US). Olancho: Juticalpa, P.H. Gentle 281 (US).

EL SALVADOR. Sansonate: Juayua, J.L. Morrison 8765 (US).

NICARAGUA. León: Nagarote, W.D. Stevens 23090 (TEX, US). Managua: Managua, D. Chaves 12 (US).

COSTA RICA. Alajuela: San Mateo, P. Biolley 2663 (US). Cartago: Turrialba, H.F. Pittier 14036 (US). Limón: Limón, C. Cowan 4575 (TEX). Puntarenas: Pitahaya, A. Molina 27406 (US).

PANAMA. Chiriquí: Los Algarrobos, W.H. Lewis 736 (US). Colón: Bocas del Toro, P.M. Peterson 6431 (US); Colón, P.C. Standley 25495 (US); Frijoles, P. Standley 30899 (US); Lago Gatún, J.D. Dwyer 7519 (US). Herrera: Chepo, H. Pittier 4669 (US); El Cañaistulo, H. Pittier 3624 (US). Panamá: Bella Vista, P. Standley 27745 (US); Colina, E.P. Killip 12109 (US); Isla San José, C.O. Erlanson 453 (US); Miraflores, W.L. Stern 70 (US); San Miguelito, E.P. Killip 3328 (US).

BAHAMAS. Andros: Central Andros, D. Goldman 424 (TEX). Bimini: South Bimini, D.S. Correll 42069 (TEX), W. Stimson 1106 (TEX), W. Stimson 716 (TEX).
JAMAICA. Hanover: Hanover, G.R. Proctor 23894 (TEX). Saint Andrew: Kingston, M.R. Crosby 97 (TEX).
DOMINICAN REPUBLIC. La Altagracia: Punta Cana, D. Goldman 1960 (TEX).
DOMINICANA. Saint Andrew: Woodfors Hill, W.R. Ernst 2075 (MEX).

***Spigelia ayotzinapensis*** S. Islas, L.O. Alvarado & R. Bustamante, Phytotaxa 331(2): 244 (2017).
TYPE: MEXICO: Guerrero: Chilapa de Álvarez, Parque Nacional General Juan N. Álvarez, 31-Jul-2010, *R. Bustamante, N. Diego & J. Rojas 414* (holotype: FCME162178!).

**Description**

Herbs not branched, stem quadrangular, pubescent, without lignification. Leaves opposite under the inflorescence, sessile, lamina ovate-lanceolate, chartaceous, 2.9-3.2 cm long. Stipules absent. Inflorescence terminal, monochasium, 1-2 flowers, pedicelate (Fig. 5-F). Sepals green with purple apex, linear. Corolla hypocrateriform, 8-10 cm long, tube white whit purple lines, lobes white with purple margin, lobes elliptic. Stamens insert above half the tube of the corolla, included, filament present. Pollen oblate-spheroidal, with large polar area, 4 simple apertures, without margo on the colpi. Stigma capitate, style pubescent. Capsules not seen. Seeds not seen.

**Distribution and habitat**

Endemic species of Mexico (Fig. 6). Can be found in *Quercus* forest. It has been recorded at 2078 m elevation.

**Conservation status**

Critically endangered (CR). *Spigelia ayotzinapensis* is known only from the type locality. Although the population seems abundant and the area surrounding the municipality is still conserved, the specimen was collected eleven years ago, and the locality is currently severely affected by livestock. We suggest assigning the category of critically endangered due to the very restricted area of distribution and the anthropogenic impact of the type locality (Islas-Hernández *et al.,* 2017b).

**Taxonomic remarks**

This species is similar to *Spigelia mocinoi* due to its sessile, ovate-lanceolate leaves without stipules, both endemic to Mexico. They can be easily distinguished by quadrangular stems (*vs.* cylindrical), chartaceous leaves (*vs.* membranaceous), monocasium with 1-2 flowers (*vs.* scorpioid top with 3-5 flowers), green sepals with purple apex (*vs.* green) and white corolla with purple apex (*vs.* white corolla). *S. mocinoi* is restricted to the state Estado de Mexico, while *S. ayotzinapensis* is endemic to the state of Guerrero.

**Specimens examined**

MEXICO. Guerrero: Acapulco de Juárez, R. Bustamante 414 (FCME).

***Spigelia carnosa*** Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 72 (1944). TYPE: GUATEMALA: Huehuetenango: dense rich wet woods between Yulhuitz and Maxbal, Sierra de los Cuchumatanes, 15-Jul-1942, *J.A. Steyermark 48692* (holotype: F0062160!; isotype: GH00107105!, US00112909!).

**Description**

Herbs not branched, stem quadrangular, glabrous, with lignification. Leaves pseudowhorled under the inflorescence, peciolate, lamina eliptic-laceolate, succulent, 6-13 cm long. Stipule present, deltate. Inflorescence terminal, scorpioid cyme, 12-30 flowers, pedicelate (Fig. 7-A). Sepals green, linear. Corolla infundibuliform, 1.9-2.4 cm long, tube and lobes white, lobes ovate. Stamens insert under half the tube of the corolla, included, filament present. Pollen oblate, with small polar area, 3 simple apertures, without margo in the colpi. Stigma terete, style pubescent. Capsule glabrous, 7-8 cm diameter; metastyle present, smaller than the capsule; carpoatlas elliptic (Fig. 7-B), transvers ridge absent. Seeds elliptic, testa granulate (Fig. 7-C).

**Distribution and habitat**

Species distributed in El Salvador (Fernández-Casas & Huft, 2009), Guatemala, and Mexico (Fig. 6). It inhabits cloudy mountain forest and semi-deciduous tropical forest. From 1,300 to 2,500 m elevation.

**Conservation status**

Vulnerable (VU). *Spigelia carnosa* is known from less than ten populations in Mexico and Guatemala and has not been collected in the last 30 years. In addition to this, populations are threatened by anthropogenic activities that can reduce the number of individuals. Based on the results of the occupied area (AOO=10,846.11 $km^2$), the extension of the species is very restricted.

**Taxonomic remarks**

This species is similar to *S. humboldtiana* when dry. It differs in the number of flowers, which is higher in *S. carnosa*. In addition to this, the leaves in *S. carnosa* are thicker (*vs.* membranous), stalked inflorescences (*vs.* sessile), and larger seeds.

**Specimens examined**

MEXICO. Chiapas: La Independencia, D.E. Breedlove 336464 (MEXU); La Trinitaria, D.E. Breedlove 29632 (MEXU, TEX), D.E. Breedlove 38815 (MEXU); Las Margaritas, A. Méndez 7960 (MEXU); Ocozocoautla de Espinosa, J.I. Calzada 9638 (XAL), J.L. Calzada 9638 (MEXU). GUATEMALA. Alta Verapaz: Cobán, P.C. Standley 90272 (US). Baja Verapaz: Salamá, C.L. Lundell 19390 (TEX), C.L. Lundell 21031 (TEX).

***Spigelia chiapensis*** K.R. Gould, 51(4): 410 (-411, figs. 3-4) (1999).

TYPE: MEXICO: Chiapas: Amatenango del Valle, Amawitz, 4 km al O de la cabecera municipal, 12-Jun-1988, *M. Gómez López 521* (holotype: MEXU574652!; isotype: TEX00256905!, CAS).

**Description**

Herbs not branched, stem quadrangular, pubescent, without lignification. Leaves opposite under the inflorescence, sessile, lamina ovate-elliptic, membranaceous, 2-10 cm long.

Stipule present, deltate. Inflorescence terminal, scorpioid cyme, 7-16 flowers, sessile (Fig. 7-D). Sepals green with purple apex, linear. Corolla tubular, 6-7.5 cm long, tube red, lobes yellow, lobes lanceolate. Stamens insert above half the tube of the corolla, exert, filament present. Pollen oblate-spheroidal, with large polar area, 3 simple apertures, without margo on the colpi. Stigma terete, style pubescent. Capsule not seen, Seeds not seen.

**Distribution and habitat**

Endemic species of Mexico (Fig. 6). Inhabits coniferous forest and grasslands. It has been recorded at 1800 m elevation.

**Conservation status**

Critically endangered (CR). This species is known from three localities only in Mexico and has not been collected in the last 30 years. It has a restricted distribution, being an endemic species for the state of Chiapas. The analysis carried out from the known distribution yields a value that is less than 0.1% of the country's area (AOO: 7.09 $km^2$). Considering the restricted area and the absence of new collections of this species, the category of CR is suggested.

**Taxonomic remarks**

This species is similar to *Spigelia speciosa* in the red corolla tube and lighter colored lobes, the base of the persistent style. However, *S. chiapensis* can be differentiated by shorter sepals, smaller corollas with yellow lobes, no throat constrictions, and longer anthers.

**Specimens examined**

MEXICO. Chiapas: Amatenango del Valle, E. Matuda 5886 (TEX), M. Gómez 521 (IMSS); Teopisca, D.E. Breedlove 10520 (ENCB, TEX), R. Merrill 3009 (TEX), S.M. Mertz 44 (MEXU).

***Spigelia coelostylioides*** K.R. Gould, Brittonia 51(4): 407 (-410, figs. 1-2) (1999).

TYPE: MEXICO: Chiapas: Mun. Venustiano Carranza: Aguacatenango, 19-May-1995, *K.R. Gould 139* (holotype: TEX256906!; isotype: G, MEXU854904! NY).

**Description**

Herbs branched, stem quadrangular, glabrescent, without lignification. Leaves pseudowhorled under the inflorescence, petiolate, lamina ovate-elliptic, membranaceous to subcoriaceous, 1.1-3.5 cm long. Stipules present, deltate. Inflorescence axillary, scorpioid cyme, 3-12 flowers, pedicelate (Fig. 7-E). Sepals green, triangular. Corolla infundibuliform, 0.6-1.5 cm long, tube white, lobes white with purple margin, lobes ovate. Stamens insert half the tube of the corolla, included, filament present. Pollen oblate-spheroidal, with medium polar area, 3 simple apertures, without margo on the colpi. Stigma terete, style pubescent. Capsule pubescent, 7-8 mm diameter; metastyle present, smaller than the capsule; carpoatlas oblong, (Fig. 7-F), transverse ridge absent. Seeds ovate, testa rugose (Fig. 7-G).

**Distribution and habitat**

Species distributed in Guatemala (Gould, 1999) and Mexico (Fig. 9). It inhabits tropical deciduous forest, humid tropical forest, and sub-deciduous tropical forest. Recorded from 200 to 1500 m elevation.

**Conservation status**

Least Concern (LC). This species has a wide distribution, extending from central Mexico to Guatemala (AOO: 32,500.00 $km^2$). Likewise, it has been collected in different locations in recent years. Therefore, it is not considered under any category of threat.

**Taxonomic remarks**

This species is similar to *S. hedyotidea* in herbaceous habit, leaf size, and flower appearance (Gould, 1999). However, *S. coelostylioides* differs from this by being branched plants (*vs.* monopod plants), with whorled leaves (*vs.* all-opposite leaves), sessile inflorescences (*vs.* pedunculate inflorescences), and papillose capsules (*vs.* smooth capsules). Likewise, *S. coelostylioides* is restricted to southern Mexico and northern Guatemala, while *S. hedyotidea* is distributed in northern Mexico and the United States of America.

**Specimens examined**

MEXICO. Chiapas: Altamirano, A. Pérez 1 (MEXU); Comitán de Domínguez, A. Chamé 29 (MEXU), E. Matuda 5760 (MEXU), E.A. Goldman 822 (US), J. Rzedowski 33627 (ENCB); La

Independencia, D.E. Breedlove 47799 (ENCB); Las Margaritas, K. Gould 140 (TEX); Ocosingo, E. Martínez 11306 (MEXU); Oxchuc, S. Luna 33 (IMSS); Trapichito, E. Matuda 5760 (TEX); Venustiano Carranza, D.E. Breedlove 10022 (US). Oaxaca: San Lucas Ojitlán, J.I. Calzada 14187 (MEXU); Tuxtepec, A. Arboretum 429 (US). Puebla: Hueytamalco, G. Cornejo 2781 (IEB, MEXU). Veracruz: Emiliano Zapata, W. Márquez 876 (XAL); Huatusco, S. Avendaño 493 (XAL), S. Avendaño 786 (XAL); Teocelo, A. Cruz 409 (XAL); Uxpanapa, E. Martínez 39501 (MEXU); Veracruz, V. Sosa 67 (IEB, XAL).

***Spigelia colimensis*** Fern. Casas, Fontqueria 55(65): 521 (-523, 527; fig. 1, map) (2008). TYPE: MEXICO: Colima: Tecolapa: Cerro San Miguel, 21-Ago-1987, *F. Leger CUIDA-841* (holotype: IBUG88634!; isotype: IBUG89167!).

**Description**

Herbs not branched, stem quadrangular, glabrous, without lignification. Leaves opposite under the inflorescence, petiolate, lamina ovate-elliptic, membranaceous, 6-11.8 cm long. Stipule present, deltate. Inflorescence terminal, scorpioid cyme, 5-14 flowers, pedicelate (Fig. 8-A). Sepals green, lanceolate. Corolla hypocrateriform, 2-4.5 cm long, tube pink, lobes pink with white margin, lobes deltate. Stamens insert above half the tube of the corolla, exert, filament present. Pollen not seen. Stigma capitate, style glabrous. Capsule not seen. Seeds not seen.

**Distribution and habitat**

Endemic species of Mexico (Fig. 9). It lives in sub-deciduous tropical forest. At 500m elevation.

**Conservation status**

Critically endangered (CR). This species is known only from the type specimen and has not been collected again in nearly 30 years.

**Taxonomic remarks**

*S. colimesis* shows characteristics similar to *S. longiflora* due to the branching stems, membranous leaves and red hypocrateriforme flowers. It can be distinguished from this by having petiolate leaves (*vs.* sessile leaves), smaller corollas (*vs.* longer corollas), and internally white corolla lobes (*vs.* red lobes).

**Specimens examined**

MEXICO. Colima: Tecoman, F. Weger 841 (IBUG).

***Spigelia dolichostachya*** Fern. Casas, Fontqueria 55(23): 129 (-133; figs. 5-7; map 2) (2004). TYPE: MEXICO: Chiapas: Mun. Ocosingo: Naja, 2 km al N camino de Chancalá, 17-Jun-1986, *E.M. Martínez & M.A. Soto 18778* (holotype: MEXU580222!; isotype: IEB084136!).

**Description**

Herbs not branched, stem cylindrical, glabrous, without lignification. Leaves pseudoworled under the inflorescence, petiolate, lamina lanceolate, chartaceous, 7 cm long. Stipule present, deltate. Inflorescence terminal, scorpioid cyme, more than 30 flowers, pedicelate (Fig. 8-B). Sepals green, lanceolate. Corolla hypocrateriform, 1.5-1.7 cm long, tube and lobes white, lobes deltate. Stamens insert above half the tube of the corolla, included, filament present. Pollen oblate-spheroidal, with medium polar area, 3 simple apertures, without margo on the colpi. Stigma terete, style glabrous. Capsule pubescent, 4.5 mm diameter; metastyle present, smaller than the capsule; carpoatlas elliptic (Fig. 8-C), transversal ridge present. Seeds discoid, testa reticulate (Fig. 8-D).

**Distribution and habitat**

Endemic to Mexico (Fig. 9). It inhabits cloudy mountain forest, at 900 m elevation.

**Conservation status**

Critically endangered (CR). This species is known only from a collection in the state of Chiapas, Mexico, in an area with a high anthropogenic impact. In addition, it has been more than 30 years since it has been collected.

**Taxonomic remarks**

*S. dolichostachya* is similar to *S. anthelmia* in the pseudowhorled leaves below the inflorescence, terminal inflorescences, and papillose capsules at the apex. It can be easily distinguished from it by monopodial stems (*vs.* branching stems), chartaceous leaves (*vs.* membranous leaves), and very long inflorescences with more than 30 flowers on very short peduncles (*vs.* short inflorescences with less than 20 flowers).

**Specimens examined**

MEXICO. Chiapas: Ocosingo, E. Martínez 18778 (IEB).

***Spigelia elbakyaniae*** S. Islas & L.O. Alvarado, Phytotaxa 477(2): 278 (2020).

TYPE: MEXICO: Oaxaca, Distrito: Juchitán, municipio: Santa María Chimalapa. Camino hacia Arroyo San Vicente, 11 km LR SE de la Gringa, 23 March 1995, *E. Torres 540* (holotype: SERO!; isotype: OAX!).

**Description**

Herbs not branched, stem quadrangular, pubescent, without lignification. Leaves opposite under the inflorescence, petiolate, lamina elliptic, chartaceous, 5.7-6.8 cm long. Stipule present, deltate. Inflorescence terminal, scorpioid cyme, up to 10 flowers, sessile (Fig. 8-E). Sepals green, linear. Corolla infundibuliform, 1.3-1.6 cm long, tube and lobes white with purple lines, lobes ovate. Stamens insert under half the tube of the corolla, included, filament present. Pollen not seen. Stigma terete, style glabrous. Capsule not seen. Seeds not seen.

**Distribution and habitat**

Endemic to Mexico (Fig. 9). It inhabits cloudy mountain forest. It has been recorded at 900 m elevation.

**Conservation status**

Critically endangered (CR). *Spigelia elbakyanii* is known from the type locality only. The specimen was collected over 25 years ago in the state of Oaxaca, Mexico. The forest where the species was collected is under deforestation due to timber harvesting and farming and has been subject of social and environmental problems such as the fires of 1988. Based on this and because of the very restricted area of distribution and the lack of new records of this species since the type collection.

**Taxonomic remarks**

The species is morphologically similar to *S. humboldtiana* and *S. anthelmia* in floral characters. However, it can be distinguished from these by opposite leaves below the inflorescence, chartaceous leaf texture, pedunculate inflorescences, and style less than 1 cm long. The size of the style, less than half the corolla tube, has not been reported in any other species of the genus in the NA region.

**Specimens examined**

MEXICO. Oaxaca: Santa María Chimalapa, E. Torres 540 (OAX, SERO).

***Spigelia gentianoides*** Chapm. ex A. DC., Prodr. [A. P. de Candolle] 9: 5 (1845).

TYPE: USA: Florida: Without specific locality or date *A.C. Chapman s.n.* (lectotype: G00368318!, lectotype designated by K. Gould (1996, p. 418); isolectotype: G00368317!).

**Description**

Herbs not branched, stem cylindrical, glabrous, without lignification. Leaves opposite under the inflorescence, sessile, lamina ovate-lanceolate, coriaceous, 2-4 cm long. Stipule present, linear. Inflorescence terminal, monochasium cyme, 1-2 flowers, pedicelate (Fig. 10-A). Sepals green, lanceolate. Corolla infundibuliform, 6-8 cm long, tube pink, lobes pink with purple lines, lobes lanceolate. Stamens included, filament present. Stigma terete, style not seen. Capsule glabrous, 9-9.5 mm diameter; metastyle present, longer than the capsule; carpoatlas rhombic, transversal ridge absent. Seeds not seen.

**Distribution and habitat**

Endemic species of the United States of America (Fig. 9). It lives in Pine-Oak forest (K. Gould, 1997). Recorded at 100 m elevation.

**Conservation status**

Critically endangered (CR). *Spigelia gentianoides* is listed as an Endangered species and is currently being monitored by the Florida Natural Areas Inventory program (FNAI, 2000). The species is endangered by the clearcutting of the mixed pine-hardwood habitat in northern Florida and its associated replacement with pine monoculture (Gould, 1997).

**Taxonomic remarks**

*S. gentianoides* is one of three species endemic to the United States of America along with *S. loganoides* and *S. marilandica*. Distinguished from these two morphologically by opposite leaves under the inflorescence (*vs.* pseudowhorled leaves in *S. loganioides*), white flowers with pink margin of petal lobes (*vs.* red flowers with yellow lobes in *S. marilandica*). According to the phylogenetic analysis using ITS marker, *S. gentianoides* and *S. marilandica* are sister species (Gould 1997), sharing their distribution in northern Florida. However, the floral morphology is completely different, which could be the result of the differential pressure of pollinators.

**Specimens examined**

UNITED STATES OF AMERICA. Alabama: Bibb, K. Gould 134 (TEX), S. Ginzbarg 990 (TEX).

***Spigelia guerrerensis*** L.O. Alvarado & J. Jiménez Ram., Phytotaxa 238(2): 184 (2015).
TYPE: MEXICO: Guerrero: Municipio Eduardo Neri: Cerro El Ocotal, 1.05 km al SE de Amatitlán, 11-Ago-1994, *M.A. Monroy de la Rosa 384* (holotype: FCME50441!).

**Description**

Herbs not branched, stem quadrangular, pubescent, without lignification. Leaves opposite under the inflorescence, sessile, lamina ovate-lanceolate, membranaceous, 3-4 cm long. Stipule present, deltate. Inflorescence terminal, monochasium cyme, 1-2 flowers, pedicelate (Fig. 10-B). Sepals green, linear. Corolla infundibuliform, 4.5-5.2 cm long, tube white, lobes white with purple margin, lobes ovate. Stamens insert half the tube of the corolla, included, filament present. Pollen suboblate, with medium polar area, 4 simple apertures, without margo on the colpi. Stigma capitate, style pubescent. Capsule pubescent, 6.5-7 mm diameter; metastyle present, smaller than the capsule; carpoatlas elliptic (Fig. 10-C), transversal ridge present. Seeds ovado-compressed, testa foveolate (Fig. 10-D).

**Distribution and habitat**

Endemic species of Mexico (Fig. 12). It grows in coniferous and *Quercus* forest, between 1,200 and 1,900 m elevation.

**Conservation status**

Vulnerable (VU). *Spigelia guerrerensis* is restricted to the states of Guerrero and Oaxaca, where only seven populations and one population, respectively, are known, which together cover an area close to 10,500 $km^2$ (AOO). Although populations seem abundant, anthropogenic activities in these areas could drastically reduce the number of individuals in the future. In addition, none of the known populations is included in any protected area (Alvarado-Cárdenas and Jiménez, 2015).

**Taxonomic remarks**

This species is morphologically similar to *S. scabrella* due to its infundibuliform corolla, herbaceous habit, shape and size of the leaves. *S. guerrerensis* can be distinguished by the white color of the corolla, sometimes the margins of the lobes purple, sparsely pubescent styles, inflorescences reduced to one or two flowers and apically hirsute fruits (Alvarado-Cárdenas & Jiménez, 2015).

**Specimens examined**

MEXICO. Guerrero: Atlixtac, O. Silva 22 (FCME), R. Cruz-Durán 9186 (FCME); Eduardo Neri, F. Ramos 197 (MEXU), M.A. Monroy 363 (FCME), M.A. Monroy 384 (FCME), M.A. Monroy 392 (FCME), R. Cruz-Durán 197 (FCME, MEXU), R. Cruz-Durán 931 (FCME, MEXU); General Heliodoro Castillo, R. Cruz-Durán 4203 (FCME); Taxco de Alarcon, B.E. Carreto s.n. (FCME), J.A. Almazán 1 (FCME). Oaxaca: San Bartolo Yautepec, D. López 1022 (MEXU).

***Spigelia hamelioides*** Kunth, Nov. Gen. Sp. [H.B.K.] iii. 185.

TYPE: COLOMBIA: Crescit prope Guaduas Novo-Granatensium, locis temperatis. Alt. 600 hex, floret junio, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (holotype: P0067862!).

= *Spigelia filipes* Rusby, Descr. S. Amer. Pl. 81 (1920). TYPE: Venezula: Bolivar: Eleanor Creek, lower Orinoco River, *H.H. Rusby & R.W. Squires 145* (holotype: NY00297394!; isotype: BM00757838!, US00112912!, MIN1002595!, K00573334!).
= *Spigelia killipi* Ewan, Caldasia 4: 302 (1947). TYPE: Colombia: Chocó: forest near junction of Río Condoto and Río San Juan, alt. 100-150 m, 20 Apr 1939, *E.P. Killip 35101* (holotype: US1771863!; isotype: US-00901886!, BM-00757855!).
= *Spigelia multispica* Steud., Flora 26: 764 (1843). TYPE: Suriname, in sylvis distr. Para, *W.R. Hostmann & A. Kappler 851a* (holotype: F790132!; isotype: G00368321!, K00573348!, MO1686684!, MO1954958!, P, SR5848!).
= *Spigelia persicarioides* Ewan var. *insularis* Ewan, Caldasia 4: 298 (1947). TYPE: Colombia: Gorgona Island, Dept. Nariño: S end of Gorgona island, near sea level. Bonk of small stream in dense forest. Herb; corolla white, *H. García Barriga & E.P. Killip 33105* (holotype: US1770097!; isotype: BM757854!, MO112921!, BC635667!, COL003969!, US00930981!).
= *Spigelia sessilifolia* Rusby, Bull. Torrey Bot. Club 25(10): 543 (1898). TYPE: Bolivia: Mapiri: 5000 ft., May 1886*, H.H. Rusby 1429* (holotype: MICH1191502!; isotype: NY00297400!, NY00297399!, MIN1002816!, NY00297398!, US00112926!).

**Description**

Herbs branched, stem quadrangular, glabrous, with lignification. Leaves pseudowhorled under the inflorescence, petiolate, lamina ovate, chartaceous, 10-16 cm long. Stipule present, deltate. Inflorescence axillary, scorpioid cyme, 20-30 flowers, sessile (Fig. 10-E). Sepals green, linear. Corolla infundibuliform, 0.8-1.8 cm long, tube white, lobes pink or purple, lobes lanceolate. Stamens insert under half the tube of the corolla, included, filament present. Pollen not seen. Stigma terete, style pubescent. Capsule pubescent, 4-6.5 cm diameter; metastyle present, same size as the capsule; carpoatlas rhombic (Fig. 10-F), transversal ridge absent. Seeds 16, testa rugose.

**Distribution and habitat**

Species distributed in Costa Rica, Honduras and Panama (Fig. 12). Outside the study area its distributed in Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guiana, Peru, Suriname, and Venezuela (Fernández-Casas & Huft, 2009). It lives in humid forests. It is recorded from sea level to 160 m elevation.

**Conservation status**

Least concern (LC). *S. hamelioides* is one of the species that is shared between the NA and SA region. Its distribution extends to Ecuador, Peru, Bolivia, and Brazil in the Amazon region.

**Taxonomic remarks**

This species presents morphological characteristics similar to *S. humboldtiana* in the size of the leaves and flowers, as well as in the pseudowhorled phyllotaxy under the inflorescence. It can be differentiated from this by chartaceous leaves (*vs.* membranous), flowers with pink petals (*vs.* flowers with white petals), and pubescent capsule (*vs.* capsule glabrous).

**Specimens examined**

HONDURAS. Islas de la Bahia: Brick Bay, C. Nelson 8333 (US). Panamá. Colón: Donoso, A. Fendler 283 (US); Frijoles, P.C. Standley 27389 (US), P.C. Standley 29926 (US); Gamboa, P.C. Standley 30960 (US); Palmas Bellas, P.H. Allen 902 (US); Santa Rosa, C. Galdames 7911 (US). Darién: Piaogana, P.H. Allen 929 (US); Rancho Ahogado, W.L. Stern 812 (US). Herrera: Chepo, E.P. Killip 3120 (US). Kuna Yala: Playón Chico, W.H. Lewis 78 (US). Los Santos: Pedasí, P.C. Standley 37077 (US).

COSTA RICA. Puntarenas: Corcovado, K. Gould 8 (TEX); Golfito, K. Gould 6 (TEX); Osa, K. Gould 7 (TEX), P. Acevedo-Rdgz. 487 (US); Puntarenas, P. Delprete s.n. (TEX).

PANAMA: Bella Vista, E.A. Goldman 1962 (US); Las Cumbres, S. Morí 1781 (US); San Antonio, P.C. Standley 28232 (US); Vista Bella, H. Kennedy 3117 (TEX). Veraguas: Santiago, H. Pittier 5107 (US); Soná, J.A. Duke 4761 (US).

***Spigelia hedyotidea*** A. DC., Prodr. [A. P. de Candolle] 9: 7 (1845).

TYPE: USA: Nuevo Mexico, 1851, *C. Wright 1663* (holotype: P511989!).

= *Spigelia coulteriana* Benth., J. Proc. Linn. Soc., Bot. 1: 90 (1856). TYPE: Mexico: Hidalgo: Zimapan, *T. Coulter 962* (holotype: K00573402!).

= *Spigelia lindhiemeri* A. Gray, Syn. Fl. N. Amer. 2(1): 108 (1878). TYPE: USA: Texas: Comal Co.: New Braunfels, *F.J. Lindheimer 172* (lectotype: GH00107111!, lectotype designated by Henrickson (1996, p.99)).

**Description**

Herbs branched, stem quadrangular, glabrescent, without lignification. Leaves opposite under the inflorescence, sessile o shortly petiolate, lamina lanceolate, coriaceous, 1-2.5 cm long. Stipule present, deltate. Inflorescence axillary, scorpioid cyme, 5-8 flowers, pedicelate (Fig. 11-A). Sepals green, linear. Corolla infundibuliform, 0.7-1.3 cm long, tube white, lobes white with purple margin, lobes lanceolate. Stamens insert half the tube of the corolla, included, filament present. Pollen not seen. Stigma capitate, style pubescent. Capsule pubescent, 5.3-6.2 mm diameter; metastyle present, smaller than the capsule; carpoatlas oblong (Fig. 11-B), transversal ridge present. Seeds elliptic, testa reticulate.

**Distribution and habitat**

Species distributed in the United States of America and Mexico (Fig. 12). It lives in tropical deciduous forest, from 1,400 to 1,800 m elevation.

**Conservation status**

Least concern (LC). This species has been reported with a greater distribution in the United States and Mexico, covering an area of 85,000.00 $km^2$ (AOO). Likewise, it has been collected steadily in recent years.

**Taxonomic remarks**

This species is related to *S. texana* based on the phylogenetic analysis from chloroplast DNA (Gould, 1997). *S. hedyotidea* can be morphologically differentiated from *S. texana* by having larger branceh stems (*vs.* monopodic stems), glabrous leaves (*vs.* papillose leaves), and opposite leaves at the base of the inflorescence (*vs.* pseudowhorled leaves below the inflorescence).

**Specimens examined**

UNITED STATES OF AMERICA. Arkansas: Conway, A. Haas 252 (US). Texas: Austin, B.C. Tharp 1328 (TEX), B.C. Tharp 44445 (TEX), B.C. Tharp s.n. (TEX), M.S. Young s.n. (TEX); Bandera, G. Denny 193 (TEX), G. Denny 309 (TEX), K. Gould 148 (TEX), K. Gould 157 (TEX), W.R. Carr 14586 (TEX); Bell, L.L. Hansen 5903 (TEX); Bexar, E. Lott 4406 (TEX), E. Lott 4582 (TEX), W.R. Carr 12365 (TEX), W.R. Carr 19732 (TEX); Burne, J.A. Mears s.n. (TEX); Columbia, B.F. Bush 148 (US); County, B.C. Tharp s.n. (TEX); Gillespie, K. Gould s.n. (TEX); Goliad, W.R. Carr 11814 (TEX); Guadalupe, H.B. Parks 1847 (TEX), H.B. Parks 39592 (TEX); Hays, B. Harms 3 (TEX); Karnes, D.S. Correll 16055 (TEX); Kensall , W.R. Carr 34019 (TEX); Kimble, L.L. Hansen 4846 (TEX), L.L. Hansen 6580 (TEX); Kleberg, W.R. Carr 25632 (TEX); Mclennan, L.D. Smith 507 (TEX), L.D. Smith 558 (TEX); McMullen, W.R. Carr 25288 (TEX); Palo Pinto, R. McVaugh 8342 (TEX); Parker, W.R. Carr 28161 (TEX); Terrell, G.L. Webster 392 (TEX), K. Gould 158 (TEX), W.R. Carr 23781 (TEX); Uvalde, W.R. Carr 14624 (TEX); Val Verde, B.H. Warnock 11345 (TEX), K. Gould 108 (TEX), K. Gould 111 (TEX), W.R. Carr 15909 (TEX), W.R. Carr 22009 (TEX), W.R. Carr 30330 (TEX), W.R. Carr s.n. (TEX).

MEXICO. Chihuahua: Chihuahua, C.G. Pringle 839 (MEXU); Julimes, M.C. Johnston 11389 (TEX), M.C. Johnston 12337 (TEX). Coahuila: Cuatro Ciénegas, T. Wendt 842 (TEX); Sierra de la Gloria, T. Wendt 1654 (TEX). San Luis Potosí: Ciudad Valles, E. Palmer 461 (US), E. Palmer 86 (US). Sonora: Alamos, P. Jenkins s.n. (TEX). Tamaulipas: Bustamante, G. Nesom 5989 (TEX); Gómez Farías, A. Mora-Olivo 7759 (MEXU); Jaumave, H.W. Viereck 362 (US); Tula, M.C. Johnston 11158 (TEX), M.C. Johnston 11172 (TEX).

***Spigelia humboldtiana*** Cham. & Schltdl., Linnaea 1(2): 200 (1826).

TYPE: VENEZUELA: Sucre: Habitat ad Cumaná, 1799, *F.W.H.A. Humboldt & A.J.A. Bonpland 174* (lectotype: BW3552!, (lectotype designated by Ewan (1947, p. 295), isolectotype: P507553!,).

= *Spigelia australis* L.B. Sm., Wrightia 2: 101, fig. 19p-q (1960). TYPE: Brasil: Santa Catarina, collected in pinheiral (Araucaria forest). 33km W of Cacador, *D.L. Smith & R. Reitz 9104* (holotype: US2280007!; isotype: Herb. Barbosa Rodriguez, Herb. Nacional do Rio de Janeiro).

= *Spigelia chamaedryoides* Kraensl., Repert. Spec. Nov. Regni Veg. 14: 293 (1916). TYPE: Argentina: Misiones: Posadas y suburbios, *A.A. Muniez 12* (holotype: G368322!; isotype: GH, MO1686669!).

= *Spigelia humboldtiana* var*. obtusifolia* Progel, Fl. Bras. (Martius) 6(1): 261 (1868). TYPE: Brazil: Brasilia: ad fl. Paraiba. *P.M. Vidensis s.n.* (holotype: BR6594893!).

= *Spigelia humboldtiana* var*. pubescens* Progel, Fl. Bras. (Martius) 6(1): 261 (1868). TYPE: Brazil: Brasília: in prov. Minarum sylvis orientalibus, *F. Sellow s.n.* (holotype: BR).

= *Spigelia palmeri* Rose, Contr. U.S. Natl. Herb. 1: 342 (1895). TYPE: Mexico: Colima: In wet places across the lagoon from Manzanillo, *E. Palmer 929* (holotype: US-112919!).

= *Spigelia rubelliana* Arechau., Anales Mus. Nac. Montevideo ser. 2, 1: 61, fig. 1 (1911). TYPE: Uruguay: Rivera. Cuchilla Negra, *Anon. s.n.* (holotype: SI25771).

= *Spigelia scabra* Cham. & Schltdl., Linnaea 1(2): 202 (1826). TYPE: Brazil: in provinia Cisplatina Brasiliae: Montevideo. *F. Sellow 1477* (holotype: B; isotype: HAL69906!).

= *Spigelia scabra* var *angustata* Progel, Fl. Bras. (Martius) 6(1): 261 (1868). TYPE: Brasil: Rio de Janeiro: Petrópolis, Caxambu, *A.F.M. Glaziou s.n.* (holotype: BR111043!).

**Description**

Herbs branched, stem quadrangular, glabrous, without lignification. Leaves pseudowhorled under the inflorescence, shortly petiolate, lamina ovate, membranaceous, 1.5-12 cm long. Stipule present, deltate. Inflorescence terminal, scorpioid cyme, 5-13 flowers, sessile (Fig. 11-C). Sepals green, linear. Corolla infundibuliform, 4.5-6 cm long, tube white, lobes white with purple lines, lobes ovate. Stamens insert half the tube of the corolla, include, filament present. Pollen oblate-spheroidal, with medium polar area, 3 simple apertures, without margo on the colpi. Stigma capitate, style pubescent. Capsule glabrous, 4-4.5 cm diameter; metastyle present, smaller than the capsule; carpoatlas elliptic (Fig. 11-D), transversal ridge present. Seeds trullate-ovoid, testa reticulate (Fig. 11-E).

**Distribution and habitat**

Species distributed in Belize (Fernández-Casas & Huft, 2009), Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, and Panama (Fig. 12). Outside the study area its distributed in Argentina (Bravo, 1971), Bolivia, Brazil, Colombia, Ecuador, Guiana, Honduras, Paraguay, Peru, Uruguay, and Venezuela (Fernández-Casas & Huft, 2009). It inhabits thorny forest, mesophyllous mountain forest, *Quercus* forest, deciduous and semi-deciduous tropical forest, humid tropical forest and scrub. It is found from sea level to 2700nm elevation.

**Conservation status**

Least concern (LC). This species is widely distributed from Mexico to South America. Together with *S. anthelmia*, they are the species with the largest distribution in the continent and introduced in the old world. It is distributed mainly along the coasts and has been recorded in protected areas and botanical gardens. Therefore, it is not considered under any type of threat.

**Taxonomic remarks**

*Spigelia humboldtiana,* is one of the two species with a wide distribution on the continent. Together with *S. scabra*, the species were published simultaneously by Chamisso and Schlechtendal (1826). Blackwell (1967) is the first to place *S. scabra* in synonymy under *S. humboldtiana* (Fernández Casas & Huft, 2009), so from this moment the priority of this name is established in accordance with the International Code of Nomenclature for Algae, Fungi and Plants (Art. 11.5).

In the publication of the species, Chamisso & Schlechtendal mention that, despite its similarity, *S. scabra* was more robust, which is why they separate them into different entities. Bravo (1971), in his work on the Argentine species of *Spigelia*, carried out a quantitative analysis of the variability in *S. humboldtiana* of different morphological characters (length and width of the leaf, length of the calyx, mature calyx-capsule ratio, roughness, stipules) that were considered for the separation of *S. scabra* as a different species. The characters analyzed in 201 specimens present a normal distribution and a continuous variation within the species, for which they are not considered of taxonomic importance to differentiate between species. Therefore, here we follow the proposal of Bravo to keep *S. humboldtiana* as the accepted name, subordinating *S. scabra* as a synonym.

**Specimens examined**

MEXICO. Campeche: Candelaria, Grupo Roya 37 (XAL); Tenabo, P. Zamora 5804 (CICY). Chiapas: Acacoyagua, N. Martínez 941 (FCME, MEXU), R. Hernández 529 (MEXU); Berriozábal, F. Miranda 7880 (MEXU), R.A. Palestina 2338 (XAL); Cacahoatán, F. Miranda 1771 (MEXU), G. Guzman 115 (ENCB); Chiapa de Corzo, D.E. Breedlove 27999 (MEXU); Chilón, L. Ambriz 1 (IMSS, XAL); Escuintla, E. Matuda 16989 (MEXU), E. Matuda 2113 (MEXU), E. Matuda s.n. (MEXU); Huixtla, S. Quintero 247 (XAL); Ixtacomitán, E. Martínez 3152 (MEXU); La Concordia, A. Reyes-García 1864 (INEGI, MEXU), J. Martínez 1008 (FCME), J. Martínez 517 (MEXU), J. Martínez 551 (FCME, MEXU), J. Martínez 789 (FCME, MEXU), J. Martínez 926 (FCME), N. Méndez 71 (MEXU), U. Bachem 968 (MEXU, UAMIZ); La Independencia, F. Madero 1931 (MEXU); La Trinitaria, D.E. Breedlove 53330 (MEXU, TEX); Mapastepec, M. Heath 886 (MEXU, OAX, UAMIZ, XAL); Ocosingo, A. Durán 327 (MEXU), D. Álvarez 5387 (MEXU, XAL), D.E. Breedlove 34122 (MEXU), E. Martínez 10761 (MEXU), E. Martínez 10762 (MEXU), E. Martínez 13744 (MEXU), E. Martínez 16525 (CICY, MEXU), E. Martínez 16538 (MEXU), E. Martínez 18778 (CICY), E. Martínez 19007 (CICY), E. Martínez 19028 (CICY, IEB, MEXU), E. Martínez 22666 (CICY, MEXU), E. Martínez 25841 (UAMIZ, XAL), E. Martínez s.n. (MEXU, UAMIZ), F. Miranda 6983 (MEXU), F.E. Valdivia 2314 (XAL), G. Aguilar 10022 (MEXU), G. Aguilar 10439 (MEXU), G. Aguilar 11779 (MEXU), G. Aguilar 1378 (MEXU), G. Aguilar 2330 (MEXU), G. Aguilar 2951 (MEXU), G. Aguilar 2952 (MEXU), G. Aguilar 3848 (MEXU, XAL), G. Aguilar 3911 (MEXU, XAL), G. Aguilar 4613 (MEXU), G. Aguilar 5811 (MEXU, XAL), G. Aguilar 7133 (MEXU), G. Aguilar 87 (MEXU), G. Aguilar 9016 (MEXU), G. Aguilar 9149 (MEXU), G. Castillo 4090 (IEB, MEXU, XAL), G.A. Salazar 8649 (MEXU), G.L. Webster 11662 (MEXU), I. García s.n. (INEGI), J. Calónico 23123 (MEXU), J. Calónico 23126 (MEXU, XAL), J. Calónico 23251 (IBUG, MEXU, XAL), J. Calónico 2429 (MEXU), J. Calónico 24596 (MEXU, XAL), J. Calónico 24692 (MEXU), J. Meave s.n. (ENCB, FCME, IEB, MEXU, XAL), M. Gonzáles 1008 (MEXU), M. Gonzáles 1092 (MEXU), S. Levy 483 (MEXU), S. Sinaca 1094 (MEXU); Ocozocoautla de Espinosa, F. Pimentel 59 (MEXU), P.E. Valdivia 2314 (MEXU), R.A.

Palestina 2924 (XAL), S. Ochoa 3812 (XAL); Osumacinta, D.E. Breedlove 51969 (ENCB); Palenque, D.E. Breedlove 26606 (MEXU), E. Cabrera 1927 (MEXU); Pueblo Nuevo Solistahuacán, O.F. Clarke 428 (MEXU); Reforma, P. Tenorio 19465 (MEXU); Salto de Agua, E. Cabrera 12370 (MEXU, TEX), M.J. Hutt 2423 (MEXU); Solosuchiapa, D.E. Breedlove 34889 (MEXU), D.E. Breedlove 3489 (MEXU); Suchiate, E. Ventura 3783 (OAX, XAL); Tapachula, E. Matuda 2499 (MEXU), E. Ventura 172 (MEXU), E. Ventura 1924 (MEXU, OAX, XAL), E. Ventura 2344 (MEXU, XAL), E. Ventura 318 (CICY, MEXU, UAMIZ, XAL); Totolapa, D.E. Breedlove 27025 (ENCB); Tuxtla Chico, E. Ventura 1857 (CICY, MEXU), E. Ventura 3783 (MEXU); Tuxtla Gutiérrez, A. Reyes-García 1745 (INEGI, MEXU), E. Palacios 1901 (FCME, IBUG), F. Miranda 5363 (MEXU), J.A. Espinosa 377 (MEXU), R. Torres 6368 (MEXU), T.P. Ramamoorthy 1383 (MEXU); Unión Juárez, E. Ventura 1913 (XAL), E. Ventura 2319 (HUMO), J.I. Calzada 3732 (XAL); Unión Juárez, A. Vernet s.n. (MEXU), E. Martínez 20748 (MEXU), E. Ventura 1913 (MEXU), E. Ventura 2319 (IEB, UAMIZ, XAL), E. Ventura 4612 (IEB, MEXU); Villa Corzo, A. Reyes-García 4854 (MEXU), D. Álvarez 10014 (MEXU), D.E. Breedlove 40030 (MEXU), D.N. López s.n. (MEXU, XAL), E. Meléndez s.n. (MEXU), F. Hernández s.n. (MEXU), J. Martínez s.n. (FCME, MEXU), L.O. Alvarado 257 (MEXU), L.O. Alvarado 594 (MEXU), Reyes-García 5252 (MEXU), Reyes-García 7111 (MEXU); Villa Flores, A. Reyes-García 4745 (MEXU); Villaflores, D. Álvarez 9709 (MEXU), F. Miranda 6700 (MEXU). Colima: Manzanillo, C.R. Worth 8610 (US). Guanajuato: Artarjea, E. Ventura 6345 (IEB); Xichú, E. Ventura 7255 (IEB, QMEX), J. Rzedowski 41581 (IEB, UAMIZ), S. Zamudio 13628 (IEB). Guerrero: Acapulco de Juárez, F. Miranda 3343 (MEXU); Juan R. Escudero, J. Maldonado 6799 (FCME); Mártir de Cuilapan, C. Teyuco s.n. (FCME). Oaxaca: Acatlán de Pérez Figueroa, L. Cortés 473 (IEB, MEXU); Magdalena Teitipac, C.V. Morton 2535 (US); Pluma Hidalgo, A. Campos 1502 (MEXU); Pochutla, Grupo Roya 89 (XAL); San Felipe Usila, M.A. Romero-Romero 2908 (MEXU); San José Tenango, J. Calónico 894 (FCME), X. Munn-Estrada 443 (TEX); San Juan Bautista Tuxtepec, D. Ramírez 5 (MEXU), G. Martínez 123 (MEXU), G. Martínez 226 (MEXU, TEX), G. Martínez 459 (MEXU, TEX); San Juan Lalana, J.I. Calzada 17031 (MEXU); San Miguel Chimalapa, S. Maya 1427 (MEXU), S. Maya 1882 (MEXU); San Miguel del Puerto, A. Sánchez 2814 (MEXU), A. Saynes 2180 (IEB, MEXU, QMEX), C. Perret 769 (MEXU), F. López 200

(MEXU), F. López 90 (MEXU), J. Pascual 790 (IEB, MEXU), J. Rivera 1784 (MEXU), J. Rivera H. 1784 (SERO); San Miguel Soyaltepec, L. Cortes 326 (MEXU), R. Torres 6147 (MEXU); San Pedro Pochutla, H.M. Hernández 419 (ENCB), P. Tenorio 5499 (MEXU), R. Torres 4685 (MEXU, TEX), R. Torres 5236 (MEXU, TEX); Santa María Chimalapa, J. Rivera 1347 (MEXU), P. Tenorio 19241 (MEXU), P. Tenorio 19316 (INEGI, MEXU), S. Maya 3476 (MEXU); Santa María Huatulco, C. Perret 787 (MEXU); Santa María Jacatepec, C.H. Ramos 2689 (MEXU), J.I. Calzada 15443 (MEXU). Puebla: Ahuacatlán, G. Toriz 581 (INEGI, MEXU), P. Tenorio 13859 (MEXU), P. Tenorio 8984 (MEXU); Atlequizayan, L. Caamaño 5033 (HUAP); Coatepec, L. Caamaño 7196 (HUAP); Cuetzalan del Progreso, A. Campos 391 (INEGI, MEXU), F. Basurto 111 (MEXU), F. Basurto 76 (MEXU), F. Basurto s.n. (UAMIZ), M. Martínez 1802 (ENCB), P. Lamy 243 (ENCB, IMSS), P. Lamy 38 (MEXU), P. Lamy 4 (MEXU); Hueytamalco, F. Ventura 17871 (IEB, MEXU); Ixtepec, L. Caamaño 4905 (HUAP); Jopala, E. Meza 557 (HUAP, XAL), S. Vargas 395 (XAL); Santiago Yancuictlalpan, P. Lamy 255 (IMSS), P. Lamy 4 (IMSS), R. Ibarra 16 (IMSS), X. Lozoya 68 (IMSS); Tlacuilotepec, L. Caamaño 8177 (HUAP); Tuzamapan de Galeana, E. Turra 1632 (ENCB), M.A. Martínez s.n. (IMSS), Z. Espadas 90 (IMSS); Zihuateutla, J.L. Contreras 9226 (HUAP), J.L. Contreras 9614 (HUAP); Zongozotla, J.L. Martínez 730 (XAL). Querétaro: Arroyo Seco, E. Carranza 3491 (IEB, QMEX, UAMIZ); Jalpan de Serra, E. Carranza 3134 (IEB, INEGI, QMEX), S. Zamudio 7801 (IEB, MEXU, QMEX, XAL); San Joaquín, R. Hernández 10579 (IEB, MEXU, QMEX). Quintana Roo: Bacalar, E. Cabrera 6924 (MEXU, TEX), G. Pérez 447 (MEXU), H. Cisneros 28 (MEXU), H. Cisneros 99 (MEXU); Chetumal, S.C. Sanders 10011 (HUMO, TEX); Felipe Carrillo Puerto, G. Pérez 403 (MEXU, XAL); Othón P. Blanco, E. Cabrera 332 (CICY, MEXU), G. Carnevali 4861 (CICY, ENCB), G. Davidse 20186 (MEXU), O. Téllez 2104 (MEXU), R. Duno 2105 (CICY); San Felipe Bacalar, G. Pérez 447 (XAL); San Felipe Bacalar, E. Cabrera 6924 (IBUG). San Luis Potosí: Aquismón, J.B. Alcorn 3048 (MEXU, TEX); Huehuetlán, J. Rzedowski 10464 (IEB, MEXU); San Antonio, J.B. Alcorn 2394 (MEXU, TEX); Tamasopo, C.G. Pringle 3106 (MEXU); Tamazuchale, M.T. Edwards 616 (TEX); Xilitla, E.M. Lira 1428 (MEXU), R. Merrill 4421 (TEX). Tabasco: Cárdenas, G. Ortiz 507 (UAMIZ); Centla, E. Hernández-Xolocotzi 89 (MEXU); Huimanguillo, E. Martínez 34831 (MEXU), F. Ventura 20042 (MEXU, XAL), M.A. Guadarrama 6061 (MEXU); Macuspana, C.P. Cowan 3355 (CIIDIR);

Tacotalpa, M.A. Martínez s.n. (MEXU), S. Zamudio 512 (ENCB); Teapa, E. Martínez 3128 (MEXU), E. Martínez 34915 (MEXU), F. Ventura 20376 (IEB, MEXU, XAL), F. Ventura 21096 (MEXU, TEX); Tenosique, E. Matuda 3438 (MEXU), N.C. Jiménez 506 (XAL), N.C. Jiménez 644 (XAL). Tamaulipas: Gómez Farías, L. Hernández 3003 (MEXU, XAL); Tula, G. Nelson 6030 (TEX), L. Hernández 1436 (TEX), L. Hernández 1469 (TEX); Victoria, L. Hernández 1521 (TEX), R. Runyon 905 (TEX), R. Runyon 909 (TEX). Veracruz: Agua Dulce, P. Tenorio 19567 (MEXU); Atzalan, F. Ventura 14366 (IEB, MEXU, XAL), F. Ventura 19555 (MEXU), F. Ventura 901 (ENCB), T. Krömer s.n. (MEXU, XAL); Catemaco, A. Torres 171 (MEXU), A. Torres 216 (MEXU), B. Allkin 84037 (XAL), C. Cowan 5796 (TEX), C. Gutiérrez 3106 (XAL), C. Gutiérrez 3112 (XAL), F. Ventura 12789 (MEXU, XAL), J. Gary 2048 (MEXU), M. Nee 22572 (XAL), R. Cedillo 2478 (MEXU), R. Cedillo 85 (MEXU), R.C. Trigos 85 (MEXU), S. Sinaca 768 (MEXU), S. Theodore S. 8602 (MEXU), T.B. Croat 100321 (MEXU); Coatzacoalcos, A.M. Hanan 1381 (MEXU), C.H. Ramos 2636 (MEXU), Idalia 18 (MEXU, XAL), Nevling 2545 (MEXU); Comapa, G. Castillo 1276 (XAL); Córdoba, F. Miranda 4837 (MEXU); Coxquihui, Mendoza- Evangelista s.n. (FCME), V. Evangelista 40 (MEXU); Emiliano Zapata, F. Ventura 3705 (ENCB); Hidalgotitlán, A. Juan 1 (IEB), A. Juan 1 (XAL), B. Dorantes 2875 (MEXU, XAL), B. Vázquez 196 (MEXU, XAL), B. Vázquez 432 (MEXU, XAL); Jalacingo, F. Ventura 19767 (ENCB, XAL); Jesús Carranza, L.I. Nevling 2597 (MEXU), W. Márquez 248 (XAL); Las Choapas, E. López 21 (MEXU, XAL), E. López 89 (MEXU, XAL), J. Dorantes 2292 (MEXU), R.A. Palestina 3512 (XAL); Meyacapan, G. Castillo 13215 (XAL), J.I. Calzada 12727 (XAL), J.L. Calzada 12727 (XAL); Minatitlán, G. Castillo 385 (IEB, XAL); Montepío, R. Cedillo 64 (TEX); Pánuco, R. Ramírez 7511 (IBUG); Puente Nacional, M. Cházaro 148 (MEXU), M.E. Medina 82 (IBUG, IEB, MEXU, XAL); San Andrés Tuxtla, A. Gentry 32305 (MEXU), A. Gómez-Pompa 4521 (MEXU), A. Gómez Pompa 3960 (XAL), A. Gómez Pompa 4490 (XAL), A. Lot 330 (MEXU), C. Ibarra 1986 (MEXU), CIP 494 (XAL), CIP 497 (XAL), F. Ventura 9963 (MEXU, XAL), G. Ibarra 2132 (ENCB, MEXU, XAL), G. Ibarra 2884 (MEXU, XAL), G. Martínez- Calderón 1488 (MEXU), G. Martínez 1488 (TEX), G.L. Webster 20936 (MEXU), H. Bravo s.n. (MEXU), H.E. Moore Jr. s.n. (MEXU), J.M. Poole 1445 (MEXU, TEX), M. Rosas 1214 (MEXU), M. Rosas 1238 (XAL), R. Cedillo 3091 (MEXU, XAL), R. Cedillo 64 (MEXU), R. Hernández 480 (MEXU), R. Hernández 555 (MEXU), R. Hernández 682

(MEXU), R.L. Dressles 128 (MEXU), Rico-Márquez 33 (MEXU), Rico-Márquez 44 (MEXU), Rico-Márquez 49 (MEXU), Rico-Márquez 78 (MEXU), Rico-Márquez 122 (MEXU), Rico-Márquez 155 (MEXU), S. Sinaca-Colín 1982 (MEXU), S. Sinaca 768 (XAL), S. Theodore S. 8602 (XAL); San Pedro Soteapan, J.I. Calzada 11403 (XAL), M. Leonti s.n. (IMSS, MEXU), R. Acosta 1562 (IEB, TEX), S. Mata 50 (IBUG, MEXU, XAL); Sanborn, C.R. Orcutt 3176 (TEX); Sontecomapan, J. Gary 2048 (XAL); Tecuatla, C. Gutiérrez 3257 (XAL); Tenampa, F. Ventura 8048 (IEB, MEXU, XAL); Teocelo, C. González 395 (FCME); Texistepec, C.H. Ramos 1006 (MEXU); Tezonapa, A.N. Leeds s.n. (TEX), E. Robles 231 (TEX, XAL), M.A. García 985 (XAL), R. Robles 231 (IBUG), R. Robles 483 (XAL), R. Robles 610 (XAL), R. Robles 699 (IBUG, MEXU, XAL); Tlapacoyan, F. Miranda 3328 (MEXU); Totutla, A. Espíritu 240 (XAL), F. Ventura 13949 (IEB, MEXU); Xalapa, K. Fabian 245 (XAL), L. Nevling 1518 (MEXU), M. Cházaro 2221 (IEB); Xico, J.J. Fay 786 (MEXU, XAL). Yucatán: José María Morelos, R. Duno 2207 (MEXU).

GUATEMALA. Alta Verapaz: Lanquín, K. Gould 53 (TEX), K. Gould 54 (TEX), K. Gould 55 (TEX); San Bartolomé de las Casas, E. Contreras 4222 (TEX); San Pedro Carchá, E. Contreras 4791 (TEX); Senahú, K. Gould 58 (TEX), K. Gould 59 (TEX). Baja Verapaz: La Unión Barrios, C.L. Lundell 19204 (TEX). Izabal: Chinebal, G.C. Jones 3426 (TEX); El Estor, E. Contreras 11434 (TEX); Sabana Arriba, J.A. Steyermark 41720 (TEX). Petén: Machaquila, E. Contreras 2169 (TEX), E. Contreras 2170 (TEX), E. Contreras 2813 (TEX); San Fernando, E. Contreras 3367 (TEX); San Luis, E. Contreras 2386 (TEX). Quetzaltenango: Nahuala, K. Gould 20 (TEX); Retalhueu, K. Gould 23 (TEX).

Costa Rica. Puntarenas: Golfito, D. Goldman 1543 (TEX), K. Gould 162 (TEX). San José: Rofeo, O. Dobbeler 1648 (MEX).

HONDURAS. Atlántida: Agua Blanca, D. Hunt 163 (TEX). Colón: Trujillo, J. Saunders 198 (TEX). Copán: Fraternidad, J.M. Poole 900 (TEX). Cortez: Omoa, P.H. Gentle 5008 (TEX). Francisco Mozarán: Nueva Armenia, P.H. Gentle 4672 (TEX). Olancho: Silca, P.H. Gentle 6990 (TEX).

EL SALVADOR. Morazán: Los Cimientos, J.M. Tucker 632 (TEX).

NICARAGUA. Managua: Granada, A. Molina 27274 (US).

PANAMA. Bocas del Toro: Buenas Esperanzas, P.M. Peterson 6946 (US). Colón: Bajo de la Pava, M. Huft 1626 (TEX).

***Spigelia loganioides*** (Torr. & A. Gray in Endl.) A. DC., Prodr. [A. P. de Candolle] 9: 4 (1845). TYPE: U.S.A. Florida: Marion Co., near Fort King, without date, *J.E. Burrows & Lt.B. Alden s.n.* (holotype: NY00180342!, isotype: NY00180341!).

≡ *Coelostylis loganioides* Torr & A. Gray in Endl., Nov. Stirp. Dec. 33 (-34) (1839).

**Description**

Herbs branched, stem cylindrical, glabrous, without lignification. Leaves pseudoworled under the inflorescence, sessile, lamina elliptic-lanceolate, membranaceous, 3.5-4.5 cm long. Stipule present, deltate. Inflorescence terminal, monochasium cyme, 2-4 flowers, pedicelate (FI. 11-F). Sepals green, linear. Corolla infundibuliform, 1.6-2 cm long, tube white, lobes white with pink lines, lobes lanceolate. Stamens insert above half the tube of the corolla, included, filament present. Pollen not seen. Stigma terete. Capsules glabrous, 3.5-5.5 mm diameter; metastyle present, same size as the capsule; carpoatlas oblong (Fig. 11-G), transversal ridge absent. Seeds 8, testa reticulate.

**Distribution and habitat**

Endemic to the United States of America (Fig. 12). It inhabits moist forests, watersheds, and floodplain swamps (Gould, 1997). Registered from sea level to 100 m elevation.

**Conservation status**

Least concern (LC). *S. loganoides* is widely distributed in the United States of America. Although its area of occupation is not very extensive (AOO= 15,000.00 km$^2$), it is distributed in several states with abundant populations.

**Taxonomic remarks**

*S. loganioides* is similar in vegetative and floral characters to *S. humboldtiana*. It can be distinguished from this by monochasium inflorescences (*vs.* scorpioid cymes), terete stigma (*vs.* capitate stigma), and oblong carpoatlas without transverse crest (*vs.* elliptic carpoatlas with transverse crest).

**Specimens examined**

UNITED STATES OF AMERICA. Florida: Levy, D. Goldman 433 (TEX), K. Gould 128 (TEX), K. Gould 129 (TEX), K. Gould 130 (TEX), K. Gould 149 (TEX), S.L. Orzell 21694 (TEX); Marion, K. Gould 133 (TEX), K. Gould 153 (TEX); Sumter, K. Gould 151 (TEX). Maryland: Prince Georges, K.M. Van Neste 593 (US). Texas: Brazoria, E.P. Killip 42115 (US); Columbia, B.F. Bush 1288 (US); Matagorda, E.J. Palmer 9642 (US).

***Spigelia longiflora*** M. Martens & Galeotti, Naturaleza (Mexico City) ser. 2, 2, app. 34 (1893). TYPE: MEXICO: Hidalgo: les environs de Regla, pres Real del Monte, Sep-1835, *H.G. Galeotti 1477* (holotype: BR).

*Spigelia longiflora* Sessé & Moc. n*om. ileg.*, Bull. Acad. Roy. Sci. Bruxelles xi. I. (1844) 376. TYPE: Mexico: Veracruz: Habitat in Olivo de Maltrata, *M. Sessé & J.M. Mociño s.n.* (holotype: BM).

**Description**

Herbs not branched, stem cylindrical, pubescent, without lignification. Leaves opposite under the inflorescence, sessile, lamina ovate-elliptic, membranaceous, 6.3-15.75 cm long. Stipule present, linear. Inflorescence terminal, scorpioid cyme, 5-12 flowers, pedicelate (Fig. 13-A). Sepals green, lanceolate. Corolla hypocrateriform, 4.9-5.5 cm long, tube and lobes red, lobes lanceolate. Stamens insert above half the tube of the corolla, exert, filament present. Pollen oblate-spheroidal, with medium polar area, 3 simple apertures, without margo on the colpi. Stigma capitate, style pubescent. Capsule glabrous, 7-8.5 mm diameter; metastyle present, longer than the capsule; carpoatlas elliptic (Fig. 13-B), transversal ridge present. Seeds semi-spheric, testa reticulate (Fig. 13-C).

**Distribution and habitat**

Endemic species of Mexico (Fig. 14). It inhabits coniferous and Quercus forests, tropical deciduous forest, and scrub. Registered between 1100 to 2900 m elevation.

**Conservation status**

Least concern (LC). This species has a wide distribution in several states of Mexico, covering an AOO of 50,000 $km^2$. *S. longiflora* has been collected from numerous populations in recent years. Therefore, it is not considered under any type of threat.

**Taxonomic remarks**

*Spigelia longiflora* it can be confused with *S. speciosa*, mainly because of the shape of the leaves. In collections, these species are often wrong determined. However, they can be easily distinguished by the branched inflorescences (*vs.* solitary inflorescences) and corollas with red tube and lobes (*vs.* corollas with red tube and green-yellow lobes).

**Specimens examined**

MEXICO. Guanajuato: Xichú, E. Ventura 9191 (IEB, MEXU, XAL). Hidalgo: Huejutla de Reyes, J. Salazar 5 (MEXU); Jacala de Ledesma, E. Lyonnet 1301 (IEB); Jacala de Ledezma, E. Lyonnet 1301 (MEXU); Mineral del Chico, E. Berthris 99 (MEXU), E. Lyonnet 99 (IEB), H. Sánchez 2776 (MEXU), I. Berlín 25 (ENCB), IMN 5 (MEXU), J. Rzedowski 36318 (ENCB, XAL), M. Contreras 6 (MEXU), M. Medina 2090 (IBUG, MEXU), M.A. Villavicencio s.n. (FCME), P. Lamy 222 (IMSS, MEXU), X. Madrigal S. 1476 (MEXU); Tianguistengo, R. Hernández 6902 (MEXU); Tlanchinol, I. Luna 298 (FCME), O. Alcántara 3153 (FCME); Zacualtipán de Ángeles, F. Miranda 3260 (MEXU), F. Miranda 3280 (MEXU), J.L. López 146 (MEXU). Jalisco: Autlán de Navarro, V. Santos 81 (INEGI). Morelos: Tepoztlán, L. Hernández 3993 (MEXU, QMEX). Puebla: Cuautempan, G. Toriz 547 (MEXU); Nicolás Bravo, A. Mayfield 951 (MEXU, TEX); Tepanco de López, C.E. Smith 3927 (US); Tepetzintla, A. Campos 498 (MEXU), P. Tenorio 13853 (MEXU, UAMIZ); Teziutlán, D. Gold 291 (MEXU), D. Gold 306 (MEXU). Querétaro: Arroyo Seco, J. Treviño 639 (QMEX); Cadereyta de Montes, R. Hernández 11644 (MEXU, QMEX); Ezequiel Montes, H. Díaz Barriga 4941 (IEB); Jalpan de Serra, B. Servín 1182 (IEB, QMEX, TEX), B. Servín 221 (CIIDIR, IEB, MEXU, QMEX, XAL), R. Fernández 4578 (ENCB); Landa de Matamoros, E. González 26 (ENCB, IEB), E. González 582 (ENCB, IEB, QMEX), E.M. Lira 1406 (INEGI, MEXU), G. Campo 897 (MEXU), G. Ocampo 897 (IEB), H. Díaz Barriga 3865 (IEB, MEXU, QMEX), H. Rubio 133 (IEB, MEXU, QMEX, XAL), H. Rubio 1659 (IEB, MEXU, QMEX), H. Rubio 1737 (IEB, QMEX), H. Rubio 2514 (IEB, MEXU, QMEX, XAL), H. Rubio 574 (CIIDIR, IBUG, IEB, MEXU, QMEX), H. Rubio 917 (IEB, MEXU), J. Rzedowski 10916 (ENCB), J. Rzedowski 44074 (ENCB, IBUG, IEB), J. Rzedowski 44080 (ENCB, IBUG, IEB), J. Rzedowski 444080 (CIIDIR), J. Rzedowski 46721 (IEB, MEXU), J. Rzedowski 9308 (IEB), R. Fernández 4114 (ENCB), S. Zamudio 9922 (IEB, MEXU, QMEX, XAL); Pinal de Amoles, B. Córdova 661 (CIIDIR), E. Carranza 674 (IEB, MEXU), N.B. Medina 206 (IEB, MEXU, TEX); San Joaquín, R. Hernández 10942 (QMEX). San Luis Potosí: Las Magdalenas, J. Rzedowski 7689 (CIIDIR); Río Verde, J. Rzedowski 7689 (IBUG, IEB, MEXU, OAX); San Luis Potosí, J. Rzedowski 9308 (MEXU); Zaragoza, P. Castillo L. 1001 (FCME). Veracruz: Acultzingo, F. Ventura 15436 (IEB, MEXU, OAX, XAL); Ciudad Mendoza, H. Oliva s.n. (IBUG); Huayacocotla, L. Ballesteros 226 (MEXU, XAL), R. Ortega 2673 (XAL), Y.A. Vargas 343 (MEXU); Maltrata, E. Matuda 1302 (MEXU).

***Spigelia marilandica*** (L.) L., Syst. Nat., ed. 12. 2: 734 (1767).
TYPE: U.S.A. Virginia: *J. Clayton s.n.* (lectotype: BM98044!, lectotype designated by Reveal & Jarvis (2009, p.978)).

≡ *Lonicera marilandica* L. (1753, p.175). *Spigelia lonicera* Mill., Sp. Pl. [Linnaeus] 1: 175 (1753).
= *Spigelia marilandica* forma *eburnea* Van Horn & Freeman, Sida 11: 248 (-249) (1985). TYPE: U.S.A. Tennessee: Hamilton Co., Chattanooga, growing among oaks, hickories and dogwoods in lot adjacent to 3116 Lockwood Drive, 260m, 19 May 1982, *J.R. Freeman 1* (holotype: NCU0593!).

**Description**

Herbs branched, stem quadrangular, glabrous, without lignification. Leaves opposite under the inflorescence, sessile, lamina ovate-lanceolate, membranaceous, 6-10 cm long. Stipule present, linear. Inflorescence terminal, scorpioid cyme, 3-12 flowers, sessile (Fig. 13-D). Sepals green with purple apex, lanceolate. Corolla infundibuliform, 5.5-6 cm long, tube and lobes red, lobes lanceolate. Stamens insert above half the tube of the corolla, exert, filament present. Pollen not seen. Stigma capitate, style pubescent. Capsule glabrous, 7-8 mm diameter; metastyle present, longer than the capsule; carpoatlas elliptic (Fig. 13-E), transversal ridge present. Seeds 8, ovate, testa reticulate (Fig. 13-F).

**Distribution and habitat**

Endemic species of the United States of America (Fig. 14). It inhabits the margins of forests (Gould, 1997), between 50 and 730 m elevation.

**Conservation status**

Least concern (LC). *Spigelia marilandica* is one of the endemic species of the United States of America with the largest distribution, covering an AOO of 200,000.00 $km^2$, as well as the most collected in the country. Therefore, it is not considered under any category of threat.

**Taxonomic remarks**

*Spigelia marilandica* is similar to *S. speciosa* in floral characters, because of the species distributed in the NA region, they are the only ones with corollas of red tubes and yellow petal lobes. However, these can be distinguished by green sepals with purple apex, capitate stigma and straight petal lobes in *S. marilandica*, versus entirely green sepals, terete stigma with pubescent style and reflexed petal lobes in *S. speciosa*. Likewise, the disjunct distribution of both species allows us to identify them as different taxa.

**Specimens examined**

UNITED STATES OF AMERICA. Alabama: Birmingham, S.B. Bucley s.n. (MEX); Chilton, C.L. Pollard 267 (US); Madison, R. Kral 92807 (US); Mobile, A. Winchell s.n. (US), C. Mohr s.n. (US). Arkansas: Chicot, R.D. Thomas 166040 (TEX); Cleburne, D. Demaree 30478 (MEX, TEX); Fort Smith, J.M. Bigelow s.n. (US); Lee, R. Kral 61820 (TEX); Marion, D.M. Moore s.n. (TEX); Polaski, H.E. Hasse 1886 (US); Polk, L.J. Dorr 1922 (TEX), R. Kral 88587 (TEX); Pulaski, J. Kessler 7096 (TEX); Sharp, D. Demaree 27736 (TEX). Carolina del Sur: Beaufort, J.H. Mellichamp 1170 (US), J.H. Mellichamp 413 (US); Berkeley, M.E. Hyams s.n. (US); Charleston, E.A. Mearns 37 (US); Columbia, K.M. Van Neste 720 (US); Oconee, H.D. House 2139 (US); Pickens, L. Rodgers 563 (TEX), S. Leonard 4865 (MEX, TEX); Seneca, G.M. McCarthy s.n. (US); Williamsburg, R.K. Godfrey 455 (US). Florida: Dade, R. Kral 51823 (TEX);

Jackson, K. Gould 163 (TEX). Georgia: Burke, L. Ellison 1003 (MEX, TEX); Clay, R. Thorne 3710 (US); Clayton, R.M. Harper 234 (US); Dade, A. Cronquist 5131 (US), W. Duncan 5395 (TEX); DeKalb, P. Wilson 50 (US); Gwinnet, H.A. Allard 190 (US), H.A. Allard 191 (US), H.A. Allard 192 (US); Lookout Mountain, A. Ruth 461 (US); Savannah, W.M. Canby s.n. (US); Toccoa, J.L. Peters 8 (US); Walton, A. Cronquist 5199 (US); Warm Springs, M. Tracy 9233 (TEX), S.M. Tracy 9233 (US); Wilcox, R.M. Harper 2209 (US). Kentucky: Allen, F.T. McFarland 94 (US); Estill, W.A. Anderson 43 (US); Perlaski, B.W. Evermann s.n. (US); Wayne, E.L. Braun 1044 (US), L.B. Smith 3896 (US). Louisiana: Acadia, N. Rich 1886 (MEX); Covington, G. Arsene 12406 (US); Lincoln, J.A. Moore s.n. (US); Lincoln, J. Moore s.n. (TEX); Pineville, E.C. Leonard 1561 (US); Rapides, S. Orzell 7070 (TEX); Shreveport, H.C. Benke 5539 (US); Winn, R.D. Thomas 154053 (TEX). Maryland: Baltimore, G. McCarthy s.n. (TEX). Mississippi: Amite, J. Pruski 2106 (TEX, US); Attala, C.A. Weatherby 6299 (US); Copiah, F.A. Cook s.n. (US); Lafayette, E.A. Smith s.n. (US); Lincoln, M.B. Flint 128 (US); Madison, W.B. McDougall 1298 (US); Natchez, J. Blake s.n. (US); Oktibbeha, S.M. Tracy 1354 (US). Missouri: Holcomb, B.F. Bush 280 (US), B.F. Bush 354 (US), B.F. Bush 6372 (US). Oklahoma: Durant, W.L. Blain 125 (US); Le Flore, E.J. Palmer 8274 (US); Leflore, O.W. Blakley 1430 (US); McCurtain, D. Demaree 12647 (US). Tennessee: Camden, J.R. Swallen 2037 (US); Chattanooga, J.R. Churchill s.n. (US); Davidson, S. Batson 23 (TEX); Gatlinburg, C.D. Walcott s.n. (US), E.H. Walker 1506 (US); Hamilton, V.E. McNeilus s.n. (MEX); Haywood, V.E. McNeilus s.n. (MEX, TEX); Jackson, V.E. McNeilus s.n. (MEX); Knox, P. Mowery s.n. (MEX); Knoxville, F. Lamson-Scribner s.n. (US); Lewis, A. Mayfield 546 (TEX); Nashville, A. Gattinger 2260 (US); Overton, V.E. McNeilus s.n. (MEX); Polk, T. Calfee s.n. (TEX). Texas: Bowie, D.S. Correll 18856 (TEX), D.S. Correll 31262 (TEX); Butter, H. Eggert s.n. (TEX); Jasper, J.R. Crutchfield 2571 (TEX); Red River, W.C. Holmes 11472 (TEX); Sabine, R. McVaugh 8414 (TEX); San Agustine, D.S. Correll 26278 (TEX), D.S. Correll 37208 (TEX), K. Gould 1 (TEX); Tarrant, A. Ruits s.n. (TEX).

***Spigelia mexicana*** A. DC., Prodr. [A. P. de Candolle] 9: 7 (1845).

TYPE: MEXICO:, sin fecha, *J.A. Pavón s.n.* (lectotype: G00368297!, lectotype designated by McVaugh (2000, p.351)).

**Description**

Herbs not branched, stem quadrangular, glabrous, without lignification. Leaves pseudowhorled under the inflorescence, sessile, lamina ovate-elliptic, membranaceous, 4.9-12 cm long. Stipule present, linear. Inflorescence axillary, scorpiod cyme, 4-6 flowers, pedicelate (Fig. 13-G). Sepals green, triangular. Corolla tubular, 2-3.8 cm long, tube and lobes red, lobes ovate. Stamens insert above half the tube of the corolla, included, filament present. Pollen oblate, with medium polar area, 3 simple apertures, without margo on the colpi. Stigma capitate, style glabrous. Capsule glabrous, 6.5-9 mm diameter; metastyle present, longer than the capsule; carpoatlas oblong (Fig. 13-H), transversal ridge present. Seeds trulate-ovoid, testa foveolate (Fig. 13-I).

**Distribution and habitat**

Endemic species of Mexico (Fig. 14). It lives in tropical deciduous and sub-deciduous forest. It is found from 1,000 to 2,500 m elevation.

**Conservation status**

Least concern (LC). This species is found distributed in an area of about 11,000.00 $km^2$ (AOO), in Mexico. Although several populations are known, and GeoCAT analysis places it in Least Concern (LC) category, the species has not been collected in over 15 years. This is mainly due to the fact that they are found in areas of difficult access, for which the populations could currently remain stable.

**Taxonomic remarks**

This species is morphologically similar to *S. splendens*, by the shape of the leaves and shape and color of the corollas, in addition to having a sympatric distribution. *Spigelia mexicana* can be distinguished by the sessile leaves (*vs.* petiolate leaves in *S. splendens*), axillary inflorescences with fewer flowers (*vs.* always terminal inflorescences, with greater number of flowers).

**Specimens examined**

MEXICO. Guerrero: Ahuacotzingo, M. Martínez 56 (FCME, HUAP, MEXU); Chilpancingo de los Bravo, R. Cruz-Durán 4764 (FCME, MEXU); Eduardo Neri, J. Jiménez 1136 (FCME, MEXU); Minatitlán, G.B. Hinton 10487 (TEX). Oaxaca: San Miguel del Puerto, F. López 161 (IEB). Puebla: Tepetzintla, P. Tenorio 13853 (MEXU).

***Spigelia mocinoi*** S. Islas & L.O. Alvarado, Phytotaxa 331(2): 247 (2017).
TYPE: MEXICO: Estado de México: Ixtapan de la Sal, Temascaltepec, 18-Jul-1935, *G.B. Hinton 8063* (holotype: MEXU102425!; isotype: ENCB!, HUMO!).

= *Bouvardia amplexicaulis* Borhidi et E. Martínez, Acta Bot. Hung. 53(1-2): 64 (-66; fig. 1) (2011), non *Spigelia amplexicaulis* E.F. Guim. & Fontella (1969). TYPE: Mexico. Edo. Mexico, Santiago Amatepec, ladera húmeda, rocosa, barranca. Alt.:1300 m, 13 Jul 1970, *E. Matuda 38039* (holotype: MEXU-133854!).

**Description**

Herbs not branched, stem cylindrical, pubescent, without lignification. Leaves opposite under the inflorescence, sessile, lamina ovate-lanceolate, membranaceous, 2.9-3.3 long. Stipule absent. Inflorescence terminal, scorpioid cyme, 3-5 flowers, pedicelate (Fig. 15-A). Sepals green, linear. Corolla hypocrateriform, 10 cm long, tube and lobes white, lobes elliptic. Stamens insert above half the tube of the corolla, included, filament present. Pollen oblate, with medium polar area, 3 simple apertures, without margo on the colpi. Stigma capitate, style pubescent. Capsule not seen. Seeds not seen.

**Distribution and habitat**

Endemic to Mexico (Fig. 14), growing in tropical deciduous forest and registered between 1000 to 1300 m elevation.

**Conservation status**

Endangered (EN). This species is only known from the type specimen collected about 50 years ago, so the category of endangered is suggested.

**Taxonomic remarks**

This species is very similar to *S. nicotianiiflora* and *S. ayotzinapensis*. These species had been considered as a single taxon, *S. nicotianiiflora*, based on their general appearance. However, it can be recognized by morphological and geographical attributes (see *S. ayotzinapensis*). Unlike *S. nicotianiiflora*, *S. mocinoi* is non-rhizomatous plant (*vs.* rhizomatous plants), inflorescences with 3-5 flowers (*vs.* 8-9 flowers) and corolla lobes 1.9-2 × 1 cm (vs 0.9-1.6 × 0.4-0.5cm). Another important attribute that shows the differences between both taxa is the pollen grains, mainly in size and type of ornamentation. *S. mocinoi* presents a more complex sculpture, with rugulae, gems and verrucae ornamentation concentrated in the apocolpium and only rugulae in the mesocolpium, while *S. nicotianiiflora* presents homogeneous rugulae in both the apocolpium and the mesocolpium. Likewise, the distribution of the *S. mocinoii* with respect to *S. nicotianiiflora*¸ marks an important biogeographic separation, from Paraguay to Mexico, where there are numerous barriers that restrict the distribution area of each of the species.

**Specimens examined**

MEXICO. Estado de Mexico: Amatepec, E. Matuda 38039 (TEX); Ixtapan de la Sal, G.B. Hinton 8063 (ENCB, HUMO), H. Kruse 8063 (MEXU); Temascaltepec de González, H. Kruse 4469 (TEX, US).

***Spigelia polystachya*** Klotzsch ex Progel, Fl. Bras. 6(1): 265.

TYPE: GUYANA: Guyana britanicae regione, 1840, *R.H. Schomburgk 412* (holotype: G; isotype: B).

≡ *Pseudospigelia polystachya* (Klotzsch ex M.R. Schomb) W. Klettt, Bot. Arch. 3: 136 (1923).

**Description**

Herbs not branched, stem quadrangular, glabrous, without lignification. Leaves opposite under the inflorescence, sessile, laminas linear, papyraceous, 2-5 cm long. Stipule present, deltate. Inflorescence axilar, scorpioid cyme, 6-19 flowers, pedicelate (Fig. 15-B). Sepals green, deltate. Corolla campanulate, 1.5-3 cm long, tube and lobes white, lobes ovate. Stamens insert half the tube of the corolla, included, filament absent. Pollen suboblate, with medium polar area, 3 simple apertures, with margo on the colpi. Stigma terete, style pubescent. Capsule glabrous, 2-2.7 mm diameter; metastyle absent; carpoatlas quadrangular (Fig. 15-C), transversal ridge absent. Seeds ovate-compressed, testa rugose (Fig. 15-D).

**Distribution and habitat**

Distributed in Belize, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, and Nicaragua (Fig. 16; Fernández-Casas & Huft, 2009). Outside the study area its distributed in Brazil, Guiana, and Venezuela (Fernández-Casas & Huft, 2009). It inhabits thorny forest, humid tropical forest, and grasslands. Recorded between 10 and 250 m elevation.

**Conservation status**

Least concern (LC). *Spigelia polystachya* is widely distributed in southern Mexico and in several Central American countries, covering an area of 25,000.00 $km^2$. Likewise, the species has been collected from abundant populations in recent years, so it is not considered endangered.

**Taxonomic remarks**

*S. polystachya* is one of the smallest plants in the genus, along with *S. pygmaea* and *S. queretarensis*. It is distinguished from *S. pygmaea* by its smaller, lanceolate (*vs.* ovate), opposite leaves below the inflorescence (*vs.* pseudowhorled leaves below the inflorescence), and smooth capsules (*vs.* apically papillose capsules). From *S. queretarensis* it is distinguished by the shape of the leaves, papyraceous (*vs.* oblong, membranous leaves), inflorescences with up to 19 flowers (*vs.* monochasium with 1-3 flowers), campanulate corolla (*vs.* hypocrateriform), as well as capsules metastyle absent (*vs.* metastyle 2-3 mm long). In herbaria, this species has been confused with *S. anthelmia*. This may be due to the lanceolate shape of the leaves, but they can be easily distinguished by the size of the plant and the ornamentation of the capsules.

**Specimens examined**

MEXICO. Campeche: Campeche, C. Gutiérrez 5901 (CICY, MEXU, UAMIZ, XAL); Hopelchén, D. Álvarez 10252 (MEXU), D. Álvarez 10260 (MEXU), D. Álvarez 10307 (IBUG, MEXU), D. Álvarez 8880 (MEXU), D. Álvarez 9106 (MEXU). Tabasco: Centro, A. Sol 174 (MEXU); Nacajuca, C. Cowan 2366 (ENCB, XAL). Veracruz: Paso de Ovejas, F. Ventura 18063 (IEB); Puente Nacional, F. Ventura 10876 (ENCB), F. Ventura 9061 (MEXU, XAL).
GUATEMALA. Petén: Cedral, J.A. Steyermark 46024 (TEX), J.A. Steyermark 46148 (TEX); El Chal, J.A. Steyermark 46024 (US), J.A. Steyermark 46148 (US); Sayaxché, C.L. Lundell 18220 (TEX).

***Spigelia pygmaea*** D.N. Gibson, Fieldiana, Bot. 32: 5, fig (1968).
TYPE: GUATEMALA: Petén: in savanna ca. 7 km W of village in zapotal, on La Gloria road, Dos Lagunas, 19-Oct-1960, *E. Contreras 1537* (holotype: LL256903!; isotype F1652726!).

**Description**

Herbs not branched, stem quadrangular, glabrous, without lignification. Leaves pseudowhorled under the inflorescence, petiolate, lamina ovate, membranaceous, 6 cm long. Stipule present, deltate. Inflorescence terminal, scorpioid cyme, 10-15 flowers, pedicelate (Fig. 15-E). Sepals green with purple margin, deltate. Corolla campanulate, 1-3 cm long, tube and lobes white, lobes deltate. Stamens insert half the tube of the corolla, included, filament absent. Pollen suboblate, with large polar area, 3 simple apertures, with margo on the colpi. Stigma capitate, style pubescent. Capsule pubescent, 1.8-2.5 mm diameter; metastyle absent; carpoatlas oblong (Fig. 15-F). transversal ridge absent. Seeds quadrangular-compress, testa rugose (Fig. 15-G).

**Distribution and habitat**

Species distributed in Guatemala and Mexico (Fig. 16). It lives in tropical deciduous and sub-deciduous forest. It is found between 50 and 850 m elevation.

**Conservation status**

Least concern (LC). *S. pygmaea* is distributed in an area of about 30,000.00 km2 AOO in Guatemala and Mexico. Several abundant populations are known in the different states, and it has been collected regularly in recent years. Therefore, it is not considered under any category of threat.

**Taxonomic remarks**

The individuals of this species are easily recognizable for being small plants, less than 10 cm tall, like *S. polystachya* and *S. queretarensis*. It presents apically papillose capsules, for which it can be related to *S. anthelmia* (Gould, 1997), in addition to presenting pseudowhorled leaves under the inflorescence. However, it is distinguished from this by the ovate shape of the leaves (*vs.* lanceolate leaves), smaller in size, as well as the carpoatlas with rounded margins (*vs.* margins with acuminate tips).

**Specimens examined**

MEXICO. Campeche: Calakmul, D. Álvarez 6699 (MEXU); Campeche, B. Fausty 941 (CICY), C. Gutiérrez 8355 (CICY), C. Gutiérrez 8720 (MEXU, XAL), C. Gutiérrez 8723 (CICY, MEXU, XAL); Champotón, G. Carnevali 4672 (CICY, MEXU); Hopelchén, E. Martínez 38272 (MEXU), G. Carnevali 5663 (CICY, MEXU, XAL). Chiapas: San Fernando, D.E. Breedlove 39969 (MEXU). Quintana Roo: José María Morelos, D. Álvarez 10389 (MEXU), D. Álvarez 10501 (IBUG, MEXU), D. Álvarez 9682 (MEXU), E. Martínez 38083 (MEXU); Othón P. Blanco, G. Carnevali 5590 (CICY, MEXU). Yucatán: Santa Elena, G. Carnevali 6408 (CICY).

GUATEMALA. Petén: Dolores, E. Contreras 3071 (TEX); Dos Lagunas, E. Contreras 1537 (TEX).

***Spigelia queretarensis*** Fern. Casas, Fontqueria 55(65): 528 (-530; figs. 2-4, map) (2008).

TYPE: MEXICO: Querétaro: La Parada, ca. 3 km al S, 20-Ago-1988, *E. Carranza 809* (holotype: IEB198324!).

**Description**

Herbs not branched, stem quadrangular, glabrous, without lignification. Leaves opposite under the inflorescence, sessile, lamina oblong, membranaceous, 2.3 cm long. Stipule present, deltate. Inflorescence terminal, monochasium cyme, 1-3 flowers, pedicelate (Fig. 17-A). Sepals green, linear. Corolla infundibuliform, 1.5-2.5 cm long, tube white with purple lines, lobes white with purple margin, lobes lanceolate. Stamens insert half the tube of the corolla, included, filament absent. Pollen oblate-spheroidal, with medium polar area, 3 simple apertures, without margo on the colpi. Stigma capitate, style glabrous. Capsule glabrous, 5 mm diameter; metastyle present, longer than the capsule; carpoatlas oblong, transversal ridge absent. Seeds semi-spheroidal, testa tuberculate (Fig. 17-B).

**Distribution and habitat**

Endemic species of Mexico (Fig. 16). It lives in *Quercus* forest and between 1,200 to 1,700 m elevation.

**Conservation status**

Critically endangered (CR). This species is known only from the type specimen and a population collected in a nearby area. The analysis carried out from these data places it under a category of critical danger.

**Taxonomic remarks**

This species can be confused with *S. polystachya* due to the size of the plants, sessile leaves, all opposite, triangular stipules, and smooth capsules. They can be distinguished by oblong leaves (*vs.* lanceolate), inflorescences with 1-3 flowers (*vs.* 19), hypocrateriform corolla (*vs.* campanulate). In addition to its distribution, since *S. polystachya* is widely distributed in Belize, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, and Nicaragua, while *S. queretarensis* is restricted to the state of Querétaro in Mexico.

**Specimens examined**

MEXICO. Querétaro: Jalpan de Serra, E. Carranza 809 (IEB); Landa de Matamoros, S. Zamudio 14782 (IEB).

***Spigelia scabrella*** Benth., Pl. Hartw. [Bentham] 45 (1840).

TYPE: MEXICO, 1837, *K.T. Hartewg 346* (holotype: P507551!).

**Description**

Herbs not branched, stem quadrangular, pubescent, without lignification. Leaves opposite under the inflorescence, sessile, lamina ovate, membranaceous, 2.1-4.3 cm long. Stipule present, linear. Inflorescence terminal, monochasium cyme, 1-3 flowers, pedicelate (Fig. 17-C). Sepals green, lanceolate. Corolla infundibuliform, 4.5-6 cm long, tube and lobes purple, lobes ovate. Stamens insert half the tube of the corolla, included, filament present. Pollen sub-oblate, with medium polar area, 3-4 simple apertures, without margo on the colpi. Stigma capitate, style glabrous. Capsule glabrous, 7-8 mm diameter; metastyle present, smaller than the capsule; carpoatlas oblong (Fig. 17-D), transversal ridge present. Seed ovate, testa reticulate (Fig. 17-E).

**Distribution and habitat**

Endemic to Mexico (Fig. 16). It lives in coniferous and *Quercus* forest and found between 1000 and 2500 m elevation.

**Conservation status**

Least concern (LC). *S. scabrella*, is one of the species with the largest distribution area in the country with 102,500.00 $km^2$ of AOO, in addition to one of the most collected for its striking pink or purple flowers. Numerous abundant populations are known in different states of Mexico and have been collected repeatedly in recent years. Therefore, it is not considered under any type of threat.

**Taxonomic remarks**

This species is similar to *S. guerrerensis* due to the shape and size of the leaves, as well as the infundibuliform corolla. It can be distinguished by the purple corolla, glabrous style, and apically smooth capsules. In addition to presenting a wide distribution towards northwestern Mexico, while *S. guerrerensis* is restricted to the southwestern region of the country.

**Specimens examined**

MEXICO. Durango: Mezquital, J.G. González-Galegos 1874 (CIIDIR). Estado de Mexico: Tejupilco, E. Guizar 610 (MEXU); Temascaltepec de González, G.B. Hinton 1380 (MEXU, TEX); Tepotzotlán, F.J. Espinosa 644 (MEXU). Guanajuato: Juventino Rosas, J. Kishler 707 (MEXU), J. Rzedowski 43781 (CIIDIR, ENCB, IBUG, IEB), J. Rzedowski 53592 (CIIDIR, IEB, MEXU, XAL). Jalisco: Arandas, A. Delgado 266 (MEXU), R. Ramírez 2793 (IBUG); Autlán de Navarro, A. Leinberger 67 (IBUG), A. Mayfield 1051 (TEX), A. Rodríguez 931 (MEXU), A. Rodríguez 931 (IEB), F.J. Santana 3730 (MEXU), R. Kral 27646 (ENCB), R. Ramírez 157 (MEXU), R. Ramírez 1579 (IBUG, MEXU), R. Ramírez 3314 (IBUG); Ayutla, P. Carrillo-Reyes 6733 (IBUG); Casimiro Castillo, C. Anaya s.n. (IBUG); Chapala, Bárcena 626 (MEXU); Concepción de Buenos Aires, J. Villa 790 (IEB), L.M.V. De Puga 3955 (IBUG, MEXU); Cuautitlán, J.A. Pérez 196 (IBUG); Gómez Farías, F. Trujillo s.n. (IBUG); Guadalajara, C.G. Pringle 1899 (MEXU), E. Palmer 160 (IEB); Ixtlahuacán de los Membrillos, L.E. Detling 9568 (ENCB); Ixtlahuacán del Río, F.J. Santana 2834 (IBUG), R. Hernández 9480 (MEXU); Jocotepec, A. Machuca 6168 (IEB, XAL), D.P. Gregory 206 (MEXU), J.A. Machuca 6168 (IBUG), L.M.V. De Puga 495 (ENCB); La Coronilla, L.M.V. De Puga 16117 (IBUG); Mixtlán, J. González-Gallegos 1052 (IBUG); Poncitlán, L.M.V. De Puga 6403 (IBUG); San Cristóbal de la Barranca, P. Carrillo-Reyes 6994 (IBUG); San Juan de los Lagos, L.M.V. De Puga 495 (IBUG); San Martín de Bolaños, R. Ramírez 1453 (IBUG); San Martín de Hidalgo, J.J. Guerrero 283 (IBUG); San Sebastián del Oeste, R. Ramírez 5598 (IBUG); Tamazula, A.S. Garza 432 (IBUG, IEB), L.M.V. De Puga 5857 (IBUG); Tecalitlán, A. Frías 1651 (IBUG), McPherson 1132 (ENCB); Tenamaxtlan, J.A. Machuca 7154 (XAL), J.A. Machuca 7923 (IBUG, TEX, XAL); Tequila, R. González 253 (ENCB); Tlajomulco, J.A. Machuca 2855 (XAL); Tolimán, F.J. Santana 4568 (MEXU); Vallarta, L.M.V. De Puga 14394 (IBUG); Zapopan, A. Rodríguez 1387 (IBUG), F.J. Santana 2738 (IBUG, MEXU), L.M. González 3123 (IBUG), L.M.V. De Puga 15933 (IBUG, MEXU), M. Cházaro 4883 (IBUG), V. Álvarez 53 (IBUG). Michoacán: Acuitzio del Canje, H. Díaz Barriga 1319 (IEB), H. Díaz Barriga 2366 (IEB); Aguililla, M. Fishbein 5118 (MEXU); Ario, J. Rzedowski 53799 (IEB); Charo, E. Carranza 5635 (IEB, MEXU, XAL), J. Santos 2118 (ENCB, IEB), S. Zamudio 4144 (IEB, MEXU, XAL), S. Zamudio 8442 (IEB, MEXU); Coalcomán de Vázquez Pallares, H. Kruse 13982 (MEXU, TEX), H. Kruse 15000 (HUMO, TEX), H. Kruse 15043 (TEX); Cotija, I. García 3325 (IEB); Dos Aguas, M. Fishbein 5118 (IEB); Lagunillas, J.M. Escobedo 2082 (IEB, MEXU, XAL); Los Reyes, J.N. Labat s.n. (MEXU); Morelia, C. Medina 1304

(IEB, MEXU, XAL), E. Pérez 2190 (IEB, MEXU, TEX, XAL), E. Pérez 3653 (MEXU), E. Sánchez 73 (IEB, MEXU), G. Cornejo 2900 (FEZA, IEB, MEXU), G. Cornejo 3453 (IEB, MEXU), J. Rzedowski 39939 (CIIDIR, IBUG, IEB, MEXU, OAX, UAMIZ, XAL), J. Rzedowski 40138 (IEB, MEXU), J. Rzedowski 50723 (IEB), J. Santos 2207 (IEB), J.G. Arsene 6016 (MEXU), J.G. Arsene 2130 (MEXU), J.M. Escobedo 1644 (IBUG, IEB, MEXU, XAL), J.M. Escobedo 2339 (IEB), J.M. Escobedo 2519 (IEB), P. Carrillo-Reyes 6438 (IBUG, IEB), P. Carrillo-Reyes 6457 (IEB), S. Zamudio 14141 (IBUG, IEB, UAMIZ), S. Zamudio 4524 (IEB, MEXU), V.M. Huerta 559 (IEB, MEXU, XAL), V.W. Steinmann 2637 (IEB); Quiroga, C. López 1025 (IEB); Tacámbaro, J. Kishler 1088 (MEXU), J. Kishler 1146 (MEXU); Taretan, V.W. Steinmann 4570 (IEB), V.W. Steinmann 5447 (IEB); Tuxcueca, Y. Ramírez-Amezcua 652 (IEB); Tzitzio, G. Cornejo 3770 (IEB). Nayarit: Compostela, J. Rzedowski 14339 (ENCB). Querétaro: Arroyo Seco, J. Rzedowski 1930 (IEB). San Luis Potosí: Cárdenas, C.G. Pringle 3198 (IEB, MEXU, TEX). Sinaloa: San Ignacio, R. Vega 759 (MEXU). Zacatecas: García de la Cadena, P. Carrillo-Reyes 7420 (IBUG); Teul de González Ortega, P. Carrillo-Reyes 6116 (IBUG).

***Spigelia speciosa*** Kunth., Nov. Gen. Sp. [H.B.K.] iii. 186. t. 224.
TYPE: MEXICO: Distrito Federal (Ciudad de Mexico): Crescit prope urbem Mexici, sin fecha, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (holotype: P, isotype: UC1098134!, S03-2467!).

**Description**

Herbs not branched, stem quadrangular, pubescent, without lignification. Leaves opposite under the inflorescence, sessile, lamina ovate, membranaceous, 5-5.7 cm long. Stipule present, linear. Inflorescence terminal, scorpioid cyme, 7-18 flowers, pedicelate (Fig. 17-F). Sepals green, linear. Corolla infundibuliform, 7-8.5 cm long, tube red, lobes yellow, lobes lanceolate. Stamens insert above half the tube of the corolla, exert, filament present. Pollen suboblate, with medium polar area, 3 simple apertures, without margo on the colpi. Stigma terete, style pubescent. Capsule glabrous, 4.5-7.6 mm diameter; metastyle present, longer than the capsule; carpoatlas elliptic (Fig. 17-G), transversal ridge present. Seeds semi-spheric, testa reticulate (Fig. 17-H).

**Distribution and habitat**

Endemic species of Mexico (Fig. 20). It lives in coniferous and *Quercus* forest. Recorded between 1,500 and 2,700 m elevation.

**Conservation status**

Least concern (LC). This species is found in various states of Mexico. Together the populations reach an area of 30,000.00 $km^2$ (AOO). It is one of the most collected species, due to its striking red flowers with large green lobes, so there is a lot of information about the populations and their abundance. They have also been collected in different locations in recent years.

**Taxonomic remarks**

This species is similar to *S. chiapensis* by the flowers shape and color, but *S. speciosa* is easily differentiated by its absent peduncles (*vs.* 2-2.5 cm), longer sepals (*vs.* shorter sepals), lobes of the corolla incurvate (*vs.* lobes of the corolla straight), and green corolla lobes (*vs.* yellow). Likewise, *S. chiapensis* is mainly distributed in grasslands and areas with greater exposure to light (Gould, 1997), while *S. speciosa* is preferably found in coniferous and cloudy mountain forests. It also shares similarities with *S. marilandica*, but its distribution and floral characters (see taxonomic remarks of the species) allow them to be easily differentiated.

**Specimens examined**

MEXICO. Guerrero: Atoyac de Álvarez, Lab. De Biogeografía 144 (FCME); Chilpancingo de los Bravo, A. Mendez 426 (FCME), H. Kruse 1807 (MEXU), H. Kruse s.n. (MEXU), W. Thomas 3709 (FCME, TEX); General Heliodoro Castillo, L. Hernández 2460 (MEXU, QMEX, TEX), R. Cruz-Durán 3892 (FCME, MEXU), R. Cruz-Durán 4045 (FCME, HUMO, MEXU); Leonardo Bravo, A. Mayfield 991 (MEXU, TEX), B. González 1840 (FCME), L.M. González 5059 (IBUG), R. Cruz-Durán 1145 (FCME, MEXU), R.M. Fonseca 2743 (FCME); Mina, H. Kruse 10371 (TEX); Quechultenango, G. Zamudio 599 (ENCB, FCME, IEB, MEXU); Taxco de Alarcón, S. Valencia 55 (ENCB, FCME); Tixtla de Guerrero, A. Hernández 335 (FCME), M. Candela 99 (FCME). Morelos: Tepoztlán, F. Miranda 3532 (MEXU), R. Cerros-Tlatilpa 301 (IEB, UAMIZ);

Tlayacapan, R. Cerros-Tlatilpa 203 (UAMIZ), R. Hernández-Cárdenas 447 (HUMO, UAMIZ), R. Hernández 447 (IEB). Oaxaca: Oaxaca de Juárez, C.G. Pringle 4652 (MEXU); San Miguel del Puerto, F. López 161 (MEXU); Santiago Juxtlahuaca, K. Gould 136 (MEXU, TEX), R. Torres 590 (MEXU); Santiago Yosondúa, A. García- Mendoza 9878 (MEXU), A. García- Mendoza 9990 (MEXU).

***Spigelia sphagnicola*** C. Wright., Fl. Cub. (Sauvalle) 116 (1870).
TYPE: CUBA: En lagunitas de la Vuelta Abajo, ca. de Pinar del Rio, *C. Wright 2701* (holotype: MO2049493!).

**Description**

Herbs not branched, stem quadrangular, glabrous, without lignification. Leaves opposite under the inflorescence, sessile, lamina lanceolate, membranaceous, 0.5-1.5 cm long. Stipula present, deltate. Inflorescence terminal, monochasium cyme, 1-3 flowers, sessile (Fig. 18-A). Sepals green with purple apex, lanceolate. Corolla hypocrateriform, 1.2-2.5 cm long, tube white, lobes purple, lobes ovate. Stamens insert half the tube if the corolla, included. Pollen not seen. Stigma capitate. Capsule glabrous, 2.73 mm diameter; metastyle present, smaller than the capsule; carpoatlas rhomboid (Fig. 18-B), transversal ridge absent. Seeds not seen.

**Distribution and habitat**

Endemic species of Cuba (Fig. 20). It inhabits humid savannahs with white sands (Fernández-Casas, 1998). Recorded at 50 m elevation.

**Conservation status**

Critically endangered (CR). This species is known only from a few specimens collected in Cuba. There are no collection records in the last 20 years, so the populations may be reduced. However, current populations need to be assessed to get a better idea of their abundance and environmental conditions.

**Taxonomic remarks**

*Spigelia sphagnicola* is one of the species distributed in Cuba and together with *S. ambigua*, endemic to the country. It can be distinguished from the latter by the monochasium inflorescence (*vs.* scorpioid inflorescences), the sepals with purple apex (*vs.* completely green sepals), as well as for being smaller herbs with lanceolate, almost linear leaves (*vs.* taller herbs with ovate leaves).

**Specimens examined**

CUBA. Pinar del Río: Pinar del Río, E.L. Ekman 17871 (TEX).

***Spigelia splendens*** H. Wendl. ex Hook., Bot Mag. 87, t.5268. 1861.

TYPE: GUATEMALA: Cultivated, 1841, *E. Friedrichstahl s.n.* (holotype: K-573396!).

≡ *Spigelia platyphylla* Progel, Fl. Bras. (Martius) 6(1): 256 (1868).

**Description**

Herbs not branched, stem cylindrical, pubescent, without lignification. Leaves pseudowhorled under the inflorescence, sessile, lamina ovate, membranaceous, 7-16 cm long. Stipule present, deltate. Inflorescence terminal, scorpioid cyme, 10-20 flowers, sessile (Fig. 18-C). Sepals green, linear. Corolla tubular, 3-4 cm long, tube and lobes red, lobes deltate. Stamens insert above half the tube of the corolla, included. Pollen suboblate, with medium polar area, 3 simple apertures, without margo on the colpi. Stigma terete, style pubescent. Capsule glabrous, 5.4-5.7 mm diameter; metastyle present, smaller than the capsule; carpoatlas elliptic (Fig. 18-D), transversal ridge absent. Seeds rhombic, testa reticulate (Fig. 18-E).

**Distribution and habitat**

Distributed in Costa Rica, El Salvador, Guatemala, Honduras, Mexico, and Nicaragua (Fig. 20; Fernández-Casas & Huft, 2009). It inhabits coniferous and *Quercus* forests, tropical deciduous, sub-deciduous and humid forests. From 500 to 2000 m elevation.

**Conservation status**

Least concern (LC). *S. splendens* is widely distributed in Mexico and Central America. It has an area of occupancy of about 35,000.00 $km^2$ and has been recently collected from different populations in various locations. Likewise, it is registered within national parks, so the populations are not considered under any category of threat.

**Taxonomic remarks**

*S. splendens* it is vegetatively similar, due to the presence of pseudwhorled leaves under the inflorescence, as well as in the shape of the corollas to *S. mexicana*. Despite the morphological similarities this species can be distinguished by its sessile leaves (*vs.* petiolate leaves), axillary inflorescences with fewer flowers (*vs.* always terminal inflorescences, with a greater number of flowers).

**Specimens examined**

MEXICO. Chiapas: Bochil, H. Mejía 331 (CICY); Chiapa de Corzo, F. Miranda 7807 (MEXU), L. Paray 6453 (MEXU), R. Ramírez 234 (MEXU, UAMIZ), R. Torres 6388 (MEXU); Coapilla, E. Palacios 2795 (MEXU); Ixtapa, D.E. Breedlove 25544 (ENCB); Juquipilas, C. Chavarría 275 (MEXU); San Fernando, F. Miranda 7218 (MEXU); Tuxtla Gutiérrez, D.E. Breedlove 10643 (ENCB, TEX), J.A. Espinosa 107 (MEXU), J.L. Panero 5758 (IEB, MEXU, TEX), L. Paray 926 (ENCB), R. Torres 6388 (IEB). Guerrero: Acatepec, A. Hernández 2462 (FCME); Chilpancingo de los Bravo, W.R. Anderson 4948 (ENCB); Galeana, G.B. Hinton 14361 (US). Oaxaca: San Miguel del Puerto, A. Saynes 2161 (SERO, TEX); San Pedro Tapanatepec, S. Maya 1670 (OAX, TEX). Querétaro: Pinal de Amoles, B. Córdova 661 (IEB, QMEX).

GUATEMALA. Huehuetenango: Jacaltenango, M. Veliz s.n. (TEX).

COSTA RICA. San José: Escazú, B. Hammen 19034 (TEX).

***Spigelia texana*** (Torr. & A. Gray) A. DC., Prodr. [A. P. de Candolle] 9: 5 (1845).

TYPE: USA: Texas: sin localidad. May-1836. *T. Drummond 321* (holotype: NY00180344!; isotype: G00368335!, GH00061252!).

≡ *Coelostylis texana* Torr. & A. Gray., Fl. N. Amer. (Torr. & A. Gray) 2(1): 44 (1841).

**Description**

Herbs not branched, steam quadrangular, pubescent, without lignification. Leaves pseudowhorled under the inflorescence, petiolate, lamina ovate-lanceolate, membranaceous, 3-5.5 cm long. Stipule present, deltate. Inflorescence axillary, monochacium cyme, 1-2 flowers, pedicelate (Fig. 18-D). Sepals green, linear. Corolla infundibuliform, 0.7-1.5 cm long, tube white, lobes white with purple lines, lobes lanceolate. Stamens insert half the tube of the corolla, included, filament present. Pollen spheroidal, with large polar area, 3 simple apertures, without margo on the colpi. Stigma capitate, style pubescent. Capsule glabrous, 4.5-6 mm diameter; metastyle present, smaller than the capsule; carpoatlas elliptic (Fig. 18-G), transversal ridge absent. Seeds elliptic, testa foveolate (Fig. 18-H).

**Distribution and habitat**

Species distributed in the United States of America and Mexico. It inhabits tropical deciduous forest (Fig. 20), and it's found between 1100 to 1600 m elevation.

**Conservation status**

Least concern (LC). This species is widely distributed in the United States of America and with some populations in northern Mexico. Likewise, there have been collections in several locations in recent years, so it is not considered under threat.

**Taxonomic remarks**

This species is similar to *S. hedyotidea*, and together with it, the only species that are distributed in the northern part of Mexico and in the southeastern United States of America. Both species differ in characters such as the pubescence of the leaves, phyllotaxy under the inflorescence and size of the flowers, characters that allow them to be clearly separated.

**Specimens examined**

UNITED STATES OF AMERICA. Texas: Austin, K. Gould 156 (TEX); Brazoria, B.C. Tharp 2805 (TEX), E.P. Killip 43289 (TEX), K. Gould 135 (TEX), K. Gould 62 (TEX), K. Gould 63 (TEX), K. Gould 64 (TEX), K. Gould 66 (TEX), R.J. Fleetwood 9753 (TEX), R.J. Fleetwood 9798 (TEX), R.J. Fleetwood s.n. (TEX), W.R. Carr 18269 (TEX), W.R. Carr 18297 (TEX), W.R. Carr 27739 (TEX);

Colorado, W.R. Carr 33254 (TEX); De Witt, D.S. Correll 17503 (TEX), K. Gould 154 (TEX), M. Riedel s.n. (TEX); Gonzales, B.C. Tharp s.n. (TEX), D. Lynch 7555 (TEX), K. Gould 155 (TEX), S. Ginzbarg 933 (TEX), S. Ginzbarg 941 (TEX); Iowa Park, E. Hall 288 (US); Jackson, W.R. Carr 30588 (TEX); Lee, W.R. Carr 15080 (TEX); Polk, K. Gould 159 (TEX); Refugio, W.R. Carr 22383 (TEX); Uvalde , J. Gregory 121 (TEX); Victoria, B.C. Tharp s.n. (TEX), W.R. Carr 22559 (TEX), W.R. Carr 22930 (TEX); Waller, D.S. Correll 16444 (TEX).

MEXICO. Coahuila: Ramos Arizpe, J.A. Villareal 4705 (MEXU); Sierra Mojada, T. Wendt 1654 (MEXU).

***Spigelia trispicata*** H. Hurley ex K.R. Gould, Brittonia 51(4): 412 (-414, figs. 4-5) (1999).
TYPE: MEXICO: Guerrero: Distrito: Mina: Aguazarca-Filo de Caballos, 07-May-1937, *G.B. Hinton 10381* (holotype: TEX256907!; isotype: G368331!, NY102692!, US00588944!).

**Description**

Herbs not branched, stem cylindrical, pubescent, without lignification. Leaves opposite under the inflorescence, sessile, lamina elliptic-ovate, membranaceous, 1.2-5.3 cm long. Stipule present, linear. Inflorescnece terminal, scorpioid cyme, 3-10 flowers, pedicelate (Fig. 19-A). Sepals green, linear. Corolla tubular, 3.5-4.5 cm long, tube and lobes red, lobes triangular. Stamens insert above half the tube of the corolla, exert, filament present. Pollen oblate-spheroidal, with large polar area, 3 simple apertures, without margo on the colpi. Stigma capitate, style pubescent. Capsule pubescent, 2.5 mm diameter; metastyle present, longer than the capsule. Seeds ovoid (Fig. 19-B).

**Distribution and habitat**

Endemic to Mexico and growing in coniferous and Quercus forests (Fig. 20). It is recorded between 900 and 1800 m elevation.

**Conservation status**

Near threatened (NT). This species has been recorded in four populations in the state of Guerrero in Mexico. It is recorded in an area close to 2,000.00 $km^2$ (AOO). The known populations are recorded in very close localities, and it has not been collected in more than 15 years. Therefore, it is suggested to evaluate the status of the populations at present.

**Taxonomic remarks**

This species is similar to *S. chiapensis*, both with small plants with ovate to elliptic leaves, tubular flowers, long corolla lobes and stamens inserted at the apex of the corolla tube. They can be distinguished by the short-pedunculate inflorescences, flowers 40-50 mm long (*vs.* 60-80 mm) and red corollas with white lobes internally (*vs.* red corollas with yellow lobes externally).

**Specimens examined**

MEXICO. Guerrero: Ajuchitlán del Progreso, G.B. Hinton 14380 (ENCB, TEX); Mina, G.B. Hinton 10453 (TEX), G.B. Hinton 10487 (US); Zirándaro, J. Calónico 4138 (MEXU), J. Calónico 4156 (ENCB, MEXU), J. Calónico 15193 (FCME), J. Calónico 15324 (FCME).

***Spigelia xochiquetzalliana*** S. Islas, Lozada-Pérez & L.O. Alvarado, Phytotaxa 303(2): 119 (2017).

TYPE: MEXICO: Guerrero: Municipio de Acapulco de Juárez. Cerro Cebadilla, 3-Ago-2003, *L. Lozada, C. Gallardo & R. de Santiago 2588* (holotype: FCME-158129!).

**Description**

Herbs not branched, stem quadrangular, glabrous, without lignification. Leaves pseudowhorled under the inflorescence, sessile, lamina elliptic-ovate, membranaceous, 9.7-17.7 cm long. Stipule present, deltate. Inflorescence terminal, scorpioid cyme, 11-17 flowers, pedicelate (Fig. 19-C). Sepals green, lanceolate. Corolla infundibuliform, 2-2.5 cm long, tube white, lobes white with purple apex, lobes deltate. Stamens insert above half the tube of the corolla, included, filament present. Pollen oblate-spheroidal, with medium polar area, 3 simple apertures, without margo on the colpi. Stigma capitate, style pubescent. Capsules not seen. Seeds not seen.

**Distribution and habitat**

Endemic species of Mexico (Fig. 20). It lives in tropical deciduous and sub-deciduous forest. Recorded between 100 and 1000 m elevation.

**Conservation status**

Vulnerable (VU). This species has been recorded in three populations in the region of the Pacific Ocean coast in Mexico, which together cover an AOO close to 6,000.00 km2. However, the known populations are in an area with significant urban growth and there are no data on the abundance of individuals.

**Taxonomic remarks**

This species is morphologically similar to *S. humboldtiana*, due to the herbaceous habit, the shape of the leaves and the infundibuliform corolla. *S. xochiquetzalliana* can be distinguished by monochasium inflorescences (*vs.* branched inflorescences in *S. humboldtiana*), internally purple corolla lobes (*vs.* internally white lobes), and potentially protogynous flowers with the style exserted prior to anthesis (*vs.* not protogynous with the style included, even at anthesis).

**Specimens examined**

MEXICO. Guerrero: Acapulco de Juárez, L. Lozada 2588 (FCME); Mochitlán, M. Venalonzo 13715 (FCME), R. Santos 13686 (FCME). Michoacán: Aquila, B. Guerrero 311 (XAL).

**Discussion and Conclusions**

The genus *Spigelia* has an important diversity in NA, with about 30% of the species in this region (Gould, 1997; Fernández-Casas & Huft, 2009; Villaseñor, 2016), distributed in tropical and subtropical zones, with an important presence along the coasts, from the United States of America to Panama. The genus inhabits mainly in tropical deciduous and sub-deciduous forests, with a high number of species also present in humid forests, mountain mesophilic forest and coniferous and *Quercus* forest (Gould, 1997; Fernández-Casas, 1998; Islas-Hernández, 2017a).

Of the 29 species distributed in the NA region, 23 of them are found in Mexico, followed by the United States of America and Guatemala with six species each. This diversity corroborates Mexico as the center of diversity in NA for the genus (Gould, 1997; Islas-

Hernández *et al.*, 2017a). In addition to this high diversity, about 80% of the species distributed in NA are exclusive to this region, with Mexico, the United States of America and Cuba as the countries with the highest number of endemic species with fourteen, three and two, respectively.

In the NA region, Mesoamerica constitutes one of the regions in which plant diversity is most concentrated, classified as a biodiversity hotspot (Sosa & De-Nova, 2012). Within this region, Mexico stands out as a country of high biological diversity and endemism, this is mainly due to the fact that the country has a complex geological history (Ferrusquía-Villafranca, 1993), which is responsible for an abrupt topography that allows the presence of practically all the major types of vegetation known on the planet (Villaseñor, 2003), a condition that is only shared with India and Peru. In addition to this, Mexico, unlike the rest of the countries in the NA region, presents a combination of boreal and southern elements, as well as a high diversity in arid zones, similar to what occurs in Brazil in the SA region (Rzedowski, 1991).

A high number of endemic species in the region, mainly in Mexico and Cuba, have restricted distributions that have been associated with the numerous biogeographic barriers in both countries (Fernández-Casas, 1998; Gould, 1999; Islas-Hernández *et al.,* 2017a, 2017b, 2020). Associated with these geographical conditions, several of the species, mainly endemic and microendemic, are known only from the type specimens (ex. *Spigelia ayotzinapensis, S. colimensis, S. dolichostachya, S. elbakyaniae, S. queretarensis, S. sphagnicola*), have distributions that are threatened by anthropogenic activities (ex. *Spigelia chiapensis, S. gentianoides, S. guerrerensis, S. mexicana, S. mocinoi, S. trispicata, S. xochiquetzalliana*) or have not been collected in about a century. Therefore, the updated knowledge of their morphology and distribution will allow the recognition of taxa, as well as the designation of areas that allow their conservation.

To this end, detailed knowledge of vegetative structures allows the elaboration of keys that facilitate identification before it is necessary to resort to reproductive structures. These characters, such as the presence of stipules or the phyllotaxis under the inflorescences, allow, in the absence of flowers, to have a closer approach to the identification of the species, which can be subsequently corroborated with the help of the diagnoses. Likewise, it has been observed that carpological characters present an important variation that allows the limitation of species for their identification, even if the plant no longer has flowers or fruits (Islas-Hernández *et al.*, 2022).

The detailed knowledge of the morphological structures that help to identify the species (ex. type of style, pollen, carpoatlas or shape of the seeds), can be integrated as morphological markers, which together with the molecular markers will allow in the future generate combine phylogenetic analyzes (Peterson & Seberg 1998). In this sense, the use of carpological characters for the separation of groups of species has been studied within the genus (Islas-Hernández *et al.*, 2022), this information will allow, together with the floral information, the proposal of new sections that have phylogenetic congruence (Gould, 1997) and that are complemented with information derived from the species of the SA region.

This study represents the first taxonomic treatment for the genus *Spigelia* that includes all the species of the central and northern region of the continent. The information collected in this work, some of it described in detail for the first time (pollen, carpoatlas, seeds), may be useful to be integrated into phylogenetic analyzes that help resolve the intrageneric relationships of the group. Likewise, the application of potential distribution modeling tools that would allow locating areas for future collection, as well as the development of biogeographic analyzes that help us understand the reason for such distributions in some species and the separation of the flora along the continent.

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Table 1. Species of the genus *Spigelia* distributed in North America, Central America, and the Caribbean with their distribution by country.

Abbreviations: BLZ = Belize, CARIB = The Caribbean, CRI = Costa Rica, CUB = Cuba, GTM = Guatemala, HND = Honduras, MEX = Mexico, NIC = Nicaragua, PAN = Panama, SLN = El Salvador, USA = United States of America.

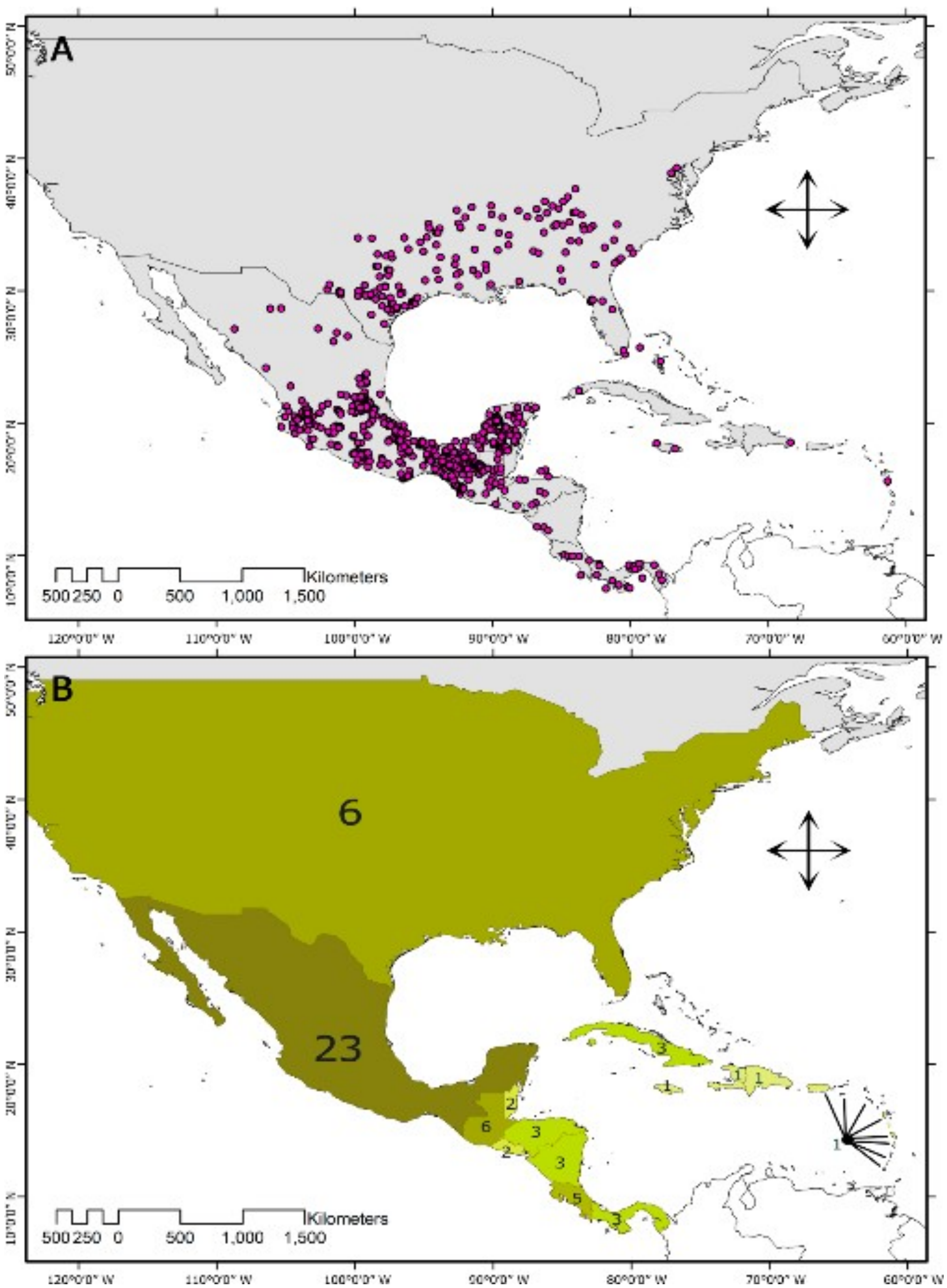


Figure 1. Distribution and species richness of the genus *Spigelia* in North America, Central America, and the Caribbean. A) Distribution of the genus *Spigelia* in the NA region. B) Species richness of the genus *Spigelia* by country in the NA region.

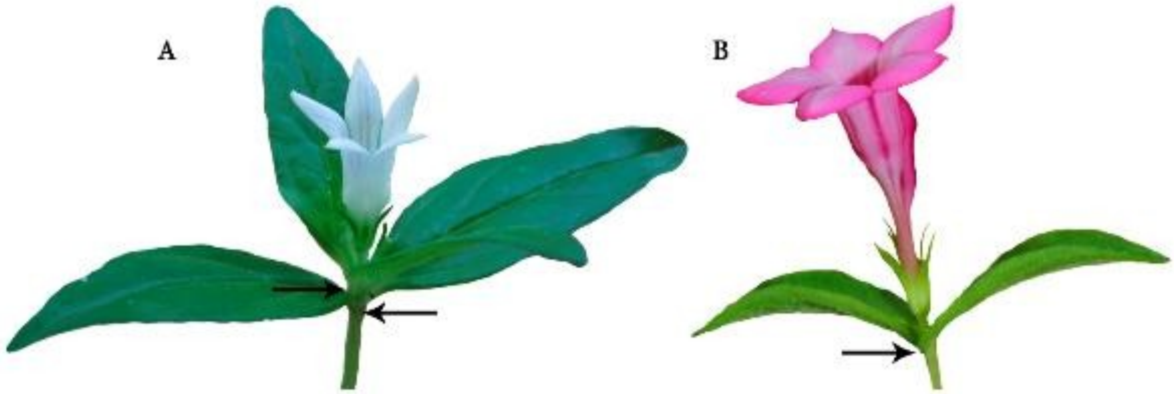


Figure 2. Phyllotaxis of the leaves under the inflorescence. A) *Spigelia loganioides* with pseudowhorled leaves and B) *S. scabrella* with opposite leaves. The black arrows show the position of the nodes.

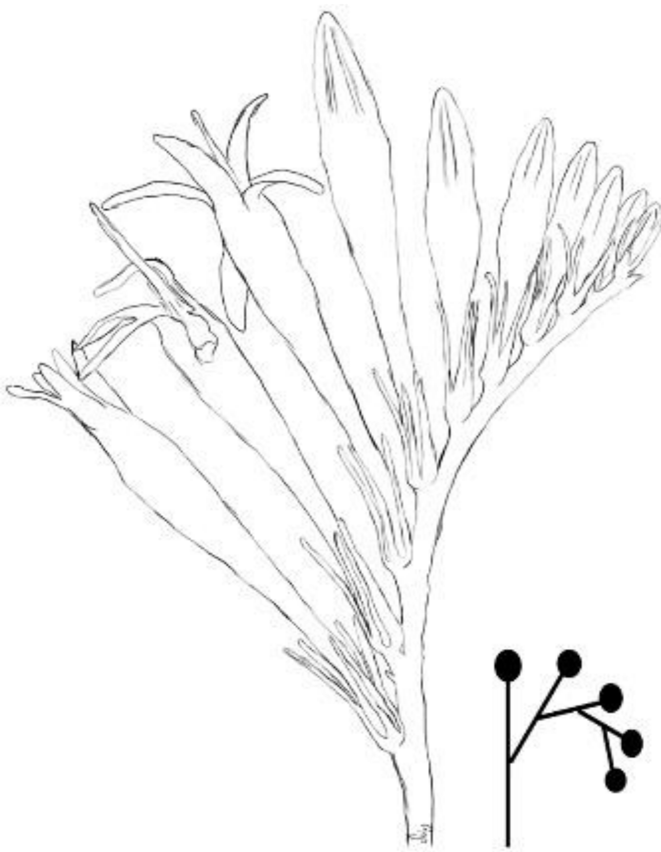

Figure 3. Drepanium-type cincinnus inflorescence in *Spigelia marilandica* (Illustration S. Islas).

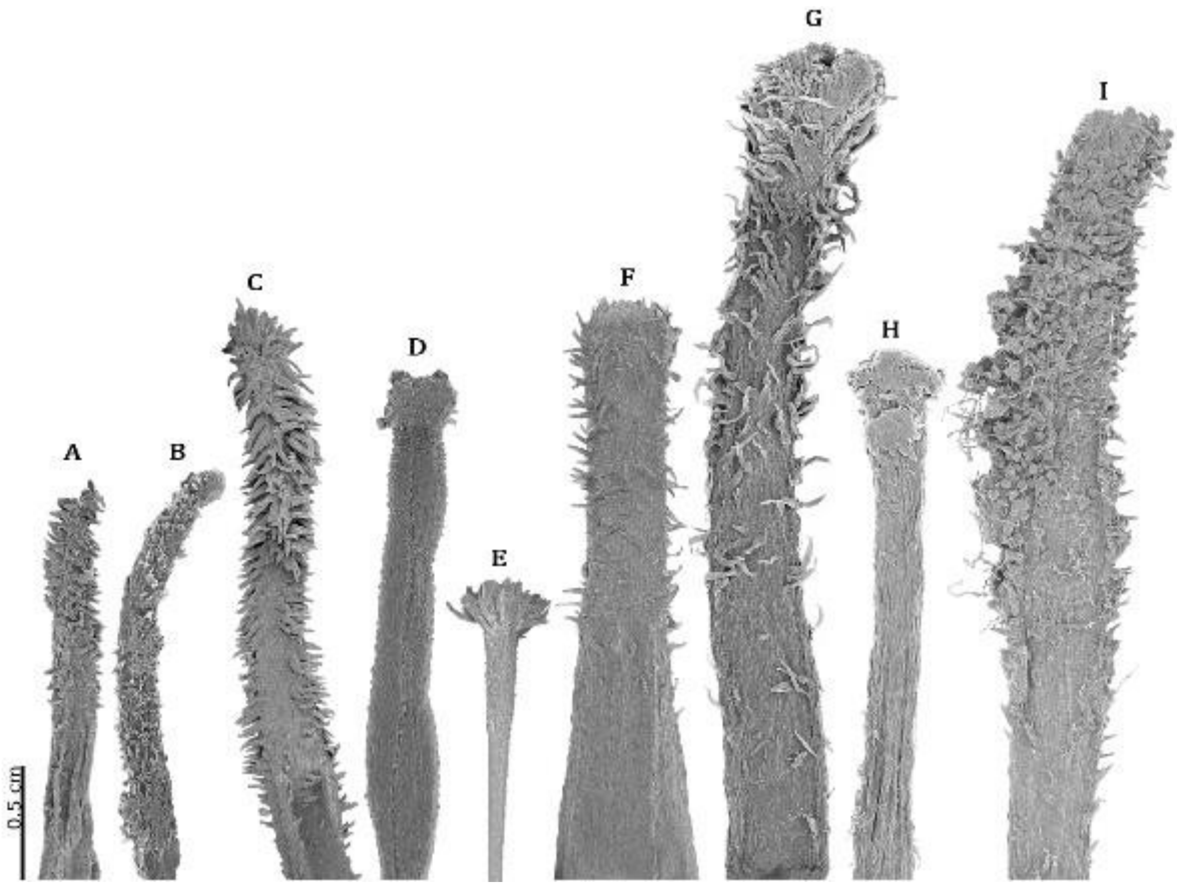


Figure 4. SEM photographs of stigmas of various *Spigelia* species, showing the trichomes along the style in some of them. A) *Spigelia anthelmia*, B) *S. hedyotidea,* C) *S. humboldtiana*, D) *S. longiflora,* E) *S. mexicana*, F) *S. scabrella,* G) *S. speciosa*, H) *S: trispicata* and I) *S. xochiquetzalliana.*

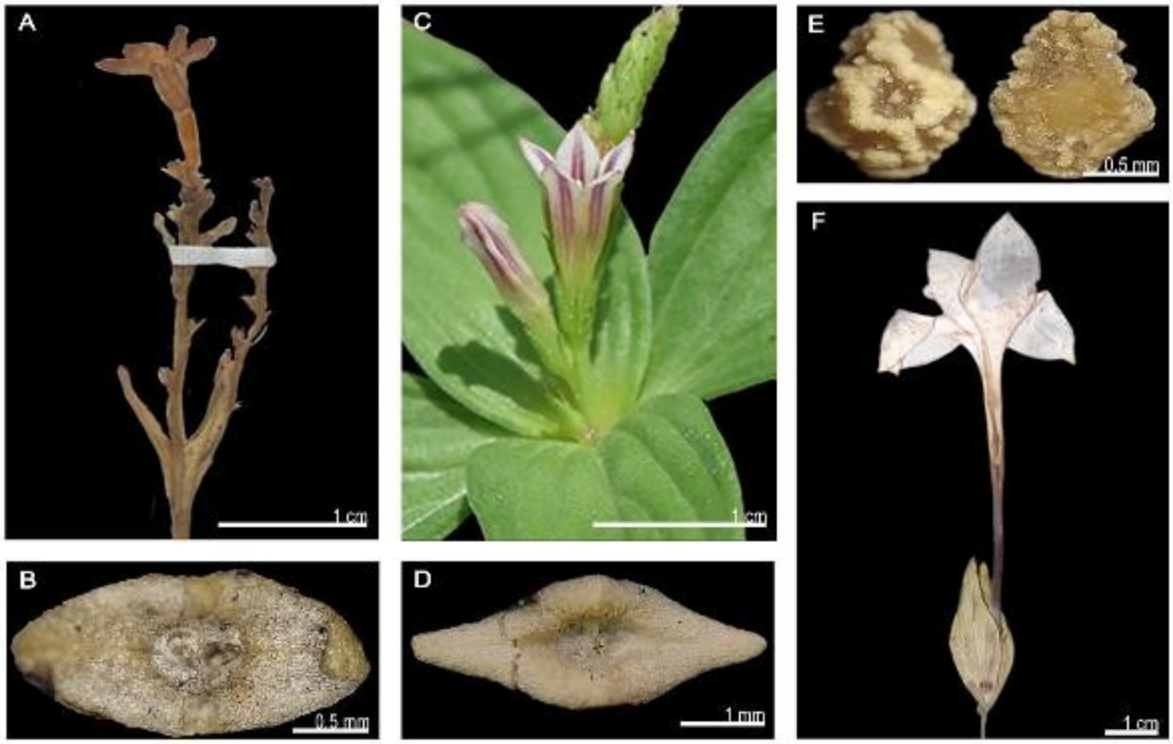

Figure 5. Morphological characters of the species *Spigelia ambigua* (A. Flower; B. Carpoatlas), *S. anthelmia* (C. Flower; D. Carpoatlas; E. Seed) and *S. ayotzinapensis* (F. Flower).

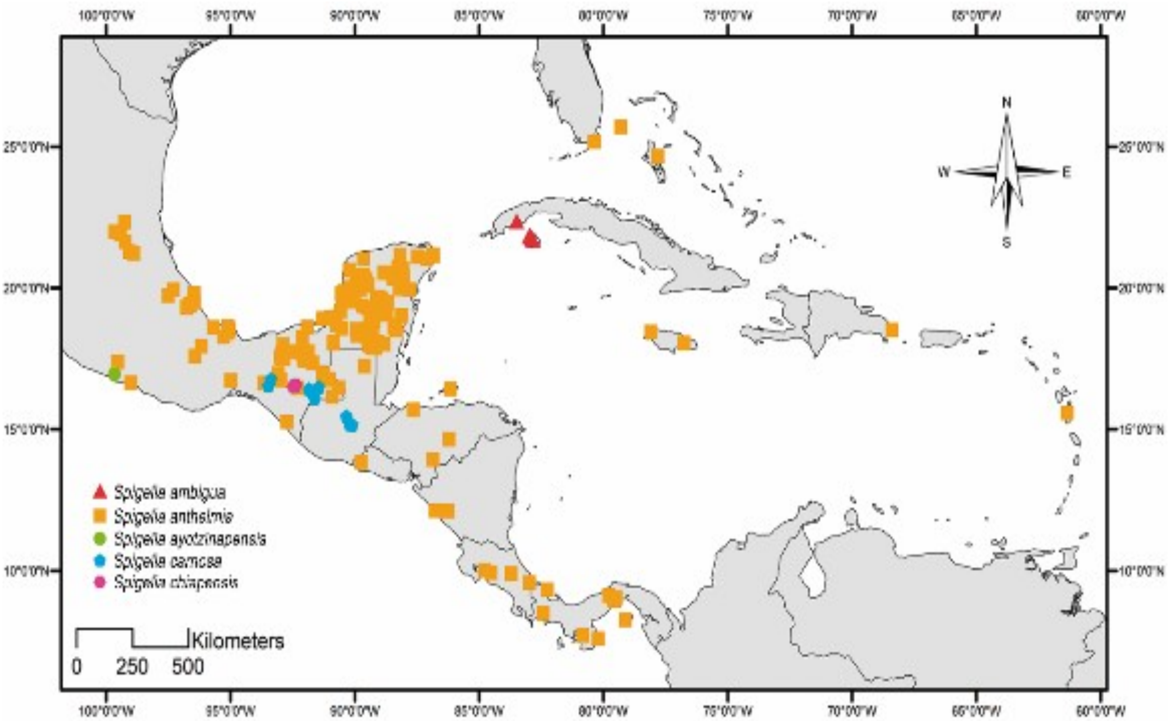


Figure 6. Map of distribution of *Spigelia ambigua, S. anthelmia, S. ayotzinapensis, S. carnosa* y *S. chiapensis.*

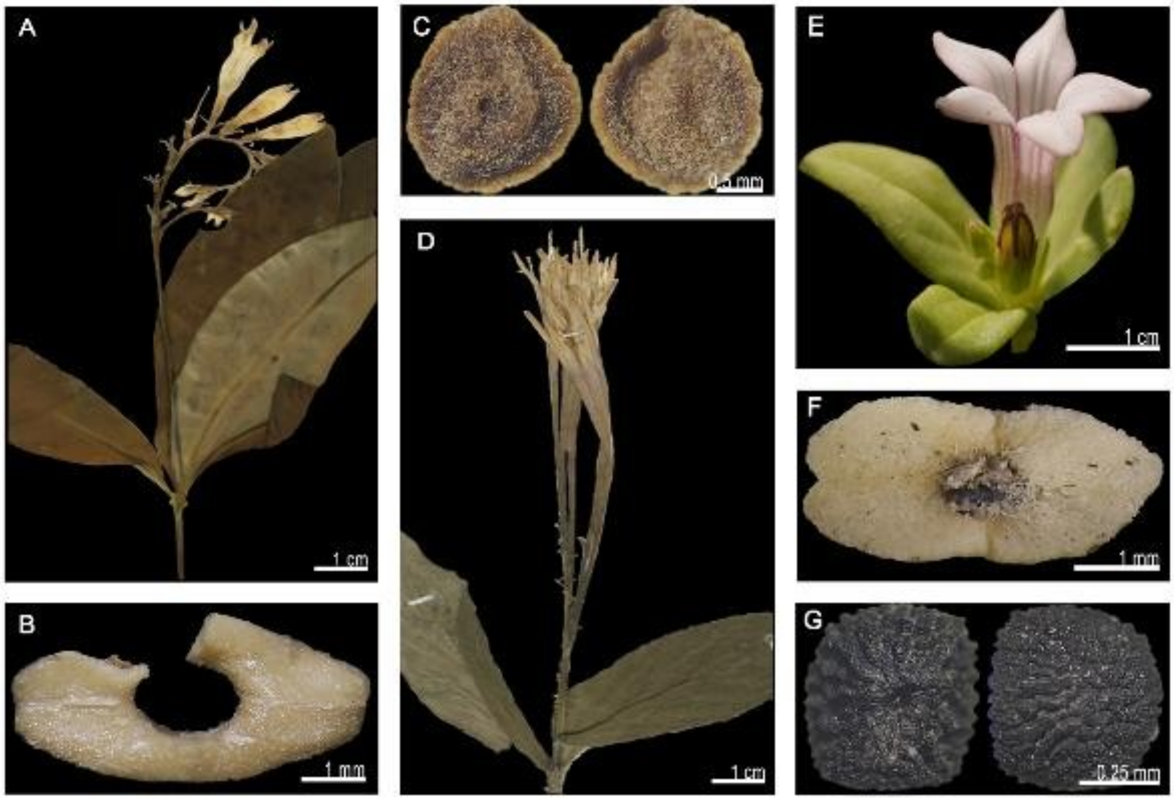


Figure 7. Morphological characters of the species *Spigelia carnosa* (A. Flower; B. Carpoatlas; C. Seed), *S. chiapensis* (D. Flower) and *S. coelostylioides* (E. Flower; F. Carpoatlas; G. Seed).

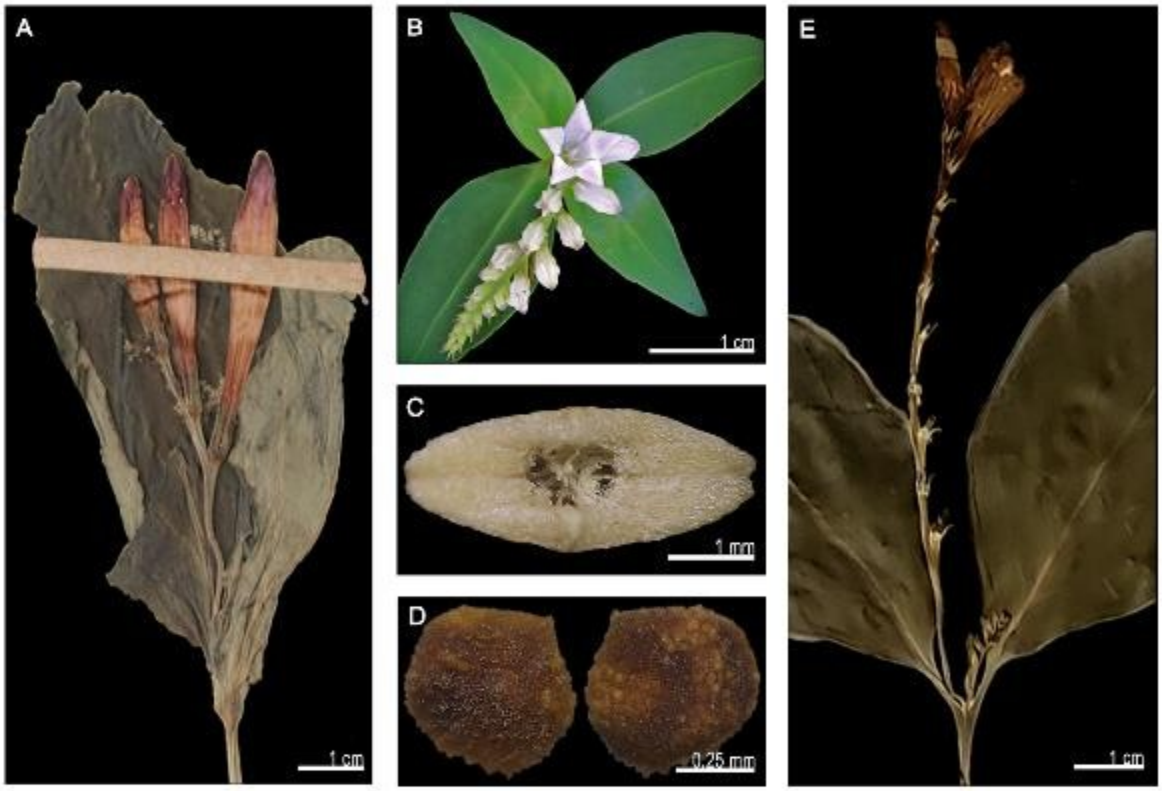


Figure 8. Morphological characters of the species *Spigelia colimensis* (A. Flower), *S. dolychostachia* (B. Flower; C. Carpoatlas; D. Seed), and *S. elbakyaniae* (E. Flower).

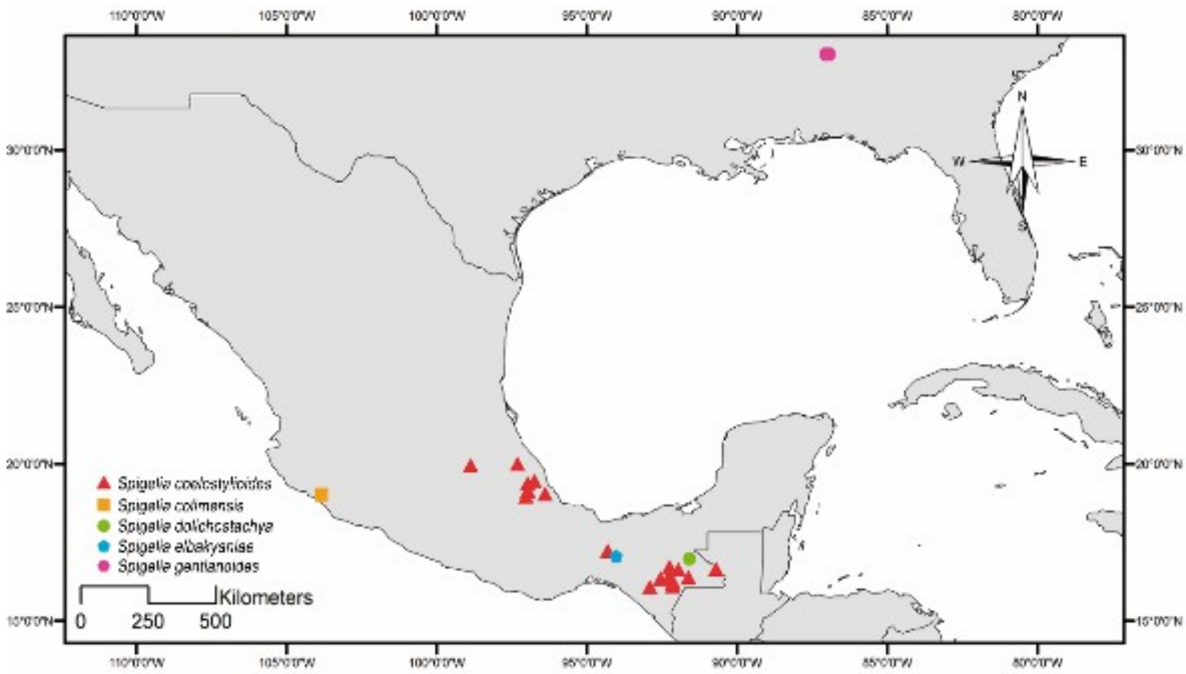


Figure 9. Map of the distribution of *Spigelia coelostylioides, S. colimensis, S. dolichostachya, S. elbakyaniae* and *S. gentianoides.*

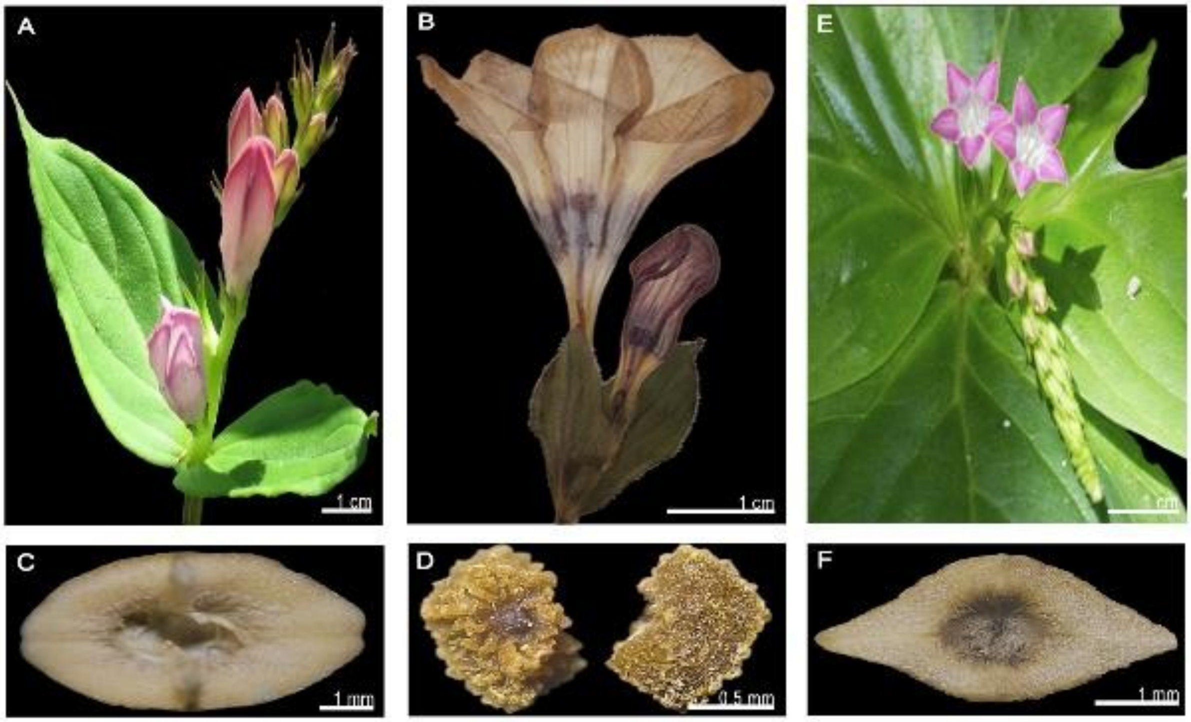


Figure 10. Morphological characters of the species *Spigelia gentianoides* (A. Flower), *S. guerrerensis* (B. Flower; C. Carpoatlas; D. Seed) and *S. hamelioides* (E. Flower; F. Carpoatlas).

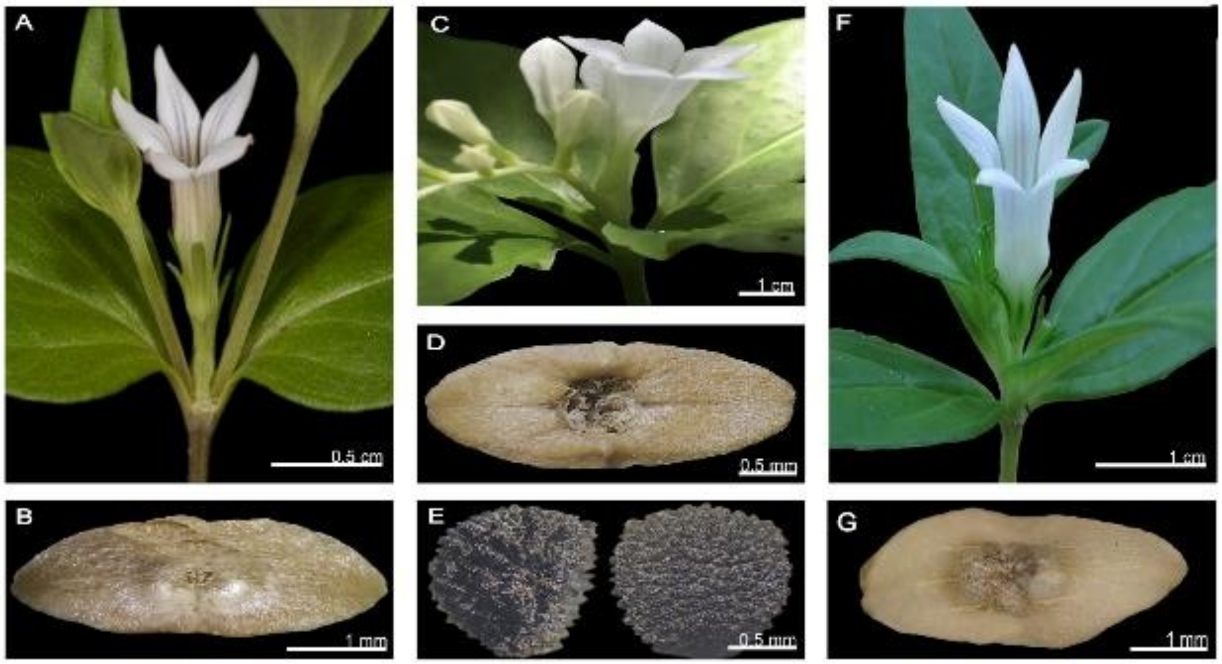


Figure 11. Morphological characters of the species *Spigelia hedyotidea* (A. Flower; B. Carpoatlas), *S. humboldtiana* (C. Flower; D. Carpoatlas; E. Seed) and *S. loganioides* (F. Flower; G. Carpoatlas).

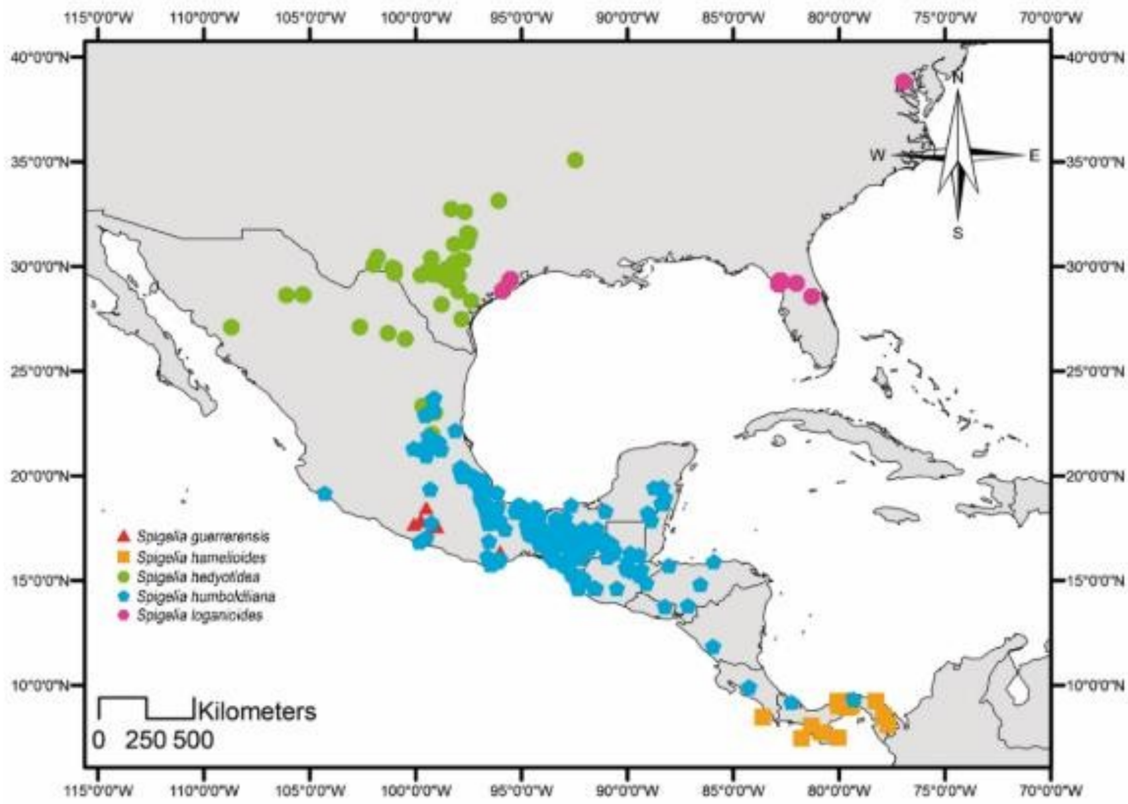


Figure 12. Map of distribution of *Spigelia guerrerensis, S. hamelioides, S. hedyotidea, S. humboldtiana* and *S. loganioides.*

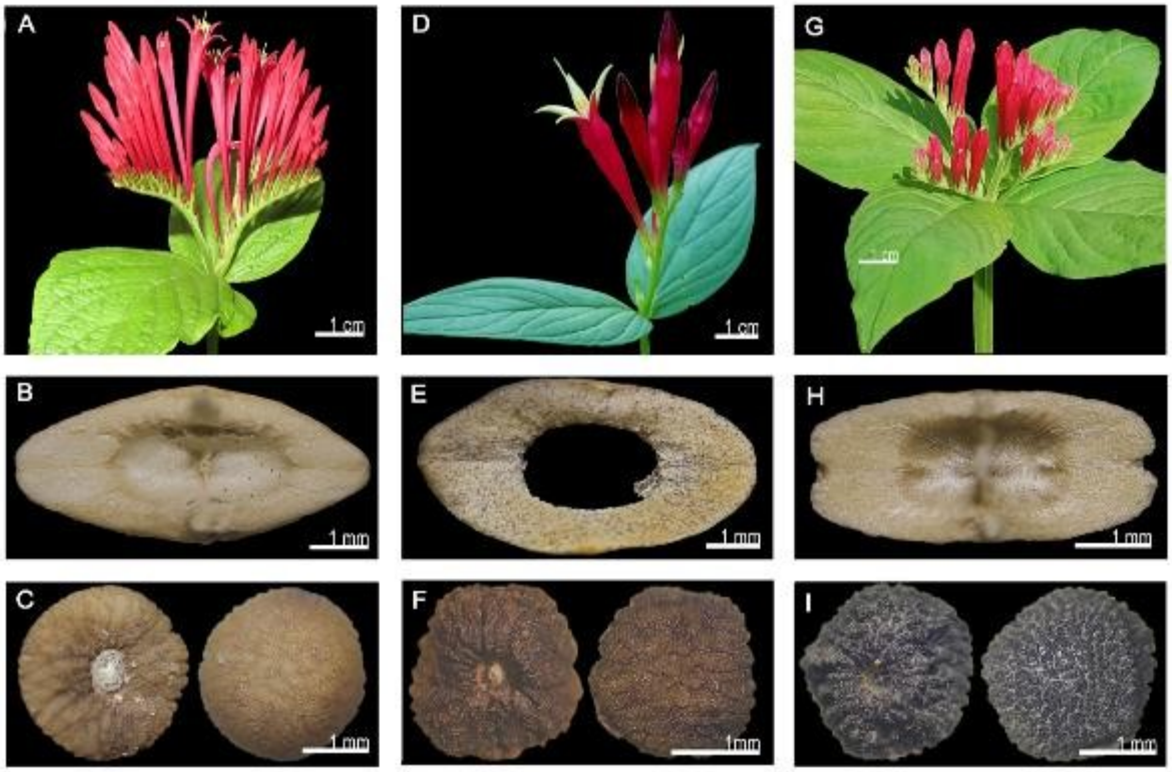

Figure 13. Morphological characters of the species *Spigelia longiflora* (A. Flower, B. Carpoatlas, C. Seed), *S. marilandica* (D. Flower, E. Carpoatlas, F. Seed) and *S. mexicana* (G. Flower, H. Carpoatlas, I. Seed).

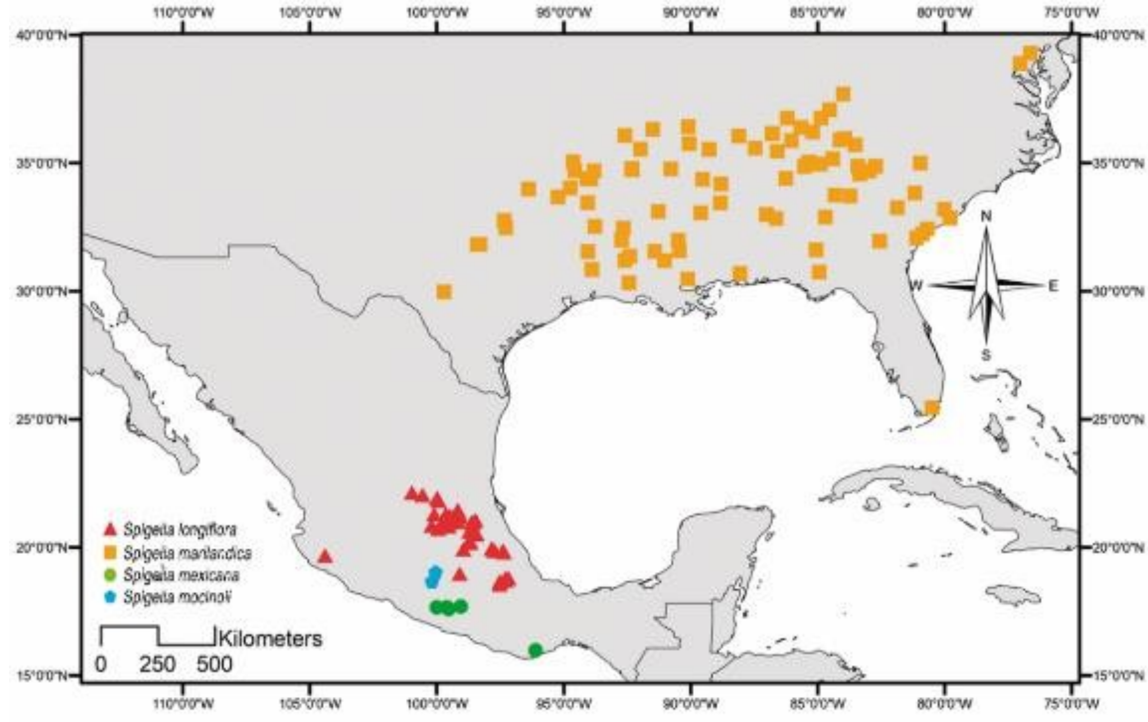


Figure 14. Map of the distribution of *Spigelia longiflora, S. marilandica, S. mexicana* and *S. mocinoi.*

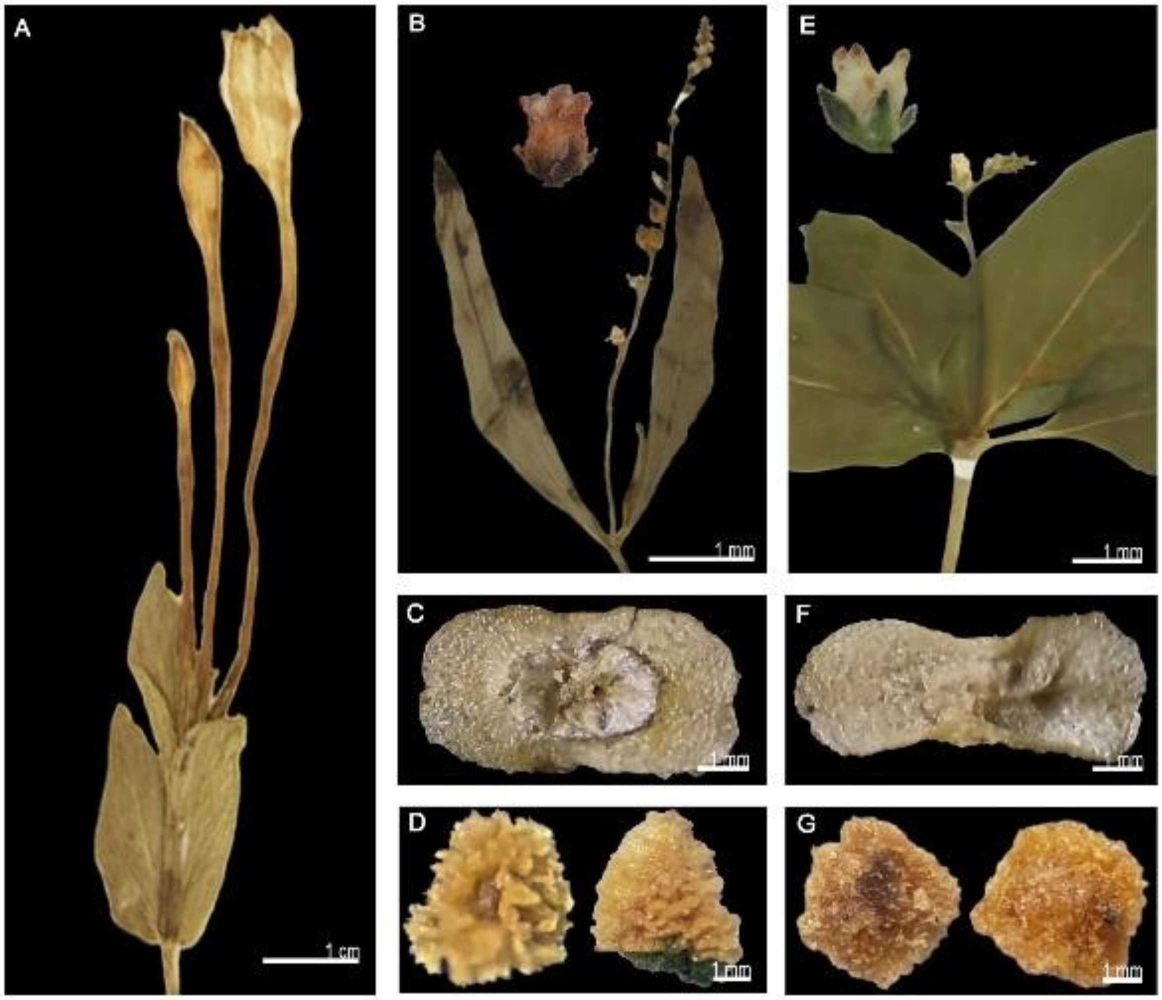


Figure 15. Morphological characters of the species *Spigelia mocinoi* (A. Flower), *S. polystachya* (B. Flower; C. Carpoatlas; D. Seed) and *S. pygmaea* (E. Flower; F. Carpoatlas; G. Seed).

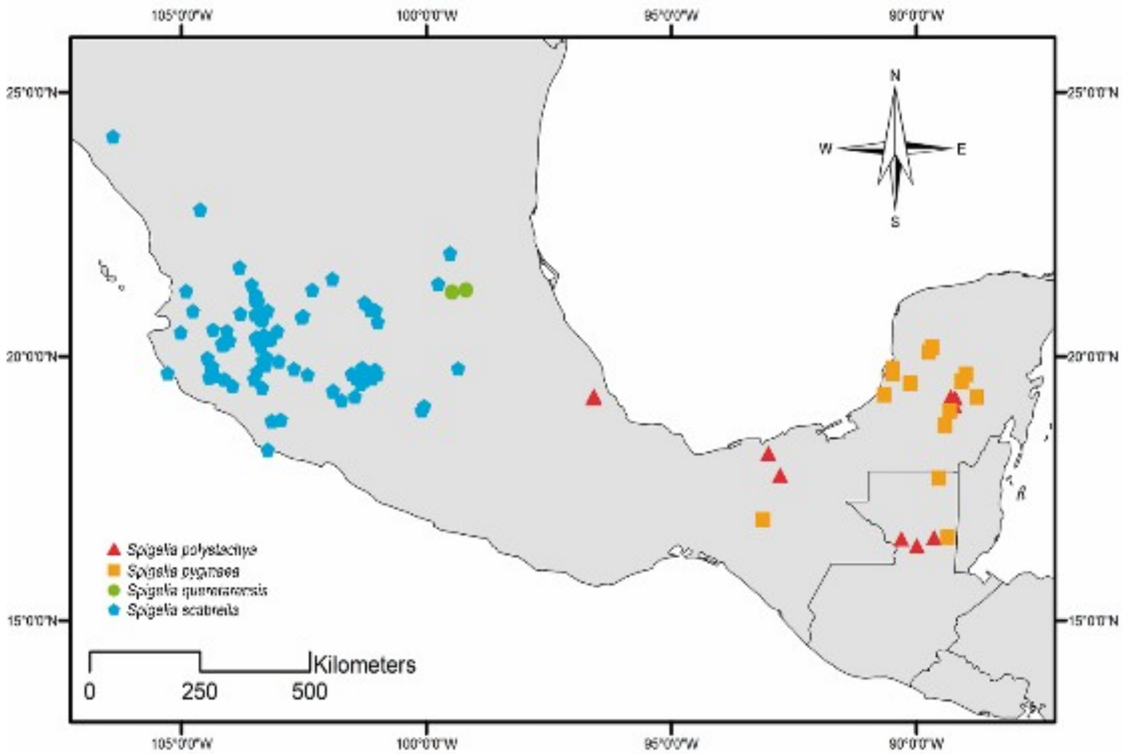


Figure 16. Map of the distribution of *Spigelia polystachya, S. pygmaea, S. queretarensis* and *S. scabrella*

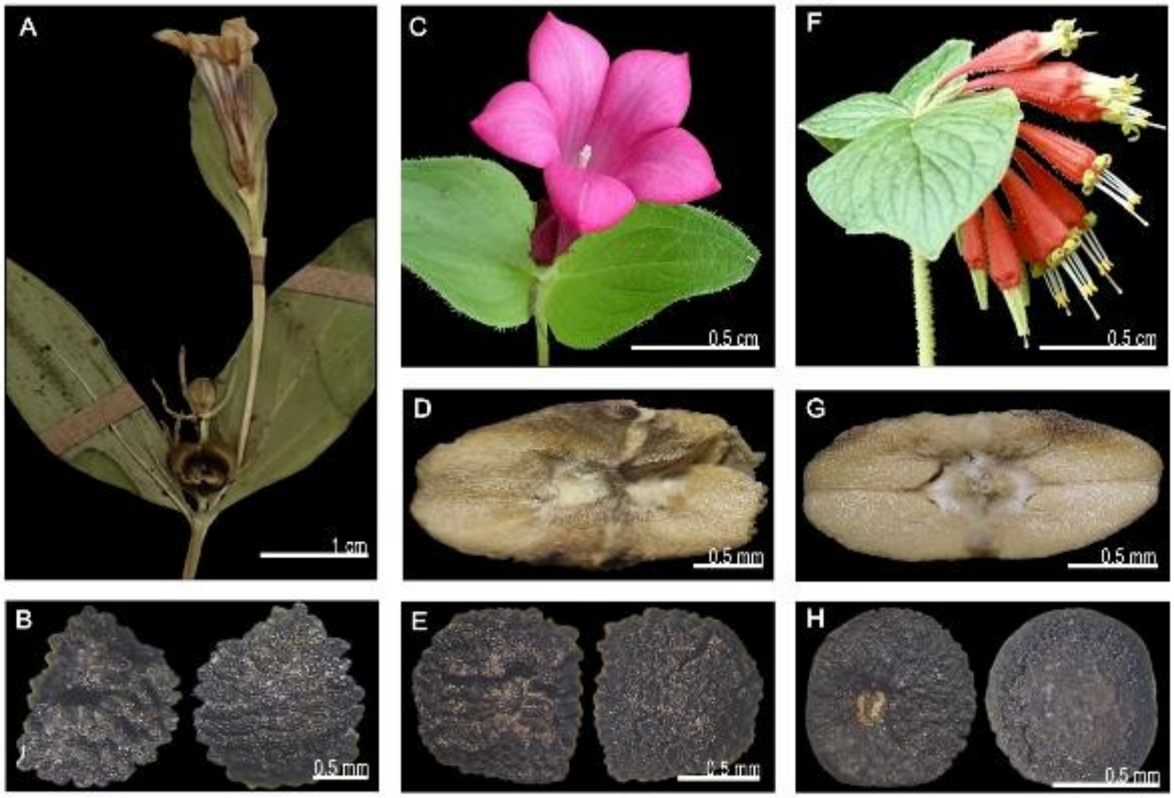


Figure 17. Morphological characters of the species *Spigelia queretarensis* (A. Flower; B. Seed), *S. scabrella* (C. Flower; D. Carpoatlas; E. Seed) and *S. speciosa* (F. Flower; G. Carpoatlas; H. Seed).

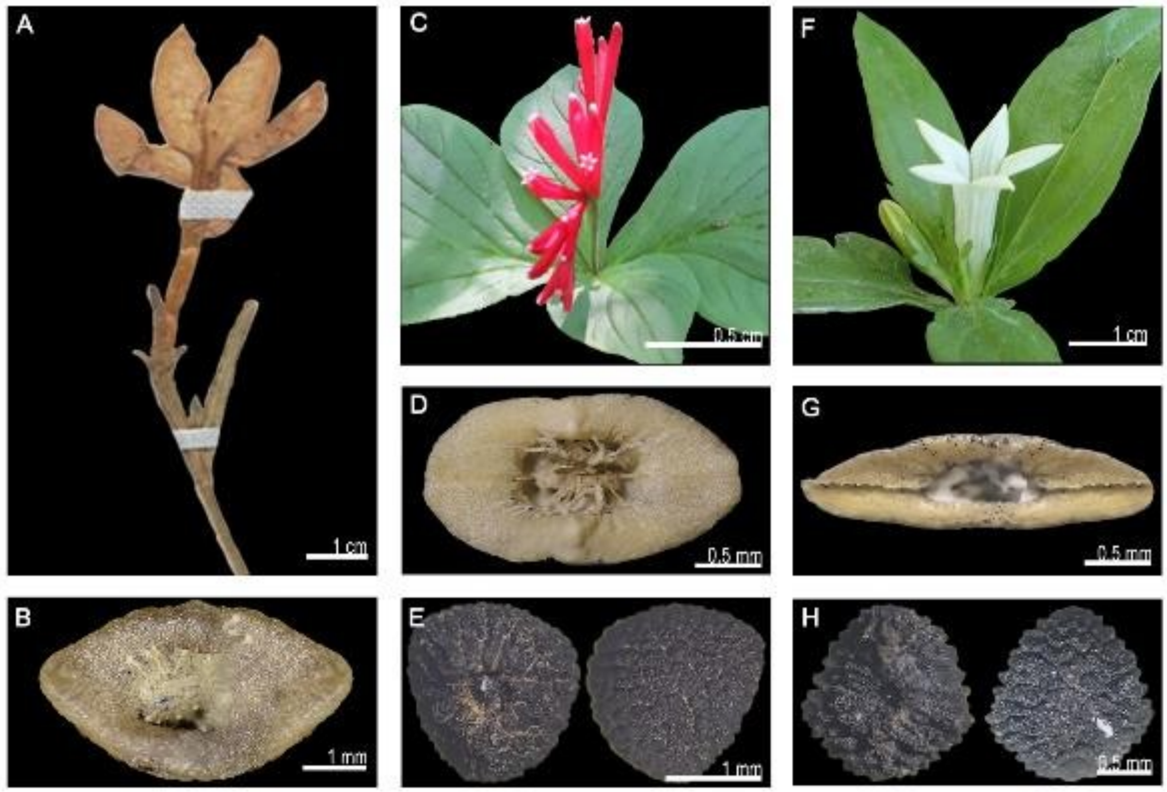


Figure 18. Morphological characters of the species *Spigelia sphagnicola* (A. Flower; B. Carpoatlas), *S. splendens* (C. Flower; D. Carpoatlas; E. Seed) and *S. texana* (F. Flower; G. Carpoatlas; H. Seed).

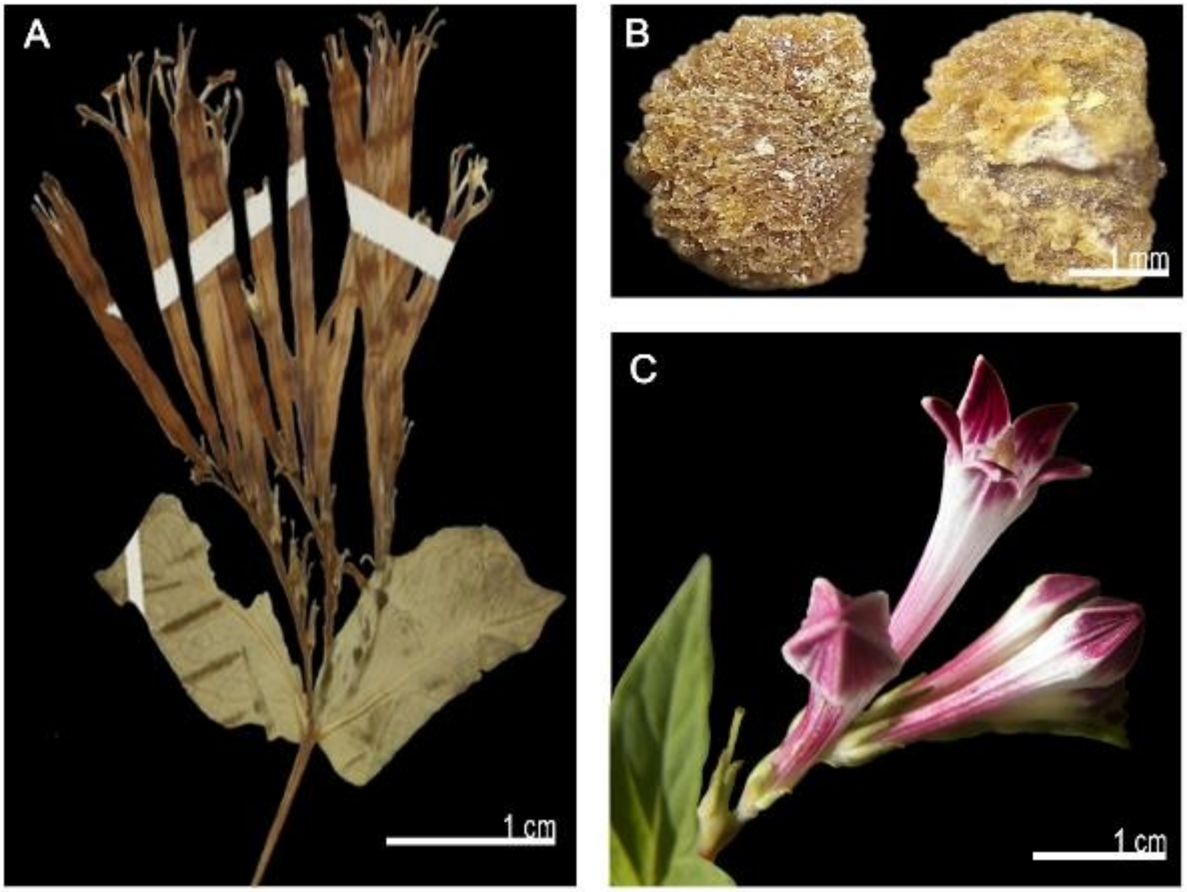


Figure 19. Morphological characters of the species *Spigelia trispicata* (A. Flower; B. Seed), *S. xochiquetzalliana* (C. Flower).

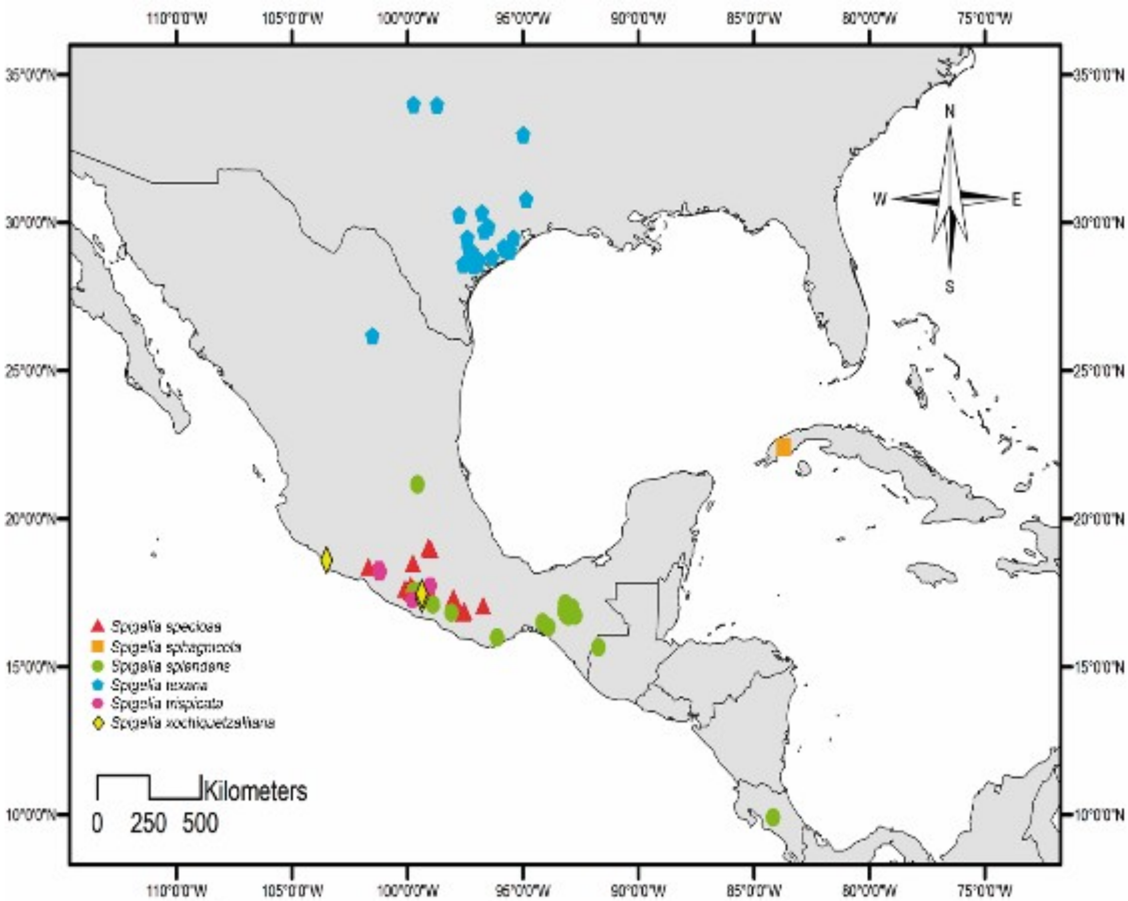


Figure 20. Map of the distribution of *Spigelia speciosa, S. sphagnicola, S. splendens, S. texana, S. trispicata* and *S. xochiquetzalliana.*

**Appendix: Photographic credits**

Figure 2: A) J. Appleget 3764461 (NatLis); B) J. Álvarez 1002431 (NatLis).

Figure 4: A-I) B. Mendoza-Garfias

Figure 5: A) E. Killip 45200 (US); C) Joe MDO 82893865 (NatLis); F) R. Bustamante 414 (FCME); B, D, E) S. Islas.

Figure 7: A) D.E Bredlove 29632 (MEXU); D) M. Gómez 521 (MEXU); E) F. Manuel 33303999 (NatLis); B, C, F, G) S. Islas.

Figure 8: A) F. Weger CUIDA-841 (IBUG); B) B. Jiménez (NatLis); E) E. Torres (SERO); C, D) S. Islas.

Figue 10: A) J. Appleget 124512093 (NatLis); B) R. Cruz-Duran 197 (FCME); E) H. Szczygiel 76279597 (NatLis); C, D, F) S. Islas.

Figure 11: A) T. Eubanks 65348344 (NatLis); F) J. Appleget 37464461 (NatLis); B, C, D, E, G) S. Islas.

Figure 13: A) M.E. Mendiola 44336379 (NatLis); D) E. Keith 7075719 (NatLis); G) R. Ramírez; B, C, E, F, H, I) S. Islas.

Figure 15: A) H. Hurley 8063 (MEXU); B) D. Álvarez 10389 (MEXU); E) D. Álvarez 10389 (MEXU); C, D, F, G) S. Islas.

Figure 17: A) T. Carranza 809 (IEB); C) I. Torres 6911904 (NatLis); F) R.M. Fonseca; B, D, E, G, H) S. Islas.

Figure 18: A) E. Killip 45873 (US); C) B. Jiménez 8526700 (NatLis); F) A. Newman 70342005 (NatLis); B, D, E, G, H) S. Islas.

Figure 19: A) J.C. Soto 4156 (MEXU); C) E. Barrera 51641972 (NatLis); C) S. Islas.

# CAPÍTULO DOS

UNAM POSGRADO

POSGRADO CIENCIAS BIOLÓGICAS

**OF/CPCB/428/2022**

**LIC. DIANA GONZÁLEZ NIETO**
Directora de Certificación y Control Documental
Dirección General de Administración Escolar
Universidad Nacional Autónoma de México
**P r e s e n t e**

Por medio del presente me permito informar a usted, que el Comité Académico del Posgrado en Ciencias Biológicas en su sesión ordinaria (*virtual*) del día 23 de mayo del año en curso, acordó aprobar el Artículo publicado en la *Revista Systematic Botany* **"MORPHOLOGICAL DIVERSITY AND TAXONOMIC IMPORTANCE OF FRUITS AND SEEDS OF THE GENUS SPIGELIA (LOGANIACEAE) IN MEXICO"**, presentado por la alumna del Doctorado en Ciencias ***CARLA SOFÍA ISLAS HERNÁNDEZ*** con número de cuenta 306270318.

De acuerdo con lo anterior, el Artículo cubre el punto 3.4.7 inciso c) Requisitos para obtener el grado de Doctora del Posgrado en Ciencias Biológicas, y así la alumna pueda solicitar el examen de grado correspondiente.

Agradeciendo la atención que se sirva dar al presente sin más por el momento le envío un cordial saludo.

Atentamente
"POR MI RAZA HABLARA EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 24 de mayo del 2022

DR. ADOLFO GERARDO NAVARRO SIGÜENZA
COORDINADOR

**COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS**
Unidad de Posgrado, Edificio D, 1° Piso. Circuito de Posgrados, Ciudad Universitaria
Alcaldía Coyoacán. C. P. 04510 CDMX Tel. (+5255)5623 7002 http://pcbiol.posgrado.unam.mx/

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# Morphological Diversity and Taxonomic Importance of Fruits and Seeds of the Genus *Spigelia* (Loganiaceae) in Mexico

**C. Sofía Islas-Hernández,[1,4] Leonardo O. Alvarado-Cárdenas,[1] Julieta A. Rosell,[2] Helga Ochoterena,[3] and José Luis Villaseñor[3]**

[1]Departamento de Biología Comparada, Facultad de Ciencias, Universidad Nacional Autónoma de México, Apartado Postal 70-282, 04510, Ciudad de México, México
[2]Instituto de Ecología, Universidad Nacional Autónoma de México, Tercer Circuito s/n de CU, Apartado Postal 70-282, 04510, Ciudad de México, México
[3]Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Tercer Circuito s/n de CU, Apartado Postal 70-282, 04510, Ciudad de México, México
[4]Author for correspondence (sofilasagesse@ciencias.unam.mx)

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*Abstract*—The genus *Spigelia* (Loganiaceae) is a Neotropical genus that includes more than 80 species distributed from the United States to Argentina. Systematic studies of the group have rarely considered the carpological characters, so their taxonomic importance has not been analyzed in detail. The aim of this study is to analyze the morphological characteristics of these organs to provide more information for a better species separation and for a more robust infra-generic classification. We provide a detailed description of *Spigelia* fruits and seeds of the Mexican species since the country represents one of its main centers of diversification. Fruits and seed samples from 54 individuals across 14 species were measured and photographed to describe each one, maintaining as much detail as possible. With the morphological matrix a DFA, PCA, and a dendrogram using the NJ method was performed. The fruits and seeds of the Mexican *Spigelia* species proved to be taxonomically useful, allowing the differentiation of four main clusters of species separated by the size of the analyzed structures in the three analyses (DFA, PCA, NJ). The results show the variation in size and shape of the structures analyzed, which shows the taxonomic importance of fruits and seeds of the genus *Spigelia*. Our work represents an advance in the detailed knowledge of structures, which are rarely considered in the descriptions, and which allows us to have a separation of species. A taxonomic treatment and photographs of the fruits and seeds are also included.

*Keywords*—Metastyle, carpoatlas, discriminant function analysis, principal component analysis, morphological comparison.

*Spigelia* L. (Loganiaceae) is a Neotropical genus distributed from the southeastern United States to northern Argentina, including the Caribbean. The genus includes more than 80 species with two main centers of diversity, one in Brazil with 56 species and another in Mexico with 23 species (BFG 2015; Islas-Hernández et al. 2017a, 2017b). The taxonomic history of the genus is complicated, and its circumscription has changed over the years (Hutchinson 1973; Cronquist 1981; Thorne 1983; Gould 1997; Backlund et al. 2000). Currently, based on molecular phylogenies, it has been recovered as a monophyletic genus; *Spigelia* in its monogeneric tribe Spigelieae is a sister group of *Mitreola* L. This last genus together with *Geniostoma* and *Logania* form the Loganieae tribe. These two tribes form a sister group to the Strychneae tribe (Backlund et al. 2000; Frasier 2008; Popovkin et al. 2011; Gibbons et al. 2013; Yang et al. 2016).

In addition to the molecular data, the morphology is of great importance to separate *Spigelia* from other phylogenetically close taxa in the country. For example, members of this genus are annual herbs (vs. lianas and trees in *Strychnos* L.), some with pseudoverticillate leaves under the inflorescences (vs. always opposite leaves in *Mitreola* and *Strychnos*), with interpetiolar stipule, inflorescences on a scorpioid cyme (vs. dichotomous cyme in *Mitreola* and corymbs in *Strychnos*), capsule fruits (vs. berries in *Strychnos*), persistent style, with septicidal, loculicidal, and circumcissile dehiscence (vs. loculicidal capsules in *Mitreola*) (Henrickson 1996; Alvarado-Cárdenas 2007; Fernández-Casas 2009). Two other important characters that allow us to recognize the genus are the metastyle, lower part of the style joint that remains in the capsule (Fernández-Casas 2003), and the carpoatlas differentiated basal portion, hardened, and thickened of the capsule resulting from the circumcissile dehiscence (Fernández-Casas 2003).

Also, within the genus, morphology remains an important attribute to separate species, especially floral and pollen grain attributes (Gould 1999; Fernández-Casas 2003; Alvarado-Cárdenas 2007; Fernández-Casas and Huft 2009; Alvarado-Cárdenas and Jiménez Ramírez 2015; Islas-Hernández et al. 2017a, 2017b). To date, systematic studies of the group for Mexico have rarely considered the carpological characters, so they have been little used, and their taxonomic importance has not been assessed in detail (Gould 1999; Alvarado-Cárdenas 2007; Fernández-Casas and Huft 2009; Islas-Hernández and Alvarado-Cárdenas 2017, 2018).

It has been pointed out that the fruits and seeds of the species in *Spigelia* show significant variations in size, shape, and ornamentation, which can be especially useful in the taxonomy of the genus (Fernández-Casas 2003; Alvarado-Cárdenas and Jiménez Ramírez 2015; Islas-Hernández et al. 2017a, 2017b). The infra-generic classifications of *Spigelia* have been based mainly on vegetative and floral characters, without including carpological characters. The Mexican species belong to three of the nine sections recognized in *Spigelia* (Bravo 1971; Progel 1986; Henrickson 1996; Gould 1997). However, the sections were proposed based on a reduced number of floral characters, for which it has been suggested that they are artificial, since the few characters used overlap or do not clearly define the separation between them (Gould 1997). Therefore, it is necessary to look for other attributes that provide systematic information, both at a supra-specific level and at more inclusive levels. Knowledge and detailed description of carpological characters could provide relevant information for species recognition, as well as for re-evaluation of previous classification. Similarly, the subsequent integration of morphological knowledge with molecular phylogeny as a frame of reference will help us to propose a more sustained classification for the genus (Stull et al. 2017; Wei et al. 2018; Tyrrell et al. 2018; Bao-Jian et al. 2019).

The aim of this study is to provide a comparative analysis and a detailed description of *Spigelia* fruits and seeds, complemented with information of taxonomic importance the previous descriptions. Special emphasis was placed on the Mexican species, since Mexico represents one of its main centers of diversification and could contain an important variation of the group. Analyzing the morphological characteristics of these organs allowed evaluating their potential usefulness in the genus systematics, mainly to reach a better species separation and to improve the infra-generic classification.

## Materials and Methods

***Botanical Material***—The specimens of the *Spigelia* species present in Mexico, with fruits and seeds deposited in different Mexican herbaria, were selected (FCME, ENCB, IBUG, and MEXU). For some species, where herborized material was scarce, carpological descriptions were complemented with data from the bibliography (Gould 1999; Fernández-Casas 2003; Alvarado-Cárdenas 2007; Fernández-Casas and Huft 2009; Alvarado-Cárdenas and Jiménez Ramírez 2015; Islas-Hernández et al. 2017a, 2017b). At the same time, fruits and seeds were collected in different areas of the country, in order to obtain complete characters for some species.

Seed samples were mounted on metal plates and covered with a gold layer to be observed and photographed under a Hitachi branded electron microscope, model SU1510 at 10 kV, at the Laboratorio de Microscopía Electrónica y Fotografía de la Biodiversidad, Instituto de Biología, Universidad Nacional Autónoma de México (UNAM). The seeds were photographed in both ventral and dorsal view, and the testa ornamentation.

From the observations, measurements, and photographs, descriptions for each of the species were made, maintaining as much detail as possible to identify as accurately as possible the differences between the species.

***Measures and Qualitative Data Analyzed***—Material belonging to 14 of the 23 species distributed in Mexico was measured and analyzed, having a minimum of five replicates for each one of the species (Table 1). The carpological characters were measured from all the herbarium specimens that had the mature structures.

The characters that were measured in the fruit were the length of the metastyle (style reminiscence), length, width, and shape of the capsule and ornamentation of the pericarp (Fig. 1) as well as the length, width, and shape of the carpoatlas (Fig. 2). For the seeds, the length, width, and depth were also measured (Fig. 3), as well as the testa ornamentation (Table 1).

The shape of the seeds may vary greatly, and it has been suggested that it depends on the number of seeds per capsule (Fernández-Casas 2003). However, most seeds have a pyramidal shape in which a ventral face can be distinguished, where the hilum is located, and a smaller dorsal face. In the ventral face, the length, width, and depth were measured, as well as the distance from the ventral to the dorsal face (Fig. 3).

Detailed descriptions of the fruits and seeds for the 14 species analyzed were made, integrating as much information as possible, as well as photographs of the structures that allow the observation of variation (see Taxonomic Treatment).

From the data obtained, a normality test was performed using the Shapiro-Wilks statistical test (Shapiro and Wilk 1965), in the GraphPad Prism 5.0 software. The data summarized by species were analyzed using a principal component analysis (PCA). In general terms, PCA is based on

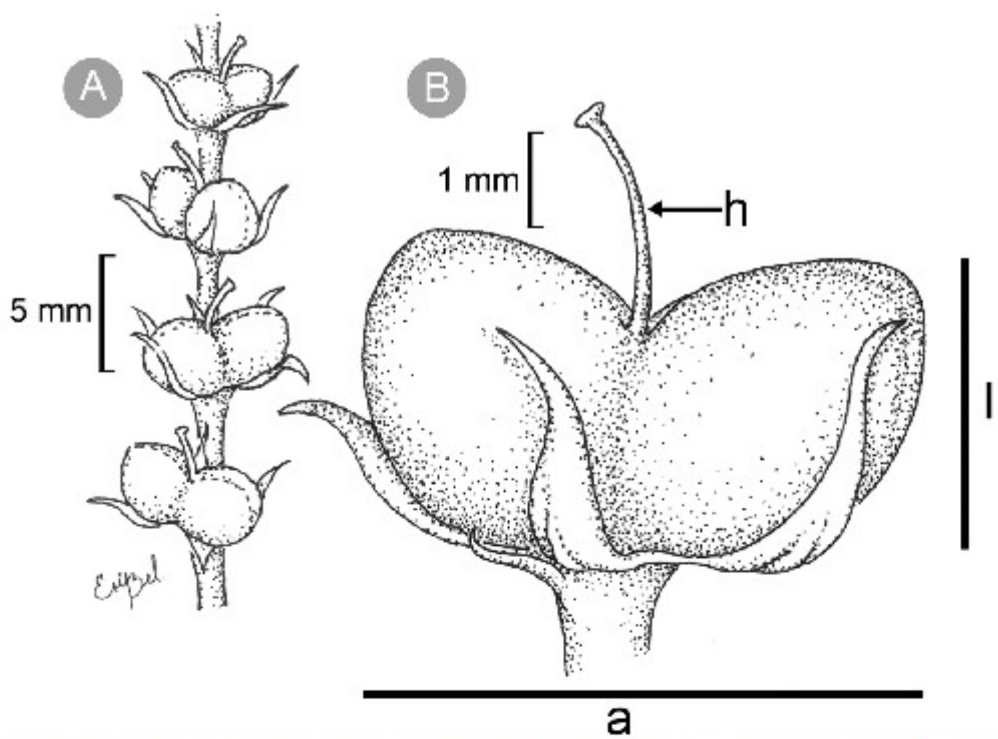


Fig. 1. *Spigelia humboldtiana* capsules. A. Fruits attached to the peduncle before dehiscence. B. Detail of the capsule showing the metastyle. l = length; a = width; h = metastyle. Illustration by Ericka B. Cortez.

TABLE 1. Fruit and seed measurements of the Mexican species of *Spigelia*. Sections: ⬢ = *Anthelmiae*; ↄ = *Coelostylis*; ▣ = *Speciosae*.

| Species | Measured specimen | Section | Metastyle | Capsule length | Capsule width | Carpostiles length | Carpostiles width | Seed length | Seed width | Seed depth |
|---|---|---|---|---|---|---|---|---|---|---|
| *Spigelia anthelmia* | *D. Álvarez 250* | ⬢ | 1.9 | 4.5 | 3.93 | 3.57 | 1.47 | 1.36 | 0.79 | 0.58 |
| *Spigelia anthelmia* | *D. Álvarez 251* | ⬢ | 1.9 | 4.1 | 3.55 | 3.8 | 1.67 | 1.25 | 0.7 | 0.41 |
| *Spigelia anthelmia* | *B. Serrín 1369* | ⬢ | 1.9 | 4.7 | 3.46 | 3.84 | 1.4 | 1.16 | 0.73 | 0.65 |
| *Spigelia anthelmia* | *B. Serrín 1369* | ⬢ | 1.9 | 4.6 | 4.41 | 3.5 | 1.47 | 1.45 | 0.89 | 0.31 |
| *Spigelia anthelmia* | *G. Castillo 18371* | ⬢ | 1.9 | 4.45 | 3.3 | 3.31 | 1.27 | 1.3 | 0.73 | 0.51 |
| *Spigelia carnosa* | *D. Breedlove 336464* | | 2.5 | 7.5 | 4.4 | 5.7 | 2.87 | 3 | 1.85 | 1 |
| *Spigelia carnosa* | *D. Breedlove 29632* | | 2.39 | 5.9 | 3.71 | 5.46 | 2.93 | 3.2 | 2.32 | 1.13 |
| *Spigelia carnosa* | *D. Breedlove 29632* | | 2.24 | 6.32 | 4.98 | 5.48 | 3.52 | 2.48 | 1.92 | 1.06 |
| *Spigelia carnosa* | *J. I. Calzada 9638* | | 2.18 | 7.4 | 6.04 | 5.62 | 4.02 | 3.12 | 2.22 | 0.98 |
| *Spigelia carnosa* | *J. I. Calzada 9638* | | 2.6 | 6.74 | 5.18 | 5.33 | 4.48 | 2.83 | 2.1 | 1.09 |
| *Spigelia coelostylioides* | *G. Cornejo 2781* | ↄ | 1.24 | 3.5 | 3.44 | 3.94 | 0.68 | 1.15 | 1.03 | 0.87 |
| *Spigelia coelostylioides* | *G. Cornejo 2781* | ↄ | 2.47 | 4.14 | 3.18 | 1.62 | 1 | 1.37 | 1.09 | 0.84 |
| *Spigelia coelostylioides* | *G. Cornejo 2781* | ↄ | 2.98 | 3.28 | 2.49 | 1.33 | 0.86 | 1.39 | 0.89 | 0.73 |
| *Spigelia coelostylioides* | *E. Martínez 39501* | ↄ | 1.74 | 3.92 | 3.24 | 1.28 | 1.12 | 1.08 | 0.92 | 0.58 |
| *Spigelia coelostylioides* | *E. Martínez 39501* | ↄ | 2 | 3.69 | 2.69 | 1.58 | 1.5 | 0.91 | 0.58 | 0.3 |
| *Spigelia guerrerensis* | *R. Cruz Durán 196* | | 1.5 | 7 | 5.3 | 6.1 | 3.9 | 1.48 | 0.95 | 0.65 |
| *Spigelia guerrerensis* | *R. Cruz Durán 196* | | 1 | 6.5 | 3.47 | 6.48 | 5.14 | 1.75 | 1.28 | 0.22 |
| *Spigelia guerrerensis* | *R. Cruz Durán 931* | | 2 | 7 | 3.23 | 6.99 | 4.58 | 1.71 | 1.38 | 0.89 |
| *Spigelia guerrerensis* | *M.A. Monroy 384* | | 1 | 6.8 | 4.58 | 6.47 | 4.4 | 1.63 | 1.15 | 0.83 |
| *Spigelia guerrerensis* | *M.A. Monroy 363* | | 1.5 | 6.65 | 4.4 | 5.2 | 5.45 | 1.86 | 1.23 | 0.58 |
| *Spielia hedyotidea* | *C.G. Pringle 839* | ↄ | 1.5 | 3.5 | 3.44 | 3.94 | 1.33 | 1.86 | 1.18 | 0.56 |
| *Spielia hedyotidea* | *C.G. Pringle 839* | ↄ | 1.18 | 5.53 | 4.92 | 3.98 | 2.94 | 2.01 | 1.21 | 0.53 |
| *Spielia hedyotidea* | *C.G. Pringle 839* | ↄ | 1.48 | 6.7 | 5.28 | 4.13 | 1.91 | 1.96 | 1.17 | 0.62 |
| *Spielia hedyotidea* | *A. Mora-Olivo 7758* | ↄ | 1.54 | 4.98 | 4.71 | 3.82 | 1.79 | 1.84 | 1.15 | 0.8 |
| *Spielia hedyotidea* | *A. Mora-Olivo 7758* | ↄ | 1.32 | 5.71 | 3.87 | 3.9 | 1.54 | 1.94 | 1.2 | 0.75 |
| *Spigelia humboldtiana* | *G. Pérez 403* | | 1.5 | 4.5 | 3.38 | 3.03 | 1.74 | 1.79 | 1.2 | 0.75 |
| *Spigelia humboldtiana* | *G. Pérez 403* | | 1.5 | 4.2 | 2.88 | 3.32 | 1.68 | 1.62 | 1.09 | 0.88 |
| *Spigelia humboldtiana* | *E. Carranza 3491* | | 1.45 | 4.6 | 3.48 | 3.09 | 1.53 | 1.76 | 1.23 | 0.89 |
| *Spigelia humboldtiana* | *E. Carranza 3491* | | 1.55 | 5 | 4 | 3.11 | 1.91 | 1.8 | 1.22 | 0.92 |
| *Spigelia humboldtiana* | *P. Tenorio 19567* | | 1.5 | 4.5 | 3.46 | 3.01 | 1.87 | 1.55 | 1.12 | 0.94 |
| *Spigelia humboldtiana* | *R. Duno 2207* | | 1.45 | 4.3 | 2.76 | 3.19 | 1.95 | 1.62 | 1.07 | 0.82 |
| *Spigelia humboldtiana* | *J. Maldonado 6799* | | 1.55 | 4.5 | 3.38 | 2.75 | 1.85 | 1.56 | 1.38 | 0.91 |
| *Spigelia longiflora* | *G.B. Hinton 14380* | | 5.42 | 7.44 | 4.83 | 6.45 | 3.48 | 4.1 | 3.6 | 1.7 |
| *Spigelia longiflora* | *F. Ventura 15436* | | 9.24 | 6.49 | 4.5 | 6.41 | 3.52 | 4.22 | 3.5 | 1.54 |
| *Spigelia longiflora* | *R. Hernández 11644* | | 6.43 | 7.19 | 4.98 | 6.5 | 3.62 | 3.54 | 3.43 | 1.73 |
| *Spigelia longiflora* | *L. Hernández 3993* | | 7.34 | 6.82 | 5.32 | 6.49 | 3.66 | 3.92 | 2.96 | 1.83 |
| *Spigelia longiflora* | *L. Hernández 3993* | | 8 | 6 | 5.4 | 6.53 | 3.46 | 3.27 | 2.79 | 1.47 |
| *Spigelia mexicana* | *M. Martínez-Cordillo 56* | | 6.12 | 4.72 | 3.18 | 4.64 | 2.84 | 2.4 | 1.56 | 1.26 |
| *Spigelia mexicana* | *M. Martínez-Cordillo 56* | | 6.43 | 5 | 2.85 | 4.43 | 2.58 | 2.2 | 1.97 | 1.13 |
| *Spigelia mexicana* | *F. López 161* | | 6.34 | 5.4 | 3.48 | 4.49 | 2.34 | 2.4 | 1.94 | 1.13 |
| *Spigelia mexicana* | *P. Tenorio L. 13853* | | 6.5 | 5.7 | 2.93 | 4.52 | 1.96 | 1.97 | 1.78 | 1.04 |
| *Spigelia mexicana* | *P. Tenorio L. 13853* | | 6.5 | 9 | 3.8 | 4.67 | 1.58 | 2.29 | 1.99 | 1.25 |
| *Spigelia polystachya* | *D. Àlvarez 8880* | ● | 0 | 2.51 | 1.63 | 1.49 | 1.09 | 0.62 | 0.5 | 0.25 |
| *Spigelia polystachya* | *D. Àlvarez 8880* | ● | 0 | 2.49 | 1.59 | 1.48 | 1.1 | 0.74 | 0.4 | 0.32 |
| *Spigelia polystachya* | *D. Álvarez 10260* | ● | 0 | 2.5 | 1.65 | 1.6 | 0.91 | 0.58 | 0.43 | 0.28 |
| *Spigelia polystachya* | *C. Cowan 2366* | ● | 0 | 2.48 | 1.58 | 1.38 | 0.91 | 0.73 | 0.51 | 0.26 |
| *Spigelia polystachya* | *F. Ventura 9061* | ● | 0 | 2.5 | 1.62 | 1.56 | 0.8 | 0.71 | 0.49 | 0.3 |
| *Spigelia pygmaea* | *C. Gutiérrez 8720* | | 0 | 2.54 | 1.48 | 1.69 | 0.74 | 0.63 | 0.51 | 0.21 |
| *Spigelia pygmaea* | *C. Gutiérrez 8720* | | 0 | 2.49 | 1.58 | 1.86 | 0.82 | 0.76 | 0.56 | 0.17 |
| *Spigelia pygmaea* | *E. Martínez 38272* | | 0 | 2.45 | 1.49 | 1.59 | 0.72 | 0.48 | 0.4 | 0.23 |
| *Spigelia pygmaea* | *D. Àlvarez 9682* | | 0 | 2.3 | 1.57 | 1.62 | 0.76 | 0.52 | 0.45 | 0.19 |
| *Spigelia pygmaea* | *D. Àlvarez 10389* | | 0 | 2.5 | 1.46 | 1.57 | 0.81 | 0.45 | 0.55 | 0.3 |
| *Spigelia scabrella* | *J. Rzedowski 53592* | | 1 | 7 | 6.84 | 4.5 | 2 | 2.4 | 1.8 | 1.5 |
| *Spigelia scabrella* | *A. Delgado 266* | | 0.8 | 5 | 6.71 | 4.6 | 2.3 | 2.12 | 1.15 | 0.89 |
| *Spigelia scabrella* | *E. Carranza 5635* | | 1.2 | 8 | 6.84 | 4.8 | 2.5 | 2.21 | 1.05 | 1.01 |
| *Spigelia scabrella* | *J. Rzedowski 14339* | | 0.9 | 5.88 | 3.47 | 4.69 | 2.71 | 2.2 | 1.84 | 1.14 |
| *Spigelia scabrella* | *J. Rzedowski 14339* | | 1.15 | 6.43 | 4.43 | 5.74 | 3.82 | 2.01 | 1.71 | 1.1 |
| *Spigelia speciosa* | *F. Miranda 3532* | ▣ | 7.5 | 6.3 | 6.2 | 6.12 | 3.63 | 3.7 | 3.15 | 1.71 |
| *Spigelia speciosa* | *F. Miranda 3532* | ▣ | 7.45 | 5.6 | 6.1 | 5.98 | 3.43 | 3.23 | 3.16 | 1.7 |
| *Spigelia speciosa* | *F. Miranda 3532* | ▣ | 7.3 | 5.8 | 5.9 | 6.31 | 4.05 | 3.62 | 3.23 | 1.88 |
| *Spigelia speciosa* | *C.G. Pringle 4652* | ▣ | 7.8 | 6.4 | 5.8 | 6.03 | 3.21 | 3.61 | 3.6 | 1.79 |
| *Spigelia speciosa* | *C.G. Pringle 4652* | ▣ | 6.5 | 6.3 | 6.2 | 5.93 | 3.7 | 3.23 | 3.06 | 1.36 |
| *Spigelia splendens* | *F. Miranda 7807* | | 1.5 | 5.56 | 3.5 | 3.41 | 2.03 | 2.2 | 1.5 | 0.95 |
| *Spigelia splendens* | *A. Hernández 2462* | | 1 | 5.56 | 3 | 3.47 | 1.82 | 2.24 | 1.84 | 1.15 |
| *Spigelia splendens* | *A. Hernández 2462* | | 1.5 | 5.4 | 3.5 | 3.57 | 2.21 | 2.07 | 1.57 | 1.27 |
| *Spigelia splendens* | *A. Hernández 2462* | | 1.2 | 5.6 | 3.2 | 3.87 | 2.09 | 2.09 | 1.79 | 0.94 |
| *Spigelia splendens* | *W.R. Anderson 4948* | | 1.3 | 5.43 | 4 | 3.56 | 2.25 | 1.9 | 1.73 | 1.17 |
| *Spigelia splendens* | *W.R. Anderson 4948* | | 1.4 | 5.56 | 3.9 | 3.18 | 2 | 2.15 | 2.05 | 1.02 |
| *Spigelia splendens* | *W.R. Anderson 4948* | | 1.5 | 5.41 | 3.5 | 2.95 | 2.02 | 2.19 | 1.93 | 1.03 |
| *Spigelia texana* | *J.A. Villareal 4705* | ↄ | 1.5 | 2.49 | 3.75 | 4.61 | 1.88 | 2.12 | 1.55 | 0.97 |
| *Spigelia texana* | *J.A. Villareal 4705* | ↄ | 1.52 | 3.02 | 3.63 | 4.58 | 1.8 | 1.88 | 1.52 | 0.86 |
| *Spigelia texana* | *T. Wendt 1654* | ↄ | 1.53 | 2.53 | 3.8 | 4.49 | 1.79 | 2.13 | 1.39 | 0.87 |
| *Spigelia texana* | *T. Wendt 1654* | ↄ | 1.55 | 3.12 | 3.14 | 4.72 | 1.85 | 2.14 | 1.63 | 1.01 |
| *Spigelia texana* | *T. Wendt 1654* | ↄ | 1.5 | 2.87 | 3.61 | 4.68 | 1.9 | 2.18 | 1.59 | 0.87 |

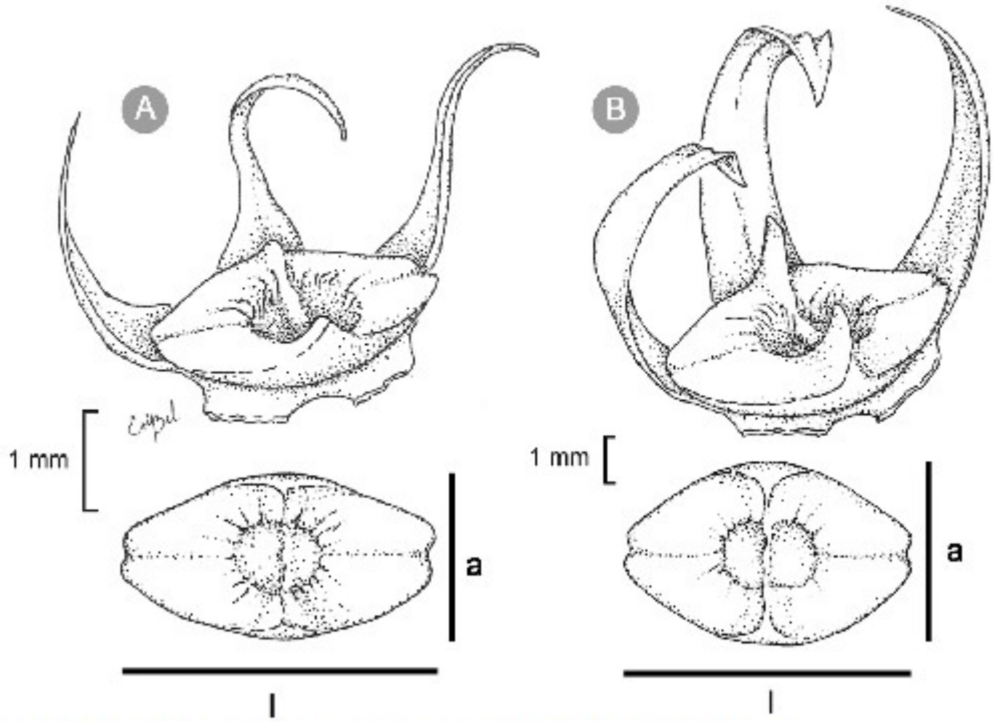


FIG. 2. Carpoatlas. A. *Spigelia humboldtiana*. B. *Spigelia guerreroensis*. l = length; a = width. Illustration by Ericka B. Cortez.

the transformation of the original variables into another set of independent variables known as principal components (Imán et al. 2011). These analyses were carried out in order to find the best summary of the data using the least number of main components; this makes it possible to identify those characteristics that have the least distance between them in the morphospace (Lever et al. 2017). In this study, PCA was applied to examine the patterns of multivariate association between the measured characteristics and to determine how far apart the species are in the space defined by the first main components. The PCA was performed with Clustvis using the probabilistic method (Metsalu and Vilo 2015).

To determine the usefulness of fruit and seed characters in the delimitation of species in *Spigelia*, a discriminant function analysis was carried out (DFA). This analysis was based on a matrix with the variables of Table 1, measured on at least five specimens of the same species. In general, the DFA is a method that allows us to identify the relationships between quantitative predictive variables and qualitative criteria variables; thus, we can identify boundaries between groups of objects (Ioffe 2006). The results indicate whether these groups can be separated by a linear combination of these predictors. The classification criterion used minimizes the probability of misclassification, that is, the rule obtained makes the rate of misclassified objects as low as possible (Casanova et al. 2009).

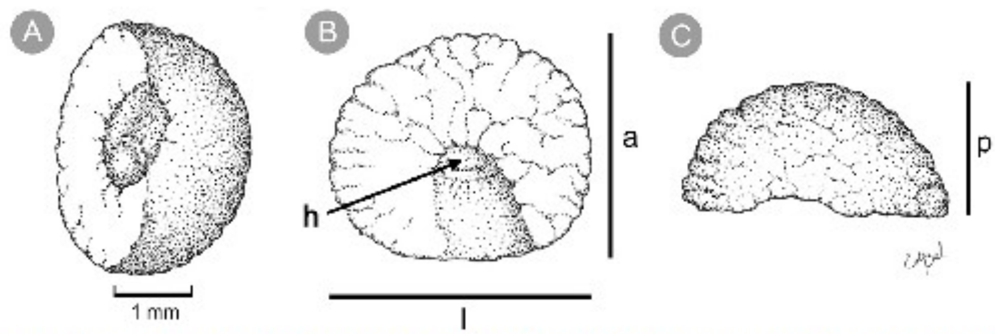


FIG. 3. *Spigelia longiflora* seeds. A. ¾ view. B. Ventral view showing the hilum. C. Side view. l = length; a = width; p = depth; h = hilum. Illustration by Ericka B. Cortez.

TABLE 2. Associated charges to the first three principal components.

| | PC1 | PC2 | PC3 |
|---|---|---|---|
| Metastyle | −3.26 | −7.53 | 0.49 |
| Capsule length | 12.58 | 0.68 | 2.91 |
| Capsule width | 6.11 | 0.85 | −0.25 |
| Carpoatlas length | 6.84 | −0.13 | −3.73 |
| Carpoatlas width | −2.56 | 1.78 | −0.4 |
| Seed length | −3.89 | 0.91 | −0.1 |
| Seed width | −6.35 | 1.08 | 0.26 |
| Seed depth | −9.47 | 2.37 | 0.82 |

The data matrix was processed with the NTSYSpc 2.11T software (Rohlf 1998) to obtain a matrix reflecting the similarity between the species. For this purpose, the neighbor joining method was used (NJ), which generates a dendrogram through distance clustering (in this case Euclidean distances), trying to minimize the total length of the branches (Saitou and Nei 1987). Thus, the DFA allowed to examine the capacity of fruit and seed characteristics to separate species. A correct classification of the specimens in species exposes the importance of including these types of characteristics in the delimitation of species in *Spigelia*.

## RESULTS

The variation in size and shape of the structures analyzed in this study (Table 1), allowed distinguishing groups of species. For the differentiation of these groups, characters such as the size of the metastyle, seed width, the capsule length, or testa ornamentation were extremely important. These variables presented a normal distribution ($p > 0.05$).

Components 1 and 2 of the PCA together explain 85.9% of the accumulated variation in the carpological and seminal structures analyzed. The characteristics with greater contribution to the main component one (CP1) were capsule length, seed width, as well as the carpoatlas length and the seed depth; in contrast, in the CP2, the metastyle length, carpoatlas width, and seed length contribute more significantly (Table 2).

Figure 4 shows the different specimens measured in the space of the first two components. The separation of species along the CP1 is remarkable, a component that gathers, to a large extent, the differences in size of fruits and seeds. In Fig. 4, this difference in size is expressed in four species clusters. One group includes *Spigelia polystachya* Klotzsch ex Progel and *S. pygmaea* D.N. Gibson, which have the smallest structures. The second group consists of the species *S. anthelmia* L., *S. coelostylioides* K.R. Gould, *S. hedyotidea* A. DC., *S. humboldtiana* Cham. & Schltdl., *S. splendens* H. Wendl., and *S. texana* (Torr. & A. Gray) A. DC. These species are grouped because they have capsules of 3.0–5.0 mm long, like the carpoatlas, as

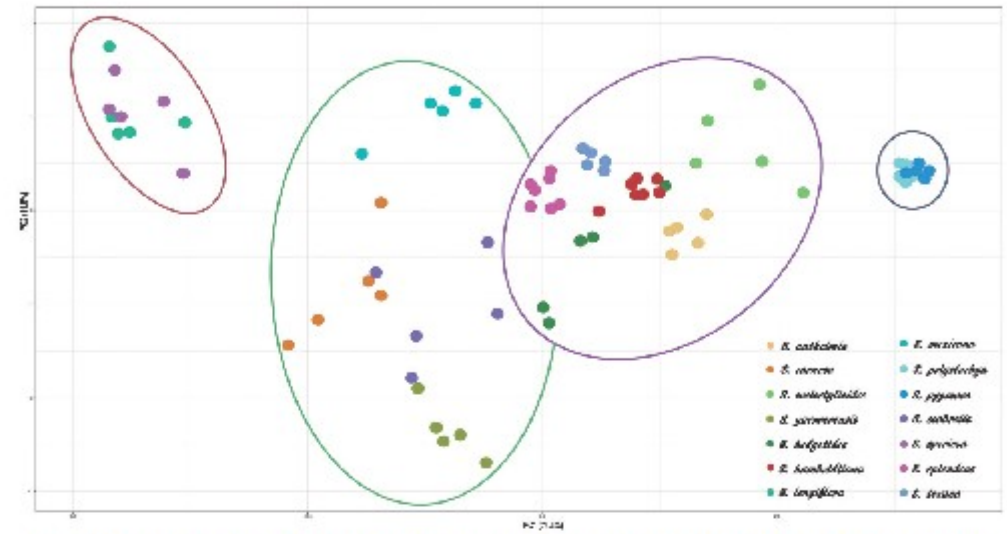

FIG. 4. Principal component analysis (PCA), using the carpological data of 14 *Spigelia* species. Blue = group 1; Pink = group 2; Green = group 3; Red = group 4.

TABLE 3. Coefficients of linear discriminants of the DFA.

| | LD1 | LD2 | LD3 | LD4 | LD5 | LD6 | LD7 | LD8 |
|---|---|---|---|---|---|---|---|---|
| Metastyle | 3.0084845 | 3.17250686 | −2.517214 | 0.7454492 | 0.3569548 | −0.36901779 | 0.32017317 | 0.5722694 |
| Capsule length | 0.6277827 | −1.07394969 | −1.9005318 | −1.8024108 | 0.6906291 | 0.22284049 | 0.46418862 | −0.8596299 |
| Capsule width | 0.5097777 | −0.0377007 | 1.2142673 | 1.0090652 | −0.5275271 | −1.7778943 | 1.01301754 | 0.1156913 |
| Carpoatlas length | 2.1358589 | −1.21236546 | −0.3268573 | 2.458969 | 0.451057 | 0.03170639 | −1.42048621 | −1.5379445 |
| Carpoatlas width | 1.2003931 | −1.42962054 | −1.0516675 | −0.7030306 | −1.4508709 | 0.38632425 | −0.00842968 | 1.5450841 |
| Seed length | 1.655441 | −1.60246379 | 2.6132497 | −0.142486 | 4.175551 | 1.73946246 | 0.28806468 | 2.2901895 |
| Seed width | 1.688485 | 1.90501761 | 1.770614 | 0.3069381 | −3.578699 | 0.32373458 | 1.84469354 | −2.8867661 |
| Seed depth | 0.3115143 | 0.07199218 | −0.459546 | −2.1615813 | −0.4165841 | −0.89691849 | −2.44124961 | 0.9055326 |

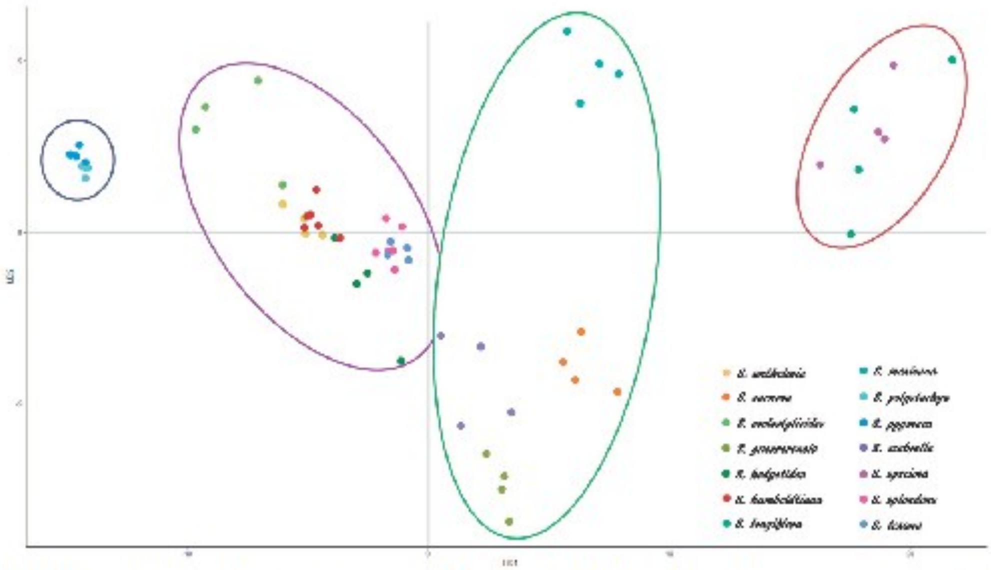

FIG. 5. Discriminant functions analysis (DFA) using morphological characteristics of fruits and seeds of *Spigelia*. Four main groupings are shown, with carpological data corresponding to 5 individuals for each of the 14 species. The first two discriminant functions (LD) explain 92% of the variation, with LD1 = 83% and LD2 = 9%.

well as seeds ranging from 0.3–0.99 mm deep, the three main characters that explain the variation in the CP1.

The third group is integrated by *S. carnosa* Standl. & Steyerm, *S. guerrerensis* L.O. Alvarado et J. Jiménez Ram., *S. mexicana* A. DC. and *S. scabrella* Benth. These species are grouped in the first component because they have capsules of about 6 mm long and carpoatlas of more than 4.5 mm long, as well as seeds of more than 1 mm deep. The last group is integrated by *S. longiflora* M. Martens & Galeotti and *S. speciosa* Kunth.; these species have the biggest seeds with more than 3 mm in diameter and 1.5 mm depth, carpoatlas more than 6 mm long, and metastyles 7 to 8 mm long.

The discriminant function analysis (DFA, Table 3) also supported the differentiation of four major clusters (Fig. 5). The first two discriminant axes explain 92% of the variation among *Spigelia* fruits and seeds. The first discriminant function contributes 83% and the second 9%. The characteristics that better explain the separation of LD1 into two groups are

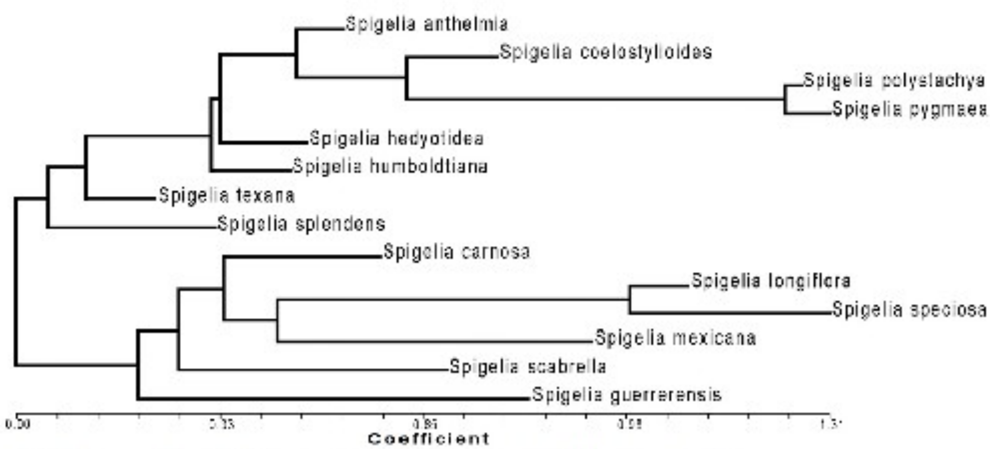


FIG. 6. Dendrogram obtained with the closest neighbor (NJ) method and using the Euclidean distance coefficient.


FIG. 7. Carpoatlas of 15 species of *Spigelia* distributed in Mexico. A. *Spigelia anthelmia*. B. *S. carnosa*. C. *S. coelostylioides*. D. *S. dolychostachya*. E. *S. guerrerensis*. F. *S. hedyotidea*. G. *S. humboldtiana*. H. *S. longiflora*. I. *S. mexicana*. J. *S. polystachya*. K. *S. pygmaea*. L. *S. scabrella*. M. *S. speciosa*. N. *S. splendens*. O. *S. texana*. Scale bar = 0.5 cm.

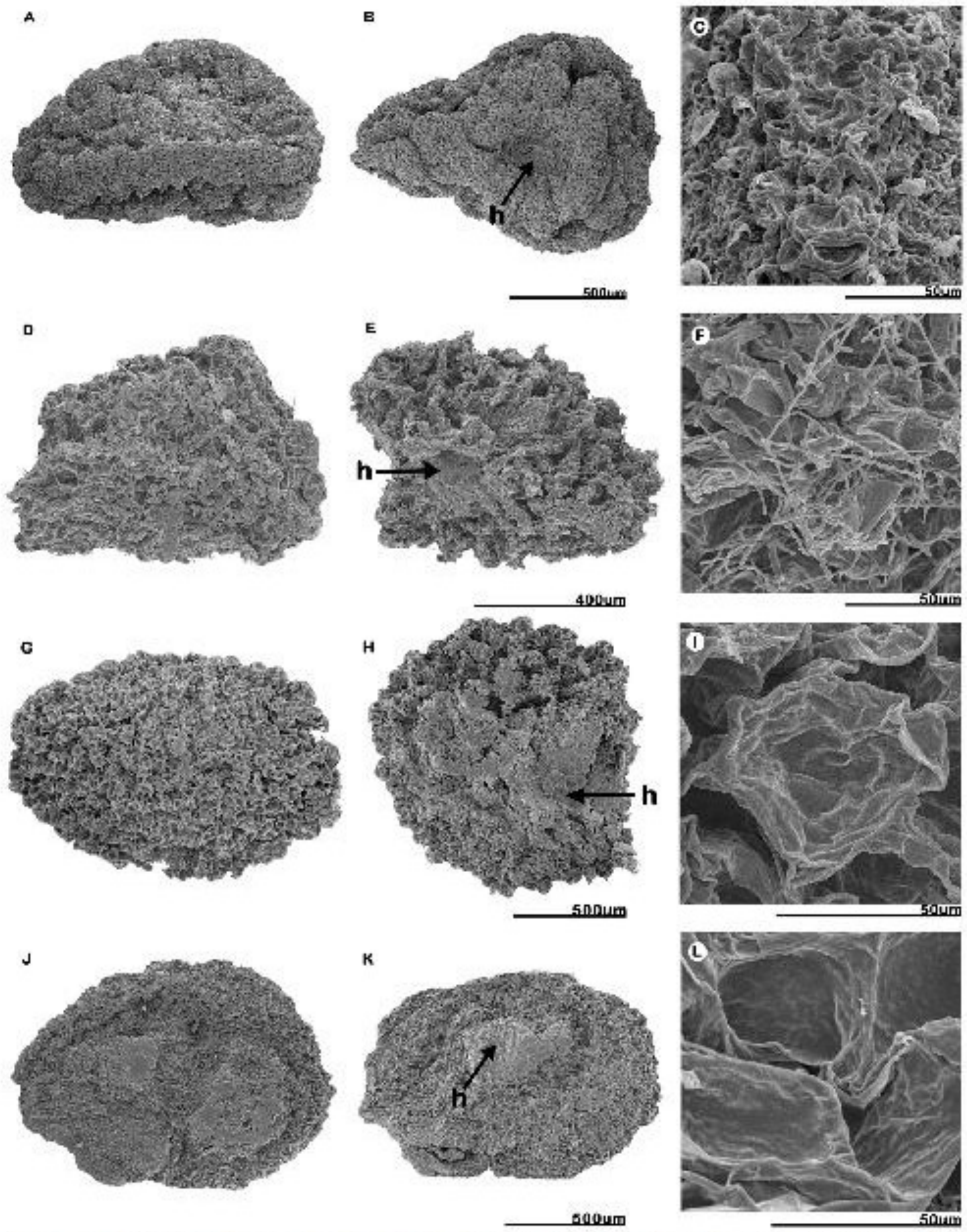


FIG. 8. Seeds in dorsal view, ventral view, and close-up of the testa ornamentation. A–C. *Spigelia anthelmia.* D–F. *Spigelia coelostylioides.* G–I. *Spigelia guerrerensis.* J–L. *Spigelia hedyotidea.* h = hilum.

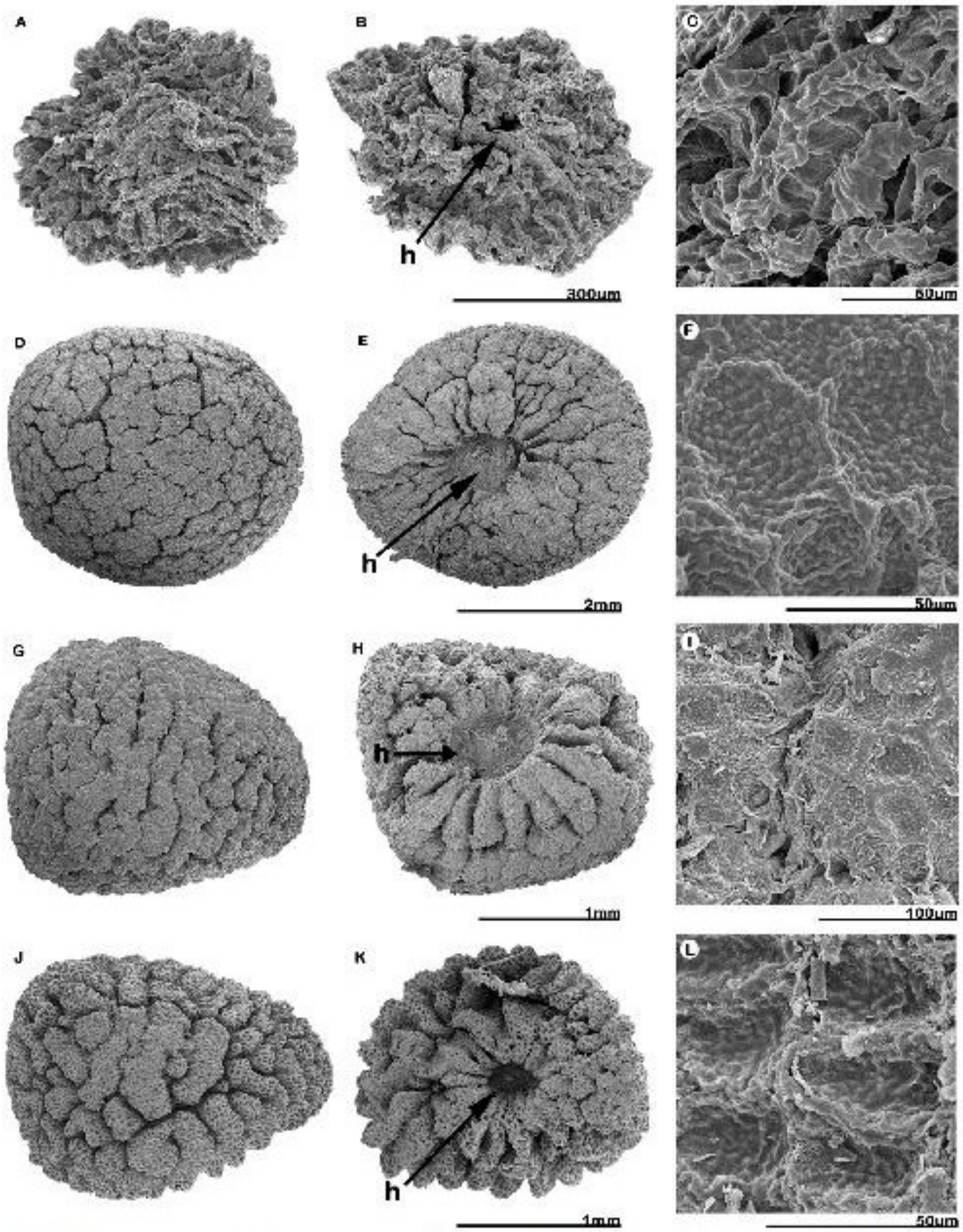


FIG. 9. Seeds in dorsal view, ventral view, and close-up of the testa ornamentation. A–C. *Spigelia humboldtiana*. D–F. *Spigelia longiflora*. G–I. *Spigelia mexicana*. J–L. *Spigelia polystachya*. h = hilum.

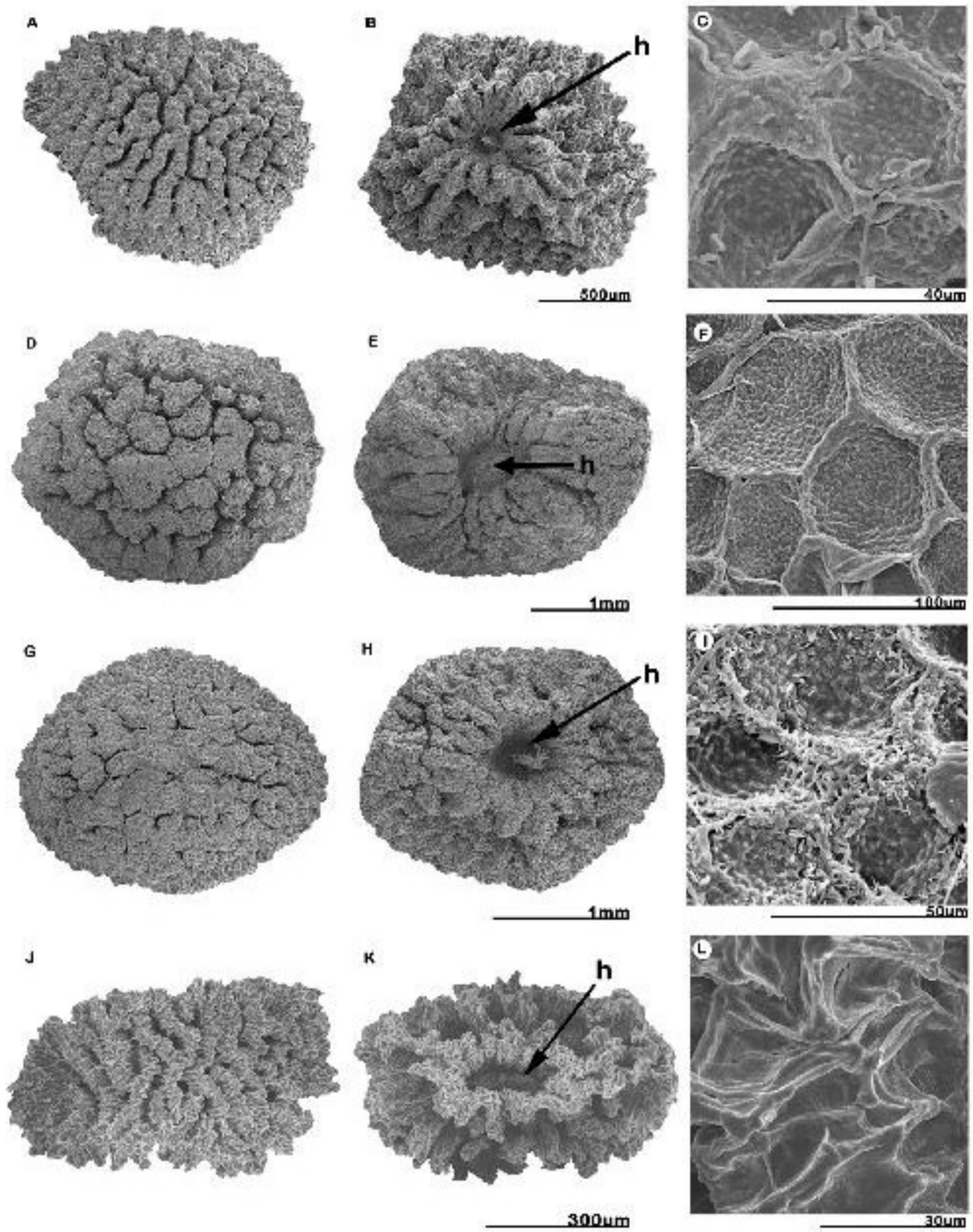


FIG. 10. Seeds in dorsal view, ventral view, and close-up of the testa ornamentation. A–C. *Spigelia pygmaea*. D–F. *Spigelia speciosa*. G–I. *Spigelia splendens*. J–L. *Spigelia texana*. h = hilum.

the length of metastyle, the length of carpoatlas, and the width of the seed, while those of LD2 are the width of carpoatlas and the length of the seed, which are divided into three additional groups. The separation of the four groups resulting from the DFA is highly significant, with a predictive value of 0.93. This suggests that the probability of misclassification from the proposed characteristics is very low.

The dendrogram generated from the clustering method (Fig. 6), largely recovers the groups formed by the PCA and the DFA. The formation of two main groups can be observed, consisting of the same species as the purple-blue and pink-green groups in the PCA analysis, where the species with the smallest fruit and seed structures (*S. polystachya* and *S. pygmaea*) are clustered within the medium structure species, formed by group two of the PCA. The second group, formed by *S. carnosa*, *S. guerrerensis*, *S. longiflora*, *S. mexicana*, *S. scabrella*, and *S. speciosa*, recovers to a great extent the group separated by the discriminant LD1 of the DFA, where, in addition, the two groups are separated in a similar way by LD2.

## Carpological Descriptions

The descriptions of the capsules and seeds for the genus were made by contrasting in the best way the structures for each of the species, described below in the taxonomic treatment. The capsules are bilobed globose, with a dry, thin, smooth or papillary, glabrous or pubescent pericarp, the apex may be reminiscent of style, called metastyle, which consists of the lower part of the style's joint. Dehiscence is loculicidal, septicidal, and circumcissile at the same time. After dehiscence, the base of the fruit is called a carpoatlas and remains attached to the stalk (Fernández-Casas 2003). The carpoatlas is a hardened disc with a central hole. In some cases, it usually shows the remains of a septal membrane. They can also present a transversal ridge, and two projections in the middle of the carpoatlas that reflect the septicidal dehiscence of the carpels. The disc may be flat or concave, and varies in shape depending on the species, ranging from oblong to elliptical or rhombic (Fig. 7).

The seeds are derived from an anatropous to semi-anatropous ovule and vary in number, ranging from 4 to 16 per capsule and from 0.4 to 6 mm in diameter (Figs. 8, 9, 10). The testa has a regular or irregular reticulated pattern, with extratectal elements in the form of warts in some species. The seeds present quadrangular, elliptical, ovoid, trullate, rhombic, and hemispherical shapes, where it is easy to distinguish a highly ornate dorsal face and a ventral one, where the hilum is located in a depression. In some cases, they become compressed.

Spigelia anthelmia L., Sp. Pl. 1:149-150, 1753. Type: Brazil. Brasilia: Habitat in Cajenna, s.d., Anon s.n. (Lectotype, designated by Leeuwenberg, Act. Bot. Neerl. 10:461-465, 1961, LINN-HL210-2!).

**Capsules** 4.1–4.7 mm long, 3.5-4.5 mm wide, bilobed, pericarp apically papillary; metastyle 1.6–1.9 mm long; carpoatlas 3.3–3.9 mm long, 1.2–1.7 mm wide, rhombic shape, transverse ridge absent. **Seeds** 1.2-1.5 mm long, 0.75–1.1 mm wide, 0.5–1.0 mm deep, ovate, with flat dorsal sides; rough testa, with small triangular projections, in some cases flattened from the tip.

*Specimens Examined*—**Mexico.** —Campeche: Municipio Calakmul: 2 km al NW de Narciso Mendoza, camino a Costa Maya, *D. Àlvarez 250* (MEXU). —Chiapas: Municipio Acapetahua: Santa Teresa, *E. Matuda 16686* (MEXU). —Guerrero: Municipio Chilpancingo de los Bravo: Cerro Del Alquitrán, delante de Petaquillas, al SE de Chilpancingo de los Bravo, *S/N W. Schwabe* (MEXU). —Oaxaca: Asunción Ixtaltepec, 1.66 km al NW del Morrito, cima cerro Timbón, *S.H. Salas M. 4656* (MEXU, SERBO). —Puebla: Municipio Hueytamalco: El cerro, *F. Ventura A. 17871* (OAX). —Querétaro: Municipio Jalpan: Tanchanaquito, *B. Serván 1369* (IEB). —Quintana Roo: Municipio Benito Juárez: Brecha camino al N, sobre carretera Cancún-Mérida, *E. Cabrera 79* (MEXU, CICY). —San Luis Potosí: Municipio Cárdenas: Poza Azul, cerca de Canoas, *J. Rzedowski 24562* (ENCB). —Tabasco: Municipio Bacalán: Ejido Faustino, *A. Ramírez B. 26* (MEXU). —Veracruz: Municipio Actopan: Pajaritos, 1 km al NE, *G. Castillo 18371* (XAL, MEXU). —Yucatán: Municipio Chemax: A 12 km al O de Chemax, sobre la carretera Valladolid- Cancún, *E. Cabrera 8887* (MEXU).

Spigelia carnosa Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23(2):72-73. 1944. Type: Guatemala. Huehuetenango: dense rich wet woods between Yulhuitz and Maxbal, Sierra de los Cuchumatanes, 15 Jul 1942, *J.A. Steyermark 48692* (Holotype: F-0062160!; Isotype: GH, US-00112909!).

**Capsules** 7.0–8.0 mm long, 4.0-4.5 mm wide, bilobed, pericarp smooth; metastyle 2.2–2.6 mm long; carpoatlas 4.5-7.5 mm long, 2.5–3.4 mm wide, elliptical, absent transverse ridge. **Seeds** 2.0–3.0 mm long, 1.85 mm wide, 0.8–1.0 mm deep, elliptical; densely grained testa.

*Specimens Examined*—**Mexico.** —Chiapas: Municipio La Independencia: Third ridge along road from Las Margaritas to Campo Alegre, *D.E. Breedlove 336464* (MEXU). Municipio La Trinitaria: Al E de la Laguna Tzikaw, Parque Nacional Monte Bello, *D.E. Breedlove 29632* (MEXU). 4 km al E de la laguna Tzikaw, cerca de Dos Lagos, *D.E. Breedlove 38815* (MEXU). Municipio Las Margaritas: Camino de terracería entre La Soledad y Tierra Fría, *A. Méndez 7960* (MEXU). Municipio Ocozocoautla: Cerro la Colmena, NE del Rancho Corocíño, Reserva Ecológica El Ocote, *J.I. Calzada 9638* (MEXU, XAL).

Spigelia coelostylioides K.R.Gould, Brittonia 51(4):407-410, f. 1-2- 1999. Type: México. Chiapas: Mun. Venustiano Carranza: Aguacatenango, 19 May 1995, *K.R. Gould 139* (Holotype: TEX-256906!; Isotypes: G, MEXU-854904! NY).

**Capsules** 7.0–8.0 mm long, 3.8–5.0 mm wide, bilobed, smooth pericarp; metastyle 2.2–2.6 mm long; carpoatlas 3.1–4.7 mm long, 1.3–1.7 mm wide, oblong shape, transverse ridge absent. **Seeds** 0.8–1.0 mm long, 0.5–0.6 mm wide, 0.25–0.40 mm deep, ovoid; rough testa.

*Specimens Examined*—**Mexico.** —Chiapas: Municipio Altamirano: El Taiamanil, lado norte del poblado ejido Puebla Nueva, *A. Pérez 1* (MEXU). —Oaxaca: Municipio San Lucas Ojitlán: Poblado de Vista Hermosa, *J.I. Calzada 14187* (MEXU). —Puebla: Municipio Hueytamalco: Campo experimental Las Margaritas, INIFAP, *G. Cornejo 2781* (IEB, MEXU). —Querétaro: Municipio San Joaquín: Apartadero, brecha hacia La Redonda, *R. Hernández 10679* (MEXU). —Veracruz: Municipio Uxpanapa: A 3.3 km al SO del Poblado II, *E. Martínez S. 39501* (MEXU).

Spigelia guerrerensis L.O.Alvarado & J.Jiménez Ram., Phytotaxa 238(2) 183-189. 2015. Type: México. Guerrero: Municipio Eduardo Neri: Cerro El Ocotal, 1.05 km al SE de Amatitlán, 11 Aug 1994, *M.A. Monroy de la Rosa 384* (Holotype: FCME-50441!).

**Capsules** 6.5–7.0 mm long, 5.0-5.5 mm wide, bilobed, hairy pericarp; metastyle 1.0–2.0 mm long; carpoatlas 5.2–7.0 mm long, 3.2–4.6 mm wide, elliptical, transverse ridge present. **Seeds** 1.8–2.0 mm long, 0.95 mm wide, 0.65 mm deep, compressed ovate; foveolate testa.

*Specimens Examined*—**Mexico.** —Guerrero: Municipio Atlixtac: Petatlán, 3.29 km al ONO, *O.S. Rodríguez 22* (FCME). 5 km al E de Atlixtac, camino a Petatlán, *R. Cruz Durán 9186* (FCME). Amatitlán, 4.7 km al O, *M.A. Monroy 363* (FCME). Cerro el Ocotal, 1.15 km al SE de Amatitlán, *M.A. Monroy 384* (FCME), *392* (FCME). Amatitlán, *R. Cruz Durán 197* (FCME). 11 km al SE de Amatitlán, carretera Amatitlan-Carrizalillo, *R. Cruz Durán 931* (FCME, MEXU). Municipio Taxco de Alarcón: Tlamacazapa, *B.E. Carreto 11* (FCME), *J.A. Almazan 1* (FCME). —OAXACA: Municipio San Bartolo: Tejón, llano para llegar a la reja, *D. López Pascual 1022* (MEXU).

SPIGELIA HEDYOTIDEA A.DC., Prodr. 9:7-8. 1845. TYPE: NUEVO MÉXICO. 1851, *C. Wright 1663* (Holotype: P-511989!).

**Capsules** 5.3–6.2 mm long, 3.8–5.0 mm wide, globose, papillary pericarp at the apex; metastyle 1.0–2.0 mm long; carpoatlas 4.5–5.5 mm long, 1.0–1.5 mm wide, oblong shape, transverse ridge present. **Seeds** 1.5–2.0 mm long, 1.0–1.3 mm wide, 0.5–0.75 mm deep, elliptical; reticulated testa.

*Specimens Examined*—**Mexico.** —CHIHUAHUA: Cerca de Chihuahua, *C.G. Pringle 839* (MEXU). —TAMAULIPAS: Municipio Gómez Farias: Río Sabies, bajo el puente en la carretera Mante-Llera, *A. Mora-Olivo 7759* (MEXU).

SPIGELIA HUMBOLDTIANA Cham. & Schltdl., Linnaea 1(2): 200-202. 1826. LECTOTYPE, designated by Ewan, VENEZUELA. Sucre: Habitat ad Cumaná, 1799, *F. Humboldt & A. Bonpland 174* (Lectotype: B-W3552!, Isolectotype: P-507553!).

**Capsules** 4.0–4.5 mm long, 2.7–4.0 mm wide, bilobed, smooth pericarp; metastyle 1.5–2.0 mm long; carpoatlas 2.7–3.4 mm long, 1.5–2.0 mm wide, elliptical, transverse ridge present. **Seeds** 1.5–1.8 mm long, 1.0–1.2 mm wide, 0.5–0.75 mm deep, trullate-ovoid; reticulated testa.

*Specimens Examined*—**Mexico.** —CHIAPAS: Municipio Acacoyagua: Cerro Ovando, polígono de Amortiguamiento, *N. Martínez 941* (FCME, MEXU). —GUERRERO: Municipio Acapulco de Juárez: Acapulco, *F. Miranda 3343* (MEXU). Municipio Juan R. Escudero: El Zapote, *J. Maldonado 6799* (FCME). Municipio Mártir de Cuilapan: La Esperanza, reserva campesina, *C. Teyuco 135-A* (FCME). —OAXACA: Municipio Acatlán de Pérez: Cerro del tigre 3 km al este de Acatlán vía Tierra Blanca-Alcatán, *L. Cortes 473* (IEB, MEXU). —PUEBLA: Municipio Agua Dulce: 4 km al SE de Ahuacatlán, brecha a Zapotitlán, *G. Toriz 581* (MEXU). —QUERÉTARO: Municipio Arroyo Seco: 7-8 km al W del Puerto de Ayutla, *E. Carranza 3491* (IEB, QMEX, UAMIZ). —QUINTANA ROO: Municipio Felipe Carrillo Puerto: 8 km al S de Yactún, *G. Pérez 403* (MEXU, XAL). —SAN LUIS POTOSÍ: Municipio Aquismon: Tamparal, *J.B. Alcorn 3048* (MEXU). —TABASCO: Municipio Centla: Cerca de San Manuel, al S del poblado a lo largo del Río Mezcalapa, *E. Hernández 89* (MEXU). —TAMAULIPAS: Municipio Gómez Farias: Rancho El Cielito, 3 km al SW del Encino, *L. Hernández 3003* (MEXU, XAL). —VERACRUZ: Municipio Agua Dulce: Ejido Gavilán, *P. Tenorio 19567* (MEXU). —YUCATÁN: Municipio José María Morelos: Carretera José María Morelos-Chetumal, aproximadamente 32 km al S de José María, desviación al poblado Gavilán, *R. Duno 2207* (MEXU).

SPIGELIA LONGIFLORA M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11(1):376. 1844. TYPE: MÉXICO. Hidalgo: les environs de Regla, pres Real del Monte, Sep 1835, *H. Galeotti 1477* (Holotype: BR).

**Capsules** 7.0–8.5 mm long, 5.0–6.0 mm wide, bilobed, smooth pericarp; metastyle 5.0–9.0 mm long; carpoatlas 6.0–7.0 mm long, 3.0–4.0 mm wide, elliptical, transverse ridge present. **Seeds** 3.5–4.2 mm long, 2.5–2.8 mm wide, 1.4–1.5 mm deep, semi-spherical; reticular testa.

*Specimens Examined*—**Mexico.** —GUANAJUATO: Municipio Xichú: El Salto, *E. Ventura 9191* (IEB, MEXU, XAL). —GUERRERO: Municipio Ajuchitlán del Progreso: Chilcayote-Carrizal, *G.B. Hinton 14380* (ENCB). —HIDALGO: Municipio Huejutla de Reyes: Pahuatlán, *J. Salazar 5* (MEXU). —MORELOS: Municipio Tepoztlan: Cerro El Tepozteco, *L. Hernández 3993* (MEXU, QMEX). —PUEBLA: Municipio Cuautempan: 1 km al W de Ixtolco, brecha de Tetela, *G. Toriz 547* (MEXU). —QUERÉTARO: Municipio Cadereyta de Montes: Maconí-Ranchería La Luz, *R. Hernández 11644* (MEXU, QMEX). —SAN LUIS POTOSÍ: Municipio Río Verde: El Agujón, 28 km al SW de Río Verde, *Rzedowski 7689* (IEB, MEXU, OAX). —VERACRUZ: Municipio Acultzingo: La Barranca del Tule, *F. Ventura 15436* (IEB, MEXU, OAX, XAL).

SPIGELIA MEXICANA A.DC., Prod. 9:7. 1845. TYPE: MÉXICO. México, s.d., *J.A. Pavón s.n.* (Lectotype, designado by McVaugh: G-00368297!).

**Capsules** 6.5–9.0 mm long, 3.5–4.0 mm wide, elliptical, smooth pericarp; metastyle 5.8–7.0 mm long; carpoatlas 4.5–5.0 mm long, 1.4–1.8 mm wide, oblong shape, transverse ridge present. **Seeds** 1.8–2.3 mm long, 1.5–2.0 mm wide, 1.25 mm deep, trullate-ovoid; foveolate testa.

*Specimens Examined*—**Mexico.** —GUERRERO: Municipio Ahuacotzingo: Aproximadamente 12 km al S de Ajuatetla, carretera Ajuatetla-Chilapa, *M. Martínez-Gordillo 56* (HUAP, FCME, MEXU). —PUEBLA: Municipio Tepetzintla: Cerro Chiquinahuimazatl, al W de Tepetzintla, *P. Tenorio L. 13853* (MEXU). —OAXACA: Municipio San Miguel del Puerto: Panteón, *F. López 161* (IEB).

SPIGELIA POLYSTACHYA Klotzsch ex Progel, Fl. Bras. 6(1):265. 1868. *Pseudospigelia polystachya* (Klotzsch ex M.R.Schomb) W. Klett, Bot. Arch. 1923. TYPE: GUYANA. Guyana britanicae regione, 1840, *R. Schomburgk 412* (Holotype: G; Isotype: B).

**Capsules** 2.0–2.7 mm long, 1.2–2.2 mm wide, globose, smooth pericarp; absent metastyle; carpoatlas 1.0–2.0 mm long, 0.5–1.0 mm wide, quadrangular in shape, transverse ridge absent. **Seeds** 0.9–1.3 mm long, 0.4–0.5 mm wide, 0.3 mm deep, compressed ovate; rough testa.

*Specimens Examined*—**Mexico.** —CAMPECHE: Municipio Campeche: 2 km al NE de China, *C. Gutiérrez B. 5901* (CICY, MEXU, UAMIZ, XAL). Municipio Holpechén: A 4.3 km al NO de Chan-Chen, *D. Álvarez 8880* (MEXU). A 9.8 km al SSE de Pachuitz, D. Álvarez 9106 (MEXU). A 9.03 km al S de Pachuitz, *D. Álvarez 10252* (MEXU). A 7.16 km al S de Pachuitz, *D. Álvarez 10260* (MEXU). A 6.47 km al E de Chan-Chen, *D. Álvarez 10307* (MEXU). —TABASCO: Municipio Centro: Rancho Dos Monte, km 12 de la carretera Villahermosa-Escárcega, atrás del aeropuerto, *A. Sol 174* (MEXU). Municipio Nacajuca: Camellones Chontales de Tucta, cerca de Nacajuca, *C. Cowan 2366* (ENCB, XAL). —VERACRUZ: Municipio Paso de Ovejas: Acazónica, *F. Ventura A. 18063* (IEB, MEXU). Municipio Puente Nacional: La Ceiba, *F. Ventura A. 9061* (MEXU, XAL); *10876* (ENCB).

SPIGELIA PYGMAEA D.N.Gibson, Fieldiana, Bot. 32(1): 5-6. 1968. TYPE: GUATEMALA. Petén: in savanna ca. 7 km W of village in zapotal, on La Gloria road, Dos Lagunas, 19 Oct 1960, *E. Contreras 1537* (Holotype: LL-256903!; Isotype F-1652726!, TEX).

**Capsules** 1.8–2.5 mm long, 1.3–1.6 mm wide, globose, papillary pericarp; absent metastyle; carpoatlas 1.0–2.0 mm long, 0.4–1.0 mm wide, oblong shape, transverse ridge absent. **Seeds** 0.4–0.5 mm long, 0.5–0.6 mm wide, 0.3 mm deep, square compressed; rough testa.

*Specimens Examined*—**Mexico.** —CAMPECHE: Municipio Calakmul: 2 km al SO de Mucuychakán, *C. Gutiérrez B. 8720* (MEXU, XAL); *8723* (CICY, MEXU, XAL). Municipio Champotón: Quebrada unos 2 km antes del desvío a Ulumal y el Zapotal, *G. Carnevalli 4672* (CICY, MEXU). Municipio Holpechén: Aguada, a 4.8 km al ENE de Bel-ha, *E. Martínez 38272* (MEXU). 11 km al S de la frontera Yucatá-Campeche, cerca de San Antonio Yax-ché, *G. Carnevalli 5663* (CICY, MEXU, XAL). —CHIAPAS: Municipio San Fernando: Mirador de Chicoasen Dam, a lo largo del camino de Tuxtla Gutiérrez a Chicoasen Dam, *D.E. Breedlove 39969* (MEXU). —QUINTANA ROO: Municipio José María Morelos: A 4.7 km al S de Venustiano Carranza, *D. Álvarez 9682* (MEXU). A 5.6 km al NO de San Carlos, *D. Álvarez 10389* (MEXU). A 2.7 km al SE de Sabana San Francisco, *D. Álvarez 10601* (MEXU). A 4.6 km al NE de Othón P. Blanco, camino a San Carlos, *E. Martínez 38080* (MEXU). Municipio Othón P. Blanco: 3-4 km al O de Margarita Maza, unos 11 km al O de Graciano Sánchez, (La patera), *G. Carnevalli 5590* (CICY, MEXU).

SPIGELIA SCABRELLA Benth., Pl. Hartw. 45. 1840. TYPE: MÉXICO, 1837, *K.T. Hartweg 346* (Holotype: P-507551!).

**Capsules** 7.0–8.0 mm long, 5.4–7.0 mm wide, bilobed, smooth pericarp; metastyle 0.8–1.2 mm long; carpoatlas 4.5 mm long, 2.0 mm wide, oblong shape, transverse ridge present. **Seeds** 2.0–2.5 mm long, 1.5–1.8 mm wide, 1.5 mm deep, ovoid; reticulated testa.

*Specimens Examined*—**Mexico.** —Estado de México: Municipio Tejupilco: Proximidades a Teneria, *E. Guizar 610* (MEX). —Guanajuato: Municipio Juventino Rosas: 23 km al NNW de Juventino Rosas, sobre carretera a Guanajuato, *J. Rzedowski 53592* (IEB, MEXU, XAL). Jalisco: Municipio Arandas: 1 km de El Mirador, *A. Delgado 266* (MEXU). —Michoacán: Municipio Charo: 1 km al SW de Pontezuelas, *E. Carranza 5635* (IEB, MEXU, XAL). —Nayarit: Municipio Compostela: 15 km al N de Compostela, sobre el camino a Tepic, *J. Rzedowski 14339* (ENCB). —San Luis Potosí: Municipio Cárdenas: Las Canoas, *C.G. Pringle 3198* (IEB, MEXU). —Sinaloa: Municipio San Ignacio: La Cebolla 40 km al N de San Ignacio, *R. Vega 759* (MEXU).

Spigelia speciosa Kunth., Nov. Gen. Sp. 3:186, t. 226. 1819. Type: México. Distrito Federal (Ciudad de México): Crescit prope urbem Mexici, sin fecha, *F. Humboldt & A. Bonpland s.n.* (Holotype: P).

**Capsules** 4.5–7.6 mm long, 5.0–6.0 mm wide, elliptical, smooth pericarp; metastyle 7.5 mm long; carpoatlas 5.9–7.0 mm long, 2.0–4.0 mm wide, elliptical, transverse ridge present. **Seeds** 3.5–3.7 mm long, 3.0–3.2 mm wide, 1.7–1.8 mm deep, semi-spherical; reticular testa.

*Specimens Examined*—**Mexico.** —Guerrero: Municipio Atoyac de Álvarez: Asoladero, km 191 Atoyac-Xochilapa, *Laboratorio de biogeografía 144* (FCME). —Morelos: Municipio Tepoztlán: Sierra Chalchi, *F. Miranda 3532* (MEXU). —Oaxaca: Municipio Oaxaca de Juárez: Sierra de San Felipe, *C.G. Pringle 4652* (MEXU).

Spigelia splendens H. Wendl. ex Hook., Bot Mag. 87, t.5268. 1861. Spigelia platyphylla Progel, Fl. Bra. 6(1): 256, f.68, f.1. 1868. Type: Guatemala. Cultivated, 1841, *E. Friedrichstahl s.n.* (Holotype: K-573396!).

**Capsules** 5.4–5.7 mm long, 3.0–4.0 mm wide, elliptical, smooth pericarp; metastyle 1.0–1.5 mm long; carpoatlas 2.9–3.9 mm long, 1.8–2.3 mm wide, elliptical, absent transverse ridge. **Seeds** 2.0–2.5 mm long, 1.5 mm wide, 0.9–1.0 mm deep, rhombic; reticular testa.

*Specimens Examined*—**Mexico.** —Chiapas: Municipio Chiapa de Corzo: Sumidero, hacia miradores Las Chiapas, *F. Miranda 7807* (MEXU). —Guerrero: Municipio Acatepec: Cerro de Mexcaltepec, *A. Hernández 2462* (FCME). Municipio Chilpancingo: 14.5 mi al W de Chilpancingo, *W.R. Anderson 4948* (ENCB).

Spigelia texana (Torr. & A. Gray) A. DC., Prodr. 9:5. 1845. *Coelostylis texana* Torr. & A. Gray. Fl. N. Amer. 2(1):44. 1841. Type: USA. Texas: May 1836, *T. Drummond 321* (Holotype: NY-00180344!; Isotype: G00368335!, GH-00061252!).

**Capsules** 4.5–6.0 mm long, 3.5–4.0 mm wide, bilobed, smooth pericarp; metastyle 1.0–2.0 mm long; carpoatlas 4.0–5.5 mm long, 1.5–2.5 mm wide, elliptical, absent transverse ridge. **Seeds** 1.0–2.1 mm long, 1.4–1.7 mm wide, 0.9–1.0 mm deep, elliptical; foveolated testa.

*Specimens Examined*—**Mexico.** —Coahuila: Municipio Ramos Arizpe: Cañada el Diente, Sierra de la Pila, *J.A. Villareal 4705* (MEXU). Sierra de la Gloria, Canon el Codo a side of Chipitin driving from N, below lowest pour off several hundred meters, *T. Wendt 1654* (MEXU).

## Discussion

Carpological and seminal characters have been little discussed in taxonomic studies. Some studies have focused on more detailed aspects of seed anatomy (Leython and Damelis 2008; Becerra-López et al. 2010; Ramírez-Sánchez et al. 2011; Espitia et al. 2017). The integration of fruit and seed attributes has proven useful in the classification of different families and angiosperm genera (Doweld 1996; Juan et al. 1998; Cabello et al. 2001; Fernández-Casas 2003; Rivera et al. 2014).

The seeds have been used in different groups and at different levels for taxonomic classification. On the other hand, fruits have been used for the description of new species (Alvarado-Cárdenas and Juárez-Jaimes 2012), for the separation at a generic level in different families (Gunn 1984; Lima 1985; Doweld 1998; Alvarado-Cárdenas and Ochoterena 2007) and for the characterization of subfamilies (Bravato 1974). It has been pointed out that fruits and seeds have had a different diversification than flowers, since they are subject to different selection pressures, so the morphology of fruits among species could present greater similarities than flowers (Schaefer et al. 2004; Whitney 2009). Because of this, when only floral attributes are used to define groups (Progel 1986; Henrickson 1996; Gould 1997; Bravo 1971), they may result in biases and not represent natural relationships, but by combining them, better defined groups with phylogenetic importance may be obtained (Kuriachen et al. 1992; Liu and Downie 2017).

This study evidences the taxonomic importance of characters in fruits and seeds of genus *Spigelia* and shows an important variation that allows separating groups of species and species from the combination of reproduction and dispersion characters. Unlike previous studies (Fernández-Casas 2003), a greater number of characters were integrated for these structures, taking into account the ornamentation of pericarp and the size of metastyle; the latter reflects the style articulation, which presents an important variation within the genus associated to the secondary presentation of pollen, described for some species (Erbar and Leins 1999). According to the DFA, the size of the metastyle turned out to be an informative character for the separation of groups.

The description of the carpoatlas could be made for 14 of the 22 species distributed in Mexico. Both shape and size were taken into account, which was useful information for the separation of the groups in the PCA (Fig. 4) and DFA analysis (Fig. 5). Previously, this character had only been described in detail for 10 species throughout the continent; however, this description was made considering only the shape of the disc and the foramen, and in some cases the size for each description (Fernández-Casas 2003). The use of the carpoatlas characteristics had not been previously considered to separate inter-generic groups (Henrickson 1996; Fernández-Casas 2001). With the analyses made in this study, the characters of the fruit can be useful to provide evidence for a more natural classification proposal for the genus.

Regarding the seed, the published works, mainly regional taxonomic treatments (Alvarado-Cárdenas 2007; Fernández-Casas and Huft 2009; Islas-Hernández and Alvarado-Cárdenas 2017, 2018) or description of new species (Gould 1999; Alvarado-Cárdenas and Jiménez Ramírez 2015; Islas-Hernández et al. 2017a, 2017b), describe it in a general way, mentioning only the diameter and color. In this study, characteristics of the seeds are described in a more specific way, from the shape, which is mainly pyramidal, which gives us three measurements that can be used (width, length, and depth), to the testa ornamentation, which has great variation between each of the species (Figs. 8, 9, 10). These two attributes present an important variation within the genus, but also a certain congruence of attributes in which patterns can be recognized, where the depth of the seed has a great contribution to the separation of different groups, according to the PCA.

The groups formed from the PCA (Fig. 4), DFA (Fig. 5), and NJ (Fig. 6) analyses are similar because of the species that form them and, in the case of the PCA and DFA analyses, because of the characteristics that separate the groups of species. However, these clusters do not recapture any of the sections previously proposed for the sub-generic classification of *Spigelia*, since the species grouped by the analyses in this work appear in several sections. For example, the group formed by *S. anthelmia*, *S. coelostylioides*, *S. hedyotidea*, *S. humboldtiana*, *S. splendens*, and *S. texana* (Fig. 4, pink), belongs to the *Anthelmiae* and *Coelostylis* sections. This result corroborates what has been mentioned in other works, in which phylogenetic analyses have been applied (Gould 1997; Frasier 2008; Popovkin et al. 2011), and have pointed out the artificiality of the infra-generic classification.

The carpological characters seem to show a positive correlation with the size of the floral structures: large flowers have large fruits and small flowers have small fruits (Primack 1987). The four groups formed in the analyses, separated mainly by the size of the carpoatlas, seeds, and metastyle, can be classified in turn by the size of the flowers. The first group (Figs. 4, 5, blue) presents fruits less than 3 mm in diameter and seeds 1 mm long, which correlates with the presence of flowers of less than 5 mm long and pollen with margo in colpus and less than 20 μm in diameter, the smallest within the genus. The second group (Figs. 4, 5, pink) is distinguished by having capsules from 3 to 5 mm in diameter and seeds from 1 to 3 mm long, as well as the corollas that range from 1 to 4 cm long, mostly with infundibuliform flowers. The third and fourth group (Figs. 4, 5, green and red), present the biggest flowers within the 14 species evaluated, with corollas ranging from 5 to 9 cm long and the biggest carpological structures with carpoatlas bigger than 6 mm long, and seeds of more than 5 mm in diameter.

When comparing the groups obtained with the carpological structures, there is no correspondence with the geographical distribution, but there is a partial similarity of the clusters obtained with respect to the existing phylogenies for the genus (Popovkin et al. 2011). The species of *S. speciosa* and *S. scabrella*, which are the ones with largest structures, are recovered in a clade of Mexican species. However, the rest of the species shared between this study and those integrated in the phylogeny (*S. anthelmia*, *S. coelostylioides*, *S. hedyotidea*, *S. humboldtiana*, and *S. splendens*), belong to group two (species with medium size structures) and are distributed along the phylogeny, so the similarity of structures in PCA and DFA could be due to the correlation with the flowers' dimensions and not necessarily to ancestry-descendence. To suggest a more natural classification, will be necessary to integrate a greater number of morphological characters, both vegetative and floral, that together with the carpological and seminal characters, allow a separation of the species with more security and clarity. Likewise, the integration of a greater sampling of species, mainly South American, will provide a more solid and stable classification for the genus.

The fruits and seeds of the Mexican *Spigelia* species proved to be taxonomically useful, allowing the differentiation of four main groups of species separated by the size of the analyzed structures. The results will serve to better classify groups within the genus (Fernández-Casas 2003) and represent an advance in the detailed knowledge of structures, taxonomically relevant, which are rarely taken into account in most of the systematic studies of angiosperms, due to their morphological plasticity (Bravato 1974; Lima 1985). Also, the characters analyzed here allow us to recognize different species.

This study is the first to provide better knowledge and detail on the descriptions of fruits and seeds of the genus *Spigelia*, but it is necessary to extend the sampling to a greater number of species. It is also important to include other qualitative characteristics, such as the ornamentation of the pericarp, the shape of the carpoatlas, and the testa ornamentation, for which it is necessary to have other tools, such as geometric morphometric analysis, which allow us to have a better comparison in terms of structure shape. Likewise, this work serves as a basis for a broader morphological analysis, which integrates vegetative, floral, and pollen data. Based on these results, a morphological phylogeny can be generated, which does not yet exist for the genus. The information presented will also serve as a reference framework for future evaluations of the evolution of the characteristics of the taxa distributed in the country and to better understand aspects of their dispersion.

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## Author Contributions

SIH and LAC conceived the project. SIH provided the data and analysis of the species (measurements and morphological data), all photographs and statistical analyses. LAC, JR, HO, JLV help improve the text and correct the statistical analyses.

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# CAPÍTULO TRES

## Distribución y diversidad del género *Spigelia* L. (Loganiaceae) en Norte América, Centro América y El Caribe.

C. Sofia Islas-Hernández[1], Leonardo O. Alvarado-Cárdenas[1], Enrique Ortíz[2], José Luis Villaseñor[2] & Helga Ochoterena[2].

[1] Departamento de Biología Comparada, Facultad de Ciencias, Universidad Nacional Autónoma de México, Apartado Postal 70--282, 04510, Ciudad de México, México.
[2] Departamento de Botánica. Instituto de Biología, Universidad Nacional Autónoma de México, Tercer Circuito s/n de CU, Apartado Postal 70--233, 04510, Ciudad de México, México.

**Resumen**

El género *Spigelia* agrupa cerca de 90 especies endémicas del continente americano, con una clara separación entre Norteamérica/Centroamérica/El Caribe (NA) y Sudamérica (SA), siendo México y Brasil los países con la mayor diversidad de especies. Los objetivos de este trabajo fueron conocer la riqueza y distribución de las especies del género en la región de NA, identificar las áreas de distribución potencial y las zonas de mayor riqueza potencial. Se elaboró una base de datos a partir de ejemplares de herbario, con más de 1500 registros. Con ellos se realizaron mapas de distribución conocida y modelos de distribución potencial, utilizando las variables bioclimáticas (WorldClim) y las ecorregiones terrestres (TEOW). Se registraron 29 especies en NA, siendo México el país con el mayor número de especies y endemismos. Los modelos de distribución potencial se realizaron para 17 de las 29 especies, que contaban con el número de registros necesarios. Estos análisis se llevaron a cabo para cada una de las especies, delimitando de manera independiente su área de movilidad (M) en relación con los registros de recolecta. A partir de estos modelos de distribución, se elaboró un mapa de riqueza potencial para localizar las ecorregiones con el mayor número de especies, la cual se encontró concentrada en 9 ecorregiones, todas ellas en México. Con

el uso de la información resultante de estos análisis como marco de referencia, se pueden sugerir nuevas zonas de recolecta, evaluar el estado de conservación de los taxones y proponer áreas de conservación en donde se distribuyen los taxones amenazados.

## 1. Introducción

El conocimiento de la distribución de las especies en un área, país o región es parte fundamental de las actividades de los biólogos (Villaseñor *et al.*, 2005). Esta información permite hacer diferentes estudios sobre la biología, sistemática, ecología, biogeografía, conservación y uso de los taxones. Diversos grupos vegetales se han estudiado sistemática o biogeográficamente, pero la gran mayoría cuenta únicamente con algunos datos sobre su variación morfológica y distribución asociada a ejemplares de herbario (Villaseñor & Téllez-Valdés, 2004). Tal es el caso del género *Spigelia* L. (Loganiaceae), grupo de herbáceas tropicales y subtropicales, el cual no cuenta con ningún trabajo que analice la distribución geográfica y el espacio climático que las especies ocupan.

*Spigelia* es un género endémico del continente americano distribuido desde el sureste de los Estados Unidos de América hasta el norte de Argentina (Fernández-Casas & Huft, 2009; BFG, 2015). A pesar de tener una distribución continua, las especies del género muestran un patrón de distribución diferencial entre Sudamérica (SA) y Norteamérica/Centroamérica/El Caribe (NA), teniendo 23 especies exclusivas de NA, 55 exclusivas de SA y 7 especies compartidas entre ambas regiones. Así mismo, Brasil en SA y México en NA representan los centros de diversidad, con 56 y 23 especies respectivamente, más de la mitad de ellas endémicas a sus territorios (Gould, 1997, 1999; BFG, 2015; Islas-Hernández *et al.*, 2017ª, 2017b; Islas-Hernández & Alvarado-Cárdenas, 2020). El conocimiento sistemático del grupo se ha abordado en tratamientos regionales para diferentes sitios de América (Bravo, 1971; Zappi, 1989; Gould, 1999; Fernández-Casas, 1998; Nurit *et al.*, 2005; Zappi, 2004; Alvarado-Cárdenas, 2007; Durán-Espinosa & Castillo-Campos, 2008; Fernández-Casas & Huft, 2009; Zappi & Setubal, 2016; Islas-Hernández & Alvarado-Cárdenas, 2017, 2018), así como en algunos trabajos sobre su filogenia (Gould, 1997; Backlund *et al.*, 2000; Popovkin *et al.*, 2011, Yang *et al.*, 2016). Sin embargo, el análisis de cómo se distribuye la diversidad del género es nulo. El conocimiento de la distribución es esencial para explicar posibles procesos biogeográficos y evolutivos (Luna-Vega, 2008), identificar áreas prioritarias para la conservación (Cuervo-Robayo & Monroy-Vilchis, 2012) y mejorar las propuestas de estado de riesgo de los taxones (Gutiérrez & Trejo, 2014; Castro-Navarro *et al.*, 2017). Asimismo, el conocimiento de los datos ambientales, recabados a través de los registros puntuales de los taxones, proporcionan información sobre sitios poco explorados en los que se puede aumentar el esfuerzo de recolecta, así como potenciales áreas para el descubrimiento de nuevos registros e incluso de especies nuevas (Raxworthy *et al.*, 2003).

Con el propósito de conocer y analizar la distribución de los organismos, se han propuesto distintos modelos predictivos que estiman su distribución potencial (por ejemplo, BIOCLIM, DOMAIN y MaxEnt). El modelado de nicho ecológico nos permite estudiar la distribución de los taxones, con el fin de identificar aquellos factores ambientales que podrían influir en dicha distribución (Peterson *et al.*, 2011; Franklin *et al.*, 2013). Entre estos factores se encuentran su tolerancia ambiental (A), la presencia de otras especies (B) y sus posibilidades de dispersión (M) (Soberón *et al.*, 2017), simplificado en el diagrama BAM, un marco de referencia conceptual para explicar el área de distribución de las especies (Cuervo-Robayo *et al.*, 2017). Estos modelos relacionan los datos de presencia de las especies, obtenidos de recolectas, con una serie de parámetros ambientales, a partir de los cuales se pueden determinar las áreas o regiones en las que se encuentran las condiciones adecuadas para que la especie prospere (Anderson *et al.,* 2003; Cuervo-Robayo *et al.*, 2017).

El nicho ecológico de las especies vegetales se ha interpretado en términos del clima, debido a que este determina en gran medida las respuestas fisiológicas y ecológicas de las especies. Debido a esto, los modelos para conocer la distribución potencial o modelos de nicho utilizan principalmente variables climáticas (Franklin, 2010; Cuervo-Robayo *et al.*, 2017). Estos modelos buscan una aproximación de la distribución de las especies a través de la estimación de las condiciones idóneas en espacios ambientales que puedan ser proyectados en el espacio geográfico (Warren, 2012).

Es importante señalar que hay varias especies de *Spigelia* bien recolectadas y de amplia distribución, pero muchas de las especies endémicas descritas en los últimos 20 años, se conocen de escasas recolectas o solo de la localidad tipo (Gould, 1999; Alvarado-Cárdenas & Jiménez-Ramírez, 2015; Islas-Hernández *et al.*, 2017ª, 2017b; Islas-Hernández & Alvarado-Cárdenas, 2020). Asimismo, las localidades donde se han recolectado los taxones del género tienen un fuerte impacto antropogéntrico y un importante cambio de uso de suelo. 119nicamente una de las cerca de 90 especies de *Spigelia* se encuentra bajo la categoría de amenazada y enlistada en peligro de extinción en el estado de Florida, USA (U.S. Fish and Wildlife Service, 2012). Por lo tanto, las especies de *Spigelia* de NA resultan un modelo de estudio idóneo para la aplicación de Sistemas de información Geográfica (SIG) y herramientas de modelado de nicho.

Nuestro trabajo tiene como finalidad evaluar la distribución geográfica y las zonas de riqueza de especies del género *Spigelia* en la región de NA, la cual muestra una importante riqueza diferencial con respecto a SA, patrón que se ha visto también en otros grupos de organismos (González, 1983; Rial, 2013; Carloni *et al.,* 2021). A partir del conocimiento ambiental, en conjunto con puntos georreferenciados, es posible definir los límites de la distribución geográfica de las especies (Lindenmayer *et al.*, 1991), lo cual nos permite generar hipótesis sobre la presencia y diversidad de los taxones en sitios específicos. Asimismo, este tipo de análisis nos permitiría encontrar o delimitar zonas potenciales de distribución, que pueden ser importantes en el diseño de estrategias de conservación de los taxones (Villaseñor & Téllez-Valdés, 2004).

## 2. Materiales y Métodos

Los registros de presencia de las especies del género *Spigelia* en México, Estados Unidos, Centroamérica y El Caribe, se obtuvieron de la revisión de 18 herbarios en México (CICY, ENCB, FCME, FEZA, HGOM, HUAA, HUAP, HUMO, IBUG, IEB, IMSS, INEGI, MEXU, OAX, QMEX, SERO, UAMIZ y XAL), así como de 3 herbarios internacionales (QCNE, LL-TEX, US), los acrónimos de los herbarios siguen a Thiers, 2022. También se incluyó información de especímenes digitalizados y accesibles en colecciones y bases de datos virtuales (Jstore, MO, NYBG, Tropicos). Adicionalmente, se realizaron salidas al campo, no consecutivas, entre 2015 y 2019 a diferentes estados de México (Estado de México, Hidalgo, Jalisco, Morelos, Oaxaca, Puebla, San Luís Potosí, Tlaxcala, Veracruz y Yucatán).

La información fue incorporada en una base de datos que contiene los registros para las 29 especies distribuidas en el área de estudio. Los registros botánicos que no contaban con coordenadas fueron georreferenciados de manera manual, utilizando Google Earth y Geo-locate (Noone *et al.*, 2019) a partir de la descripción de la localidad. La base de datos fue depurada eliminando los registros duplicados, aquellos que no contaban con la información necesaria o que era ambigua y aquellos en los que la determinación taxonómica no fue concluyente por falta de material y estructuras. Con la ayuda del programa ArcMap 10.5 (ESRI, 2011), se verificó la proyección de los puntos mediante su superposición con mapas de límites de países. Cuando se encontraron discrepancias, se revisaron las descripciones de las localidades y se asignaron nuevas coordenadas cuando así se requirió.

Se realizaron mapas de diversidad conocida de especies a partir de todos los datos conocidos para el género en NA, utilizando el programa ArcMap GIS 10.5 (ESRI, 2011) y las ecorregiones terrestres (TEOW) propuestas por Olson *et al.* (2001). Así mismo, con esta información se realizaron análisis de riqueza conocida utilizando el paquete MonographaR (Reginato, 2016) bajo la plataforma de R (R.C. Team, 2013), utilizando una cuadrícula de 1° para localizar los píxeles con la mayor riqueza. A partir de esta información se proyectaron los resultados sobre las ecorregiones de la TEOW, con la finalidad de obtener un mapa con gradientes sobre la riqueza conocida de las especies.

Los modelos de distribución de las especies se realizaron con base en los registros georreferenciados de todas las especies del género. Se seleccionaron las capas ambientales menos correlacionadas de WorldClim (http://www.worldclim.org) y el modelo digital de elevación (Hijmans *et al.*, 2005), con celdas de 30 segundos, a través de un análisis de componentes principales (PCA). Para cada uno de los puntos de distribución de todas las especies, se extrajeron los valores de las capas bioclimáticas, con la finalidad de acotar las variables a la distribución conocida. El área accesible de cada taxón (Soberón & Peterson,

2005) se definió utilizando las ecorregiones terrestres (TEOW) propuestas por Olson *et al.* (2001) y se extrajeron las máscaras (M en el modelo BAM) utilizando un script bajo la plataforma de R (R.C. Team, 2013).

Para la obtención de los modelos de distribución de las especies se utilizó el programa Maxent 3.4.1 (Phillips *et al.*, 2006; Baldwin, 2009), que estima la distribución más extendida o uniforme de los puntos conocidos en comparación con los puntos en donde se encuentran las condiciones ambientales similares en toda el área de estudio. MaxEnt proporciona la mejor aproximación de una distribución desconocida, que esté de acuerdo con todo lo que se conoce, pero que no supone nada sobre lo que no se conoce (Phillips *et al.*, 2006; Baldwin, 2009; Franklin 2010, Peterson *et al.*, 2011).

Si bien MaxEnt es elogiado por su facilidad de uso, la preparación de los datos y la determinación de los parámetros adecuados para cada modelo puede ser un desafío (Radosavljevic & Anderson, 2014). Se han desarrollado diferentes herramientas, como los paquetes de ENMeval (Muscarella *et al.*, 2014), Wallace (Kass *et al.*, 2018) o Kuenm (Cobos *et al.*, 2019), que ayudan en la toma de decisiones al respecto para la selección de los parámetros, como el valor de Regularización o el Feature Class a elegir e inclusive permiten eliminar el sesgo espacial de los datos de presencia (Phillips & Dudík, 2008; Anderson & González, 2011). Para obtener los valores más adecuados de estos parámetros y complementar los análisis realizados por MaxEnt, se utilizaron los programas Wallace (Kass *et al.*, 2018) e Ilwis (Koolhoven & Wind, 1996) como herramientas de apoyo. El programa Ilwis, a través del análisis de patrones, permitió obtener la distancia en la que los registros de los individuos dejan de tener autocorrelación espacial. Con esta distancia y con ayuda de spThin (Aiello-Lammens *et al.*, 2015), se pueden eliminar los puntos que estén autocorrelacionados espacialmente y realizar los análisis minimizando el sesgo de recolecta. En el caso de algunas especies, los siguientes pasos utilizando el programa Wallace y MaxEnt se hicieron sin aplicar la distancia de autocorrelación espacial, ya que esto dejaba un número muy bajo de registros, los cuales eran insuficientes para realizar los análisis.

El paquete Wallace trabaja bajo la plataforma de R (R.C. Team, 2013) y es una aplicación enfocada principalmente en el modelado de nicho ecológico y distribución geográfica de las especies (Guisan & Thuiller, 2005; Peterson *et al.*, 2011). Sin embargo, no ofrece tanta definición ni umbrales de corte como la interfaz de MaxEnt, por lo que únicamente fue utilizado para obtener los valores de regularización y seleccionar los Feature Class (L, Q, P, T, H o combinaciones de estos), que posteriormente se configuraron específicamente en MaxEnt para obtener los mapas finales. Esto se hizo utilizando un regularization multiplier de 0.5 y eligiendo la configuración optima mediante el valor del delta Akaike.

Para los análisis en MaxEnt, en el caso de las especies con más de 10 registros se utilizó 75 % de los datos para generar el modelo y el 25 % restante para su validación, mientras que para las que contaban con menos de 10 (mínimo 5 registros), se utilizó el método propuesto por Pearson *et al.* (2007) empleando un enfoque de jackknife modificado. En este enfoque, cada registro es removido una vez del conjunto total de datos y se generan modelos utilizando el resto de las localidades. El rendimiento se evalúa considerando la habilidad de cada modelo para predecir el registro excluido (Pearson *et al.*, 2007). Para evaluar el desempeño de los modelos, se utilizó el AUC (*Area Under the Curve*), la cual se obtiene comparando la proporción de falsos y verdaderos positivos. Se seleccionaron los modelos con valores mayores a 0.7 de AUC, los cuales indican modelos de alta precisión (Thullier *et al.,* 2009). El umbral de corte para generar los modelos binarios se seleccionó de manera particular para cada modelo de distribución, con un error de omisión menor al 10%. Los modelos de presencia-ausencia obtenidos representan el área de distribución de cada taxón. Los modelos en formato ráster fueron sumados en ArcMap GIS 10.5 (ESRI, 2011) para conocer la riqueza potencial de todas las especies modeladas.

Finalmente, con el objetivo de reconocer aquellas zonas predichas por el análisis de distribución que se encontraran en áreas vegetales conservadas, el mapa de riqueza potencial se sobrepuso al mapa de Áreas Naturales Protegidas (ANP de SEMARNAT-CONANP).

## 3. Resultados

### *3.1 Base de datos*

Se obtuvieron 1674 registros de las especies del género para NA. Se eliminaron 682 registros que no cumplían los requerimientos para el análisis, como falta de información, localidades ambiguas o determinación incorrecta de las especies. De esta manera, la base de datos final contó con 992 registros. Así mismo, cinco fueron las especies que únicamente se conocen del ejemplar tipo (*Spigelia ayotzinapensis* S. Islas, L.O. Alvarado & R. Bustamante*, S. colimensis* Fern. Casas, *S. dolichostachya* Fern. Casas*, S. elbakyaniae* S. Islas & L.O. Alvarado*, S. sphagnicola* C. Wright.), contra 301 en *Spigelia humboldtiana* Cham. & Schltdl.*,* una de las especies con la mayor distribución y recolecta en el continente (Tabla 1). En NA se distribuyen 29 de las cerca de 90 especies registradas para el género, lo que representa una tercera parte de la diversidad conocida del grupo (Fernández-Casas & Huft, 2009).

### *3.2 Área de distribución*

El género se encuentra distribuido en NA desde los 40° N en la parte sureste de Estados Unidos de América hasta los 8° N en el sur de Panamá (Fig. 1). La mayor diversidad de *Spigelia* dentro de NA se encuentra en México, con 23 especies, seguido de Estados Unidos de América y Guatemala con seis especies (Tabla 1).

Se registraron 19 especies endémicas en tres países de NA, siendo México el país con el mayor número de endemismos (14), seguido de Estados Unidos de América (3) y Cuba (2). La mayoría de las especies endémicas presentan una distribución conocida muy estrecha, algunas conocidas únicamente de la localidad tipo. *Spigelia anthelmia* y *S. humboldtiana*, son las especies con la distribución más amplia encontradas en 9 países de la zona de estudio (Belice, Costa Rica, El Salvador, Estados Unidos de América, Guatemala, Honduras, México, Panamá, Nicaragua) y en El Caribe.

El género *Spigelia* se encuentra distribuido en 61 de las 118 ecorregiones de la TEOW (A.1) propuestas para la región de NA. Las ecorregiones con la mayor riqueza conocida de especies son la Sierra Madre del Sur y la región del Petén-Veracruz con 9 especies cada una, seguidas por el Eje Volcánico Transmexicano con 8 especies y la Sierra Madre Oriental con 7 especies (Fig. 2). Estas últimas ecorregiones se encuentran en México en los estados de

Chiapas, Guerrero, Chiapas y Veracruz, que son considerados con la mayor diversidad de plantas vasculares en el país (Llorente-Bousquets y Ocegueda, 2008; Villaseñor y Ortiz, 2014).

Tabla 1. Número de registros por especie de *Spigelia* distribuidas en NA.

BLZ = Belize, CARIB = The Caribbean, CRI = Costa Rica, CUB = Cuba, GTM = Guatemala, HND = Honduras, MEX = Mexico, NIC = Nicaragua, PAN = Panama, SLN = El Salvador, USA = United States of America.

| **Especie** | **N° de registros** | **Distribución** |
|---|---|---|
| *Spigelia ambigua* | 4 | CUB |
| *Spigelia anthelmia* | 190 | BLZ, CRI, SLN, GTM, HND, MEX, PAN, USA, CARIB |
| *Spigelia ayotzinapensis* | 1 | MEX |
| *Spigelia carnosa* | 8 | SLN, GTM, MEX |
| *Spigelia chiapensis* | 7 | MEX |
| *Spigelia coelostyliodes* | 20 | GTM, MEX |
| *Spigelia colimensis* | 1 | MEX |
| *Spigelia dolichostachya* | 1 | MEX |
| *Spigelia elbakyaniae* | 1 | MEX |
| *Spigelia gentianoides* | 2 | USA |
| *Spigelia guerrerensis* | 11 | MEX |
| *Spigelia hamelioides* | 17 | CRI, HND, PAN |
| *Spigelia hedyotidea* | 48 | MEX, USA |
| *Spigelia humboldtiana* | 301 | BLZ, CRI, SLN, GTM, HND, MEX, NIC, PAN, CARIB |
| *Spigelia loganioides* | 9 | USA |
| *Spigelia longiflora* | 62 | MEX |
| *Spigelia marilandica* | 86 | USA |
| *Spigelia mexicana* | 5 | MEX |
| *Spigelia mocinoi* | 3 | MEX |
| *Spigelia polystachya* | 13 | BLZ, CRI, SLN, GTM, HND, MEX, NIC |
| *Spigelia pygmaea* | 15 | GTM, MEX |
| *Spigelia queretarensis* | 2 | MEX |
| *Spigelia scabrella* | 105 | MEX |
| *Spigelia speciosa* | 24 | MEX |
| *Spigelia sphagnicola* | 1 | CUB |
| *Spigelia splendens* | 22 | CRI, SLN, GTM, HND, MEX, NIC |
| *Spigelia texana* | 27 | MEX, USA |
| *Spigelia trispicata* | 5 | MEX |
| *Spigelia xochiquetzalliana* | 3 | MEX |

El género *Spigelia* se encuentra distribuido en 61 de las 118 ecorregiones de la TEOW (A.1) propuestas para la región de NA. Las ecorregiones con la mayor riqueza conocida de especies son la Sierra Madre del Sur y la región del Petén-Veracruz con 9 especies cada una, seguidas por el Eje Volcánico Transmexicano con 8 especies y la Sierra Madre Oriental con 7 especies (Fig. 2). Estas últimas ecorregiones se encuentran en México en los estados de Chiapas, Guerrero, Chiapas y Veracruz, que son considerados con la mayor diversidad de plantas vasculares en el país (Llorente-Bousquets y Ocegueda, 2008; Villaseñor y Ortiz, 2014).

Los factores abióticos que podrían estar influyendo en su delimitación geográfica, derivados de los análisis de PCA realizados en este trabajo, están representados por la temperatura media anual (BIO1), la isotermalidad (BIO3) y la precipitación media anual (BIO 12), en los cuales los rangos para el óptimo desarrollo de las especies se encuentran dentro de lo establecido para los climas tropicales (de Brichambaut, 1958).

### <u>3.3</u> <u>*Distribución potencial basada en modelos de distribución*</u>

Los modelos de distribución se realizaron para 17 de las 29 especies registradas en NA, las cuales contaban con 5 o más registros para realizar los análisis en MaxEnt (Tabla 1). Estos análisis se llevaron a cabo para cada una de las especies, delimitando de manera independiente las ecorregiones de la TEOW para obtener su área de movilidad (M) en relación con los registros de recolecta (A.2).

Una vez obtenidos los modelos de distribución para cada especie, se calculó un mapa de riqueza potencial para localizar las ecorregiones con el mayor número de especies (Fig. 3). De acuerdo con este mapa, las ecorregiones con la mayor riqueza potencial (5 especies), son la Sierra Madre del Sur, la Sierra Madre Oriental, la Cuenca del Balsas, la Depresión de Chiapas, El Eje Volcánico Transmexicano y la región de los bosques de Yucatán.

Dentro de las áreas de mayor riqueza potencial encontramos tres zonas asociadas a áreas naturales protegidas (ANP´s, Fig. 4). La primera es la ecorregión Trans-Mexican Volcanic Belt pine-oak forests (Fig. 3-2), cercana a las ANP Mariposa Monarca, Bosencheve, Zona Protectora Forestal de los Terrenos tonsecutivos de las Cuencas de los ríos Valle de Bravo, Malacatepec, Tilostoc y Temascaltepec, Nevado de Toluca, Lagunas de Zempoala, Corredor Biológico Chichinautzin, El Tepozteco, Iztaccíhuatl-Popocatépetl y Sierra de Huautla. La segunda, es el área comprendida entre las ecorregiones Petén-Veracruz moist forests, Chiapas depression dry forests y Central American pine-oak forests (Fig. 3-4), las ANP´s que se encuentran en esta área son la Selva del Ocote, La Sepultura, Zona de Protección Fosrestal en los terrenos que se encuentran en los municipios de La Concordia, Ángel Albino Corzo, Villa Flores y Jiquipilas y El Cañón del Sumidero. La tercera zona es la ecorregión de los bosques húmedos y secos de Yucatán (Campeche, Quintana Roo y Yucatán), dentro de esta región encontramos dos áreas con una alta riqueza potencial una en la costa de Campeche (Fig. 3-6) y otra en la región centro (Fig. 3-5), cerca del ANP Bala'an K'aax.

## 4. Discusión

El conocimiento de la distribución del género *Spigelia* en NA se ha presentado de manera general y se encuentra dispersa en numerosos trabajos regionales. Estos antecedentes proporcionan las bases para el entendimiento de dónde están las especies, pero su alcance es limitado. El presente trabajo representa el primer análisis detallado de la distribución y riqueza regional del género en NA, utilizando diferentes unidades de evaluación y numerosas colecciones biológicas. Nuestros resultados, a diferentes escalas de análisis, muestran numerosas coincidencias, la principal es que la mayor riqueza de especies se concentra en México, Estados Unidos de América y Guatemala, donde además el mayor número de endemismos se encuentra en los dos primeros. Por otro lado, la distribución y riqueza potencial del género se concentra a lo largo de las costas de México, siguiendo en gran medida la distribución actual conocida.

### *4.1 Área de distribución*

*Spigelia* se distribuye en NA abarcando las zonas más cálidas de Estados Unidos de América ubicadas en la región sureste, hasta el sur de Panamá encontrándose principalmente sobre las costas. Esta distribución sugiere la afinidad tropical y subtropical del género, concentrándose en bosques tropicales y subtropicales, tanto húmedos como mesófilos y en menor escala de coníferas (Islas-Hernández, 2017; Islas-Hernández *et al.*, 2022).

En el continente, México se reconoce como el segundo centro de diversidad y endemismos para el género, solo después de Brasil en la región de SA (BFG, 2015; Islas-Hernández *et al.*, 2022 en revisión). Las principales ecorregiones con el mayor número de especies se localizan en México (Fig. 2) y concuerdan con los estados registrados con una alta biodiversidad, especialmente de angiospermas (Villaseñor y Ortiz, 2014; Villaseñor, 2016). Esta alta riqueza de especies en el territorio nacional no es exclusiva del grupo, pues se ha visto también en otros grupos, como *Euphorbia, Mammillaria, Salvia* y *Tabernaemontana* (Villaseñor, 2004; Vargas-Amado *et al.*, 2013; Alvarado-Cárdenas *et al.*, 2019). La complejidad geológica, fisiográfica y climatológica en NA, influye en la formación de una topografía accidentada, lo que se ha visto correlacionado con la alta diversidad de plantas vasculares (Kreft & Jetz, 2007). Esto puede observarse en que más del 50% de los endemismos en la región de NA presentan una distribución restringida, asociada a numerosas barreras geográficas que proporcionan condiciones micro climáticas donde se establecen las especies (Fernández-Casas, 1998; Gould, 1999; Islas-Hernández *et al.* 2017a, 2017b, 2020).

Se ha mencionado que varias especies del género presentan distribuciones restringidas (Gould, 1997; Islas-Hernández *et al.*, 2017a, 2017b), lo cual puede asociarse, además de las condiciones ambientales, al tipo de dispersión que presentan las especies. Los frutos capsulares del género presentan una dehiscencia septicida, loculicida y circuncísil al mismo tiempo (Islas-Hernández *et al.* 2020), lo que provoca que las cápsulas exploten y expulsen las semillas lejos de la planta madre. Sin embargo, se observó que la distancia que alcanzan las semillas lejos de la planta no es mayor a dos metros, por lo que los individuos en las poblaciones se mantienen cercanos, limitando su capacidad de dispersión.

Nueve de las especies cuentan con menos de diez registros conocidos de recolecta y cinco únicamente se conocen del ejemplar tipo. Aunque esto hace que no puedan ser evaluadas mediante los modelos de distribución potencial, los registros documentados de las especies en algunos estados de México incrementan su riqueza de especies, como en el caso de los estados de Chiapas y Guerrero (Islas-Hernández, 2017). Sin embargo, debido a la falta de información sobre su distribución y abundancia, es de vital importancia aumentar los esfuerzos de recolecta y buscar alternativas de análisis para su distribución potencial (ej. modelos basados en elipsoides, Osorio-Olvera *et al.*, 2020), ya que estas especies se podría encontrar en peligro de extinción o extintas debido al impacto antropogénico o al cambio de uso de suelo.

De toda la distribución conocida del género en NA, México ocupa el primer lugar en diversidad de especies endémicas con 14 taxones de distribución restringida, concentradas en los estados de Chiapas, Guerrero y Oaxaca. Esto es consistente con lo que se conoce sobre la distribución de la biodiversidad en el país, ya que Chiapas ocupa uno de los primeros lugares en riqueza de angiospermas, con cerca de 8,000 especies (Llorente-Bousquets y Ocegueda, 2008; Villaseñor y Ortiz, 2014). Mientras que Guerrero se encuentra entre los cinco estados con mayor grado de endemismos (Villaseñor y Ortiz, 2014; Villaseñor, 2016), resultado de formar parte de la cuenca del río Balsas, una de las cuencas de mayor extensión e importancia en México (Fernández *et al.,* 1998), además de tener una topografía accidentada, por la presencia del Eje Neovolcánico y la Sierra Madre del Sur, lo que le confiere una gran variación climática y altitudinal, que permite la especiación local (Suárez-Mota & Téllez-Valdés, 2014; Martínez-Gordillo *et al.,* 2016; Solano *et al.*, 2016; Lozada-Pérez *et al.*, 2016, Flores-Tolentino *et al.*, 2021). Así mismo, estos endemismos hacen que las ecorregiones distribuidas en dichos estados (Cuenca del Balsas, Sierra Madre del Sur, Depresión de Chiapas y Eje Volcánico Transmexicano), presenten la mayor riqueza de especies (Fig. 3).

### *4.2 Modelos de distribución*

Los modelos de distribución realizados para las especies con más de 5 registros del género *Spigelia* (A.2), concentran la diversidad a lo largo de las vertientes del Golfo de México, el Océano Pacifico y la Península de Yucatán. La sumatoria de los modelos muestra que la mayor riqueza potencial en NA, al igual que la riqueza conocida, se encuentra en 10 de las ecorregiones ubicadas en México (Fig. 3). Aunque las 12 especies con menos de 5 registros no se pueden sumar a los modelos de distribución potencial, a partir de la distribución conocida observamos que únicamente dos especies (*S. mexicana* y *S. mocinoi*) se encuentran distribuidas dentro de las zonas de mayor riqueza potencial. Esto nos permite concentrar los esfuerzos de recolecta sobre estas zonas, con la finalidad de tener un mayor conocimiento de la distribución de especies que por su rareza podrían encontrarse amenazadas.

Las ecorregiones con la mayor diversidad específica conocida coinciden en gran medida con las obtenidas a través de los modelos de distribución potencial. Esto reafirma la afinidad tropical y la importancia de la diversidad climática asociada con la accidentada geografía del país que puede estar involucrada en la diversificación del grupo.

Algunas de zonas predichas por el modelo con mayor riqueza potencial se encuentran dentro o cercanas a ANP (Fig. 4). En el caso de la ecorregión Trans-Mexican Volcanic Belt pine-oak forest podemos observar que, aunque el área de mayor riqueza cae solo dentro del ANP: Z.P.F.T.C.C. de los ríos Valle de Bravo, Malacatepec, Tilostoc y Temascaltepec, alrededor de la región se encuentran 5 ANP's más. En la zona se encuentran 3 especies, que, aunque sus distribuciones actuales no se empalman, los modelos de distribución potencial muestran un área cercana al ANP Sierra de Huautla en donde podrían encontrarse. Una de las especies registradas en esta zona, *Spigelia guerrerensis*, presenta actualmente una distribución restringida, por lo que el conocimiento de su distribución potencial podría ayudarnos a conocer mejor su hábitat, entender su biología y ayudar en su conservación.

El área comprendida entre las ecorregiones Petén-Veracruz moist forests, Chiapas depression dry forests y Central American pine-oak forests (Fig. 3-4), incluye la ANP Cañón del Sumidero, la cual incluye el área predicha por los modelos de distribución potencial. El conocimiento actual que se tiene sobre la zona ha reportado únicamente dos especies, mientras que los modelos predicen la distribución de al menos 5 especies.

La tercera zona es la ecorregión de los bosques húmedos y secos de Yucatán (Campeche, Quintana Roo y Yucatán), aunque no es considerada una zona de alta diversidad conocida para el género, debido a que las condiciones, como suelos de carbonato y la falta de superficies de agua pudieran limitar la presencia de las especies de este género (Durán-García *et al.*, 2016). Sin embargo, la presencia de ANP's en esta zona permite la inclusión de áreas de vegetación más densa que podría aportar zonas con cobertura vegetal que permitan el desarrollo de microambientes apropiados para las especies de *Spigelia*; por ejemplo, la Reserva de la Biosfera de Calakmul, la cual representa una de las superficies mejor conservadas de selvas tropicales, con una alta biodiversidad representativa de las zonas tropicales de México y Centroamérica (Díaz-Gallegos *et al.*, 2002). Esto resulta novedoso para el grupo, ya que esta ecorregión representa una zona donde se podría encontrar registros nuevos de especies que en la actualidad no han sido recolectadas.

El empleo de métodos para la obtención de mapas de distribución potencial puede servir de guía para dirigir el trabajo de campo hacia sitios específicos, debido a que en la actualidad muy pocos registros de algunas de las especies se han recolectado en las ANP. Por consiguiente, el trabajo dirigido a estas zonas con potencial riqueza de especies permitirá probablemente tener un registro de las especies distribuidas dentro de ellas y de esta manera tener un mejor panorama para su conservación. Esto resulta imprescindible para el conocimiento de la biodiversidad, principalmente en un grupo como *Spigelia,* que ha sido poco estudiado en NA y en el que en los últimos años se han descrito especies nuevas con información de herbarios y de distribución restringida (Alvarado-Cárdenas y Jiménez, 2015; Islas-Hernández *et al.*, 2017a, 2017b, Islas-Hernández & Alvarado-Cárdenas, 2020).

El modelado de la distribución de las especies a partir de variables climáticas (Lindenmayer *et al.*, 2000; Fischer *et al.*, 2001), se ha utilizado en los últimos años para contestar preguntas biogeográficas, ecológicas, sistemáticas o de conservación (Gisela *et al.,* 2011; Contreras-Medina *et al.*, 2010; Palma-Ordaz & Delgadillo-Rodríguez, 2014; Gutiérrez & Trejo, 2014; Durán *et al.*, 2020). Estos modelos permiten entender aspectos relevantes sobre la distribución de los taxones, así como las variables climáticas potencialmente asociadas a dichas distribuciones. Su uso en el estudio de la distribución de las especies del género *Spigelia,* apoyan tales conclusiones.

Aunque los modelos, principalmente aquellos basados en información únicamente de presencia de los taxones, tienden a sobreestimar la distribución potencial (Contreras-Medina *et al.*, 2010), los mapas obtenidos a partir de estos métodos nos sirven como base para tomar decisiones sobre el trabajo futuro, así como sobre el conocimiento de los organismos y sus nichos ecológicos. La validación de los modelos a través del trabajo de campo resultará importante, ya que nos permitirá conocer, ajustar y cambiar los parámetros utilizados al momento de la modelación y, de encontrar las especies en las áreas predichas, evaluar la robustez de los modelos para que sirvan en la propuesta de áreas de conservación.

## 5. Conclusión

El conocimiento de la distribución de las especies es sin lugar a duda un aspecto fundamental en el conocimiento de la biodiversidad. La aplicación de análisis geográficos permite la integración de diferentes datos, como datos ambientales y nicho ecológico, que permite tener información complementaria para un mejor conocimiento de la diversidad de los taxones. Asimismo, un análisis geográfico, bajo un contexto filogenético, nos sirve como marco de referencia para conocer sobre la evolución, centros de diversificación y dispersión, lo cual ayudaría a entender aspectos sobre la diversidad del género *Spigelia* en NA, principalmente en México.

Los datos obtenidos de los ejemplares de herbario y recolectas en el transcurso del trabajo de investigación permitieron determinar los patrones de distribución de las especies del género *Spigelia,* a través del uso de sistemas de información geográfica (SIG), así como detectar las zonas de mayor riqueza.

El uso de información resguardada en herbarios y bases de datos virtuales no solo es importante en el trabajo descriptivo de la sistemática y reconocimiento de especies nuevas (Bebber *et al.*, 2010). Esta información también es muy útil en el trabajo biogeográfico, ya que permite conocer de manera indirecta las condiciones ambientales en las que se establecen las especies a partir de su distribución conocida, y como marco de referencia para otros análisis (Peterson *et al.*, 2011), como los realizados en este trabajo de distribución potencial.

Aunque los algoritmos utilizados en la modelación de la distribución potencial de las especies, basados en modelos bioclimáticos, presentan errores de omisión o comisión (Peterson y Vieglais, 2001; Anderson *et al.*, 2003), proporcionan una perspectiva útil para el conocimiento de la biodiversidad y su movimiento en el espacio geográfico debido al alto impacto antropocéntrico, para distintos grupos y en distintas escalas (Peterson y Vieglais, 2001), como el caso de las especies que cuentan con un solo registro. La distribución potencial de las especies con pocos registros se puede analizar a partir de los elipsoides de volumen mínimo (Osorio-Olvera *et al.*, 2020). Este método de evaluación en el espacio ambiental permite reconocer las características ambientales en donde la especie se encuentra distribuida, para después localizar puntos idóneos dentro del fondo ambiental (Osorio-Olvera *et al.*, 2020).

Este trabajo representa un avance en el conocimiento del género *Spigelia*, del cual un importante número de especies se encuentran fuertemente amenazadas en la actualidad por los asentamientos humanos, así como para el conocimiento de la flora de NA. Aunque aún se tienen lagunas en el conocimiento de la distribución y diversificación del género, este tipo de trabajos sientan las bases para futuros análisis en donde se incluyan más datos que permitan tener un mejor panorama, principalmente de las especies que se encuentran en peligro de extinción.

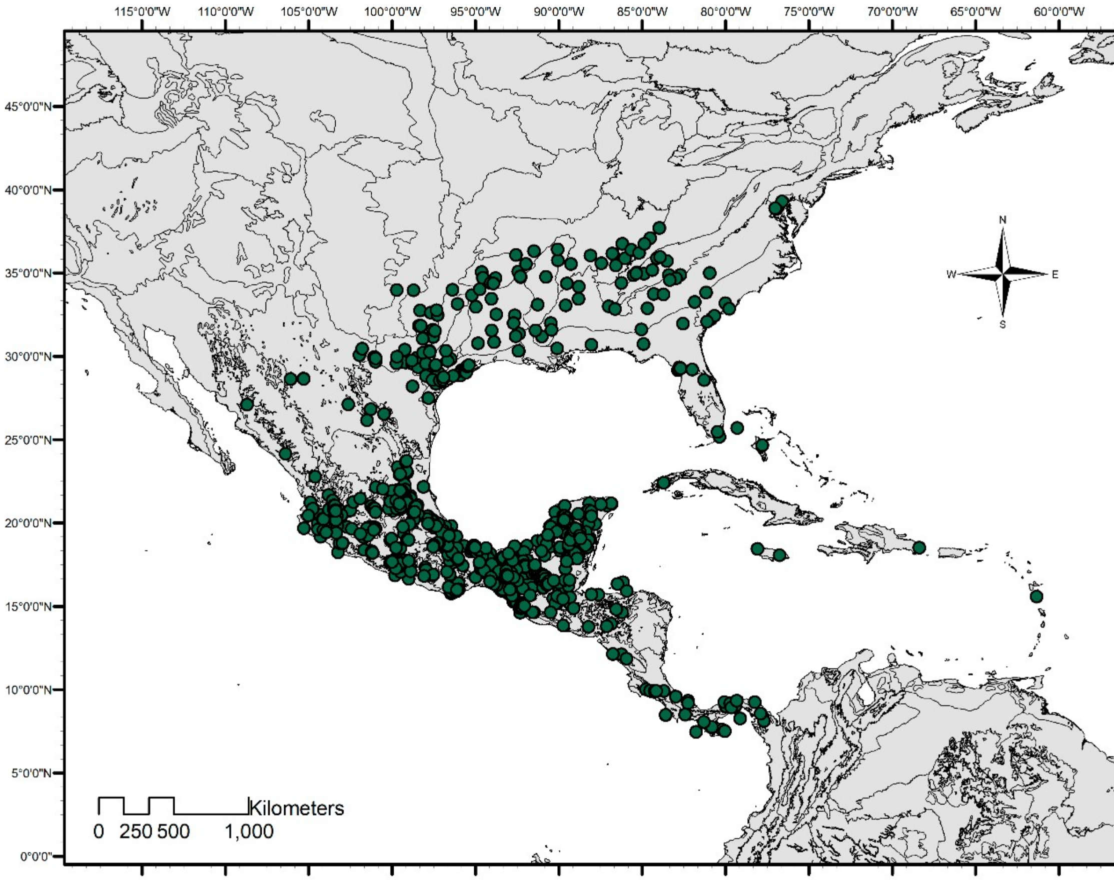


Figura 1. Distribución conocida del género *Spigelia* en Norteamérica, Centroamérica y El Caribe (NA), sobre las ecorregiones de la TEOW.

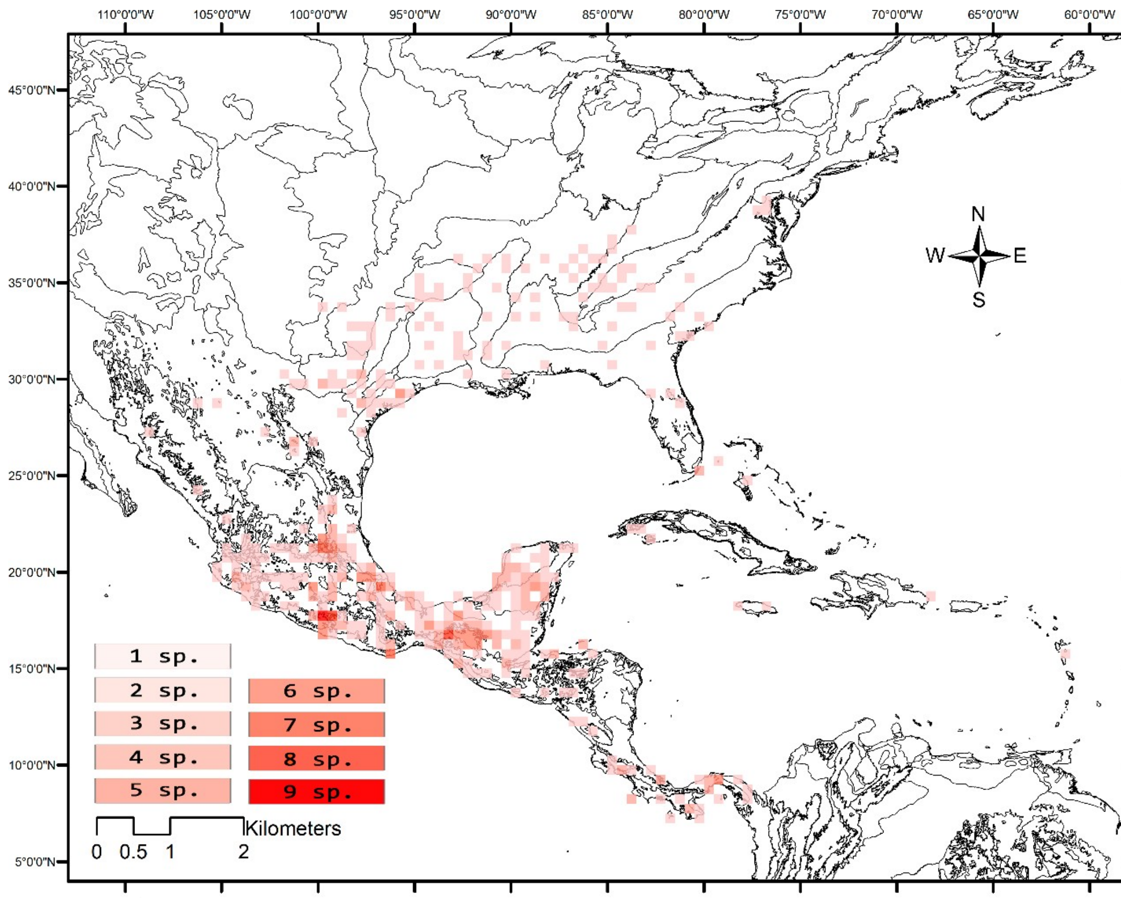


Figura 2. Riqueza conocida de *Spigelia* en Norteamérica, Centroamérica y El Caribe, sobre las ecorregiones de la TEOW. Cuadrícula de 1° de latitud y longitud.

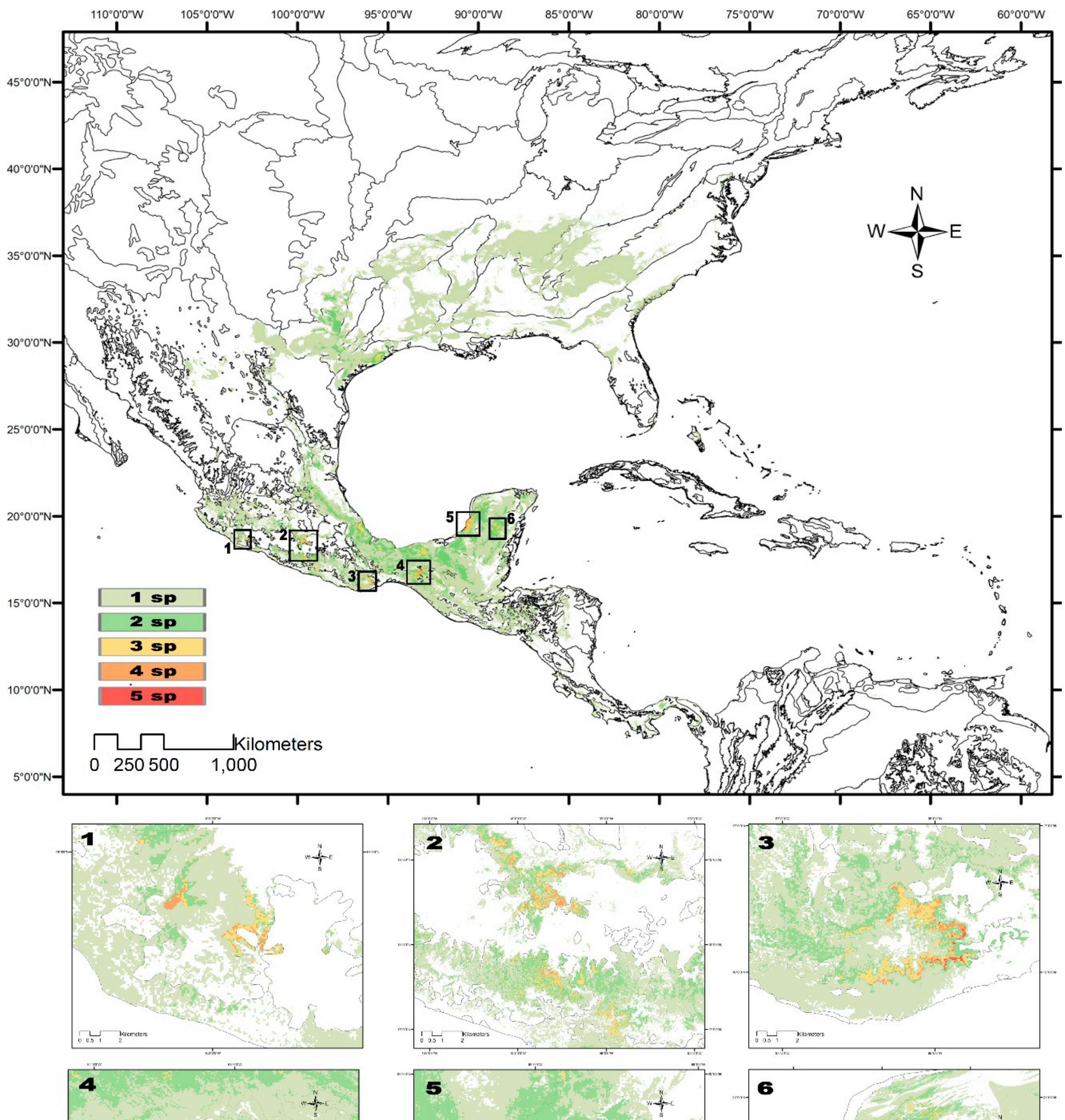


Figura 3. Riqueza potencial de especies de *Spigelia* en NA. Se resaltan las áreas con la mayor riqueza ubicadas en México. 1. Balsas dry forest, 2. Trans-Mexican Volcanic Belt pine-oak forests, 3. Sierra Madre del Sur pine-oak forests, 4. Chiapas Depression dry forests y Petén-Veracruz moist forests, 5. Yucatán moist forests y 6. Yucatán dry forests.

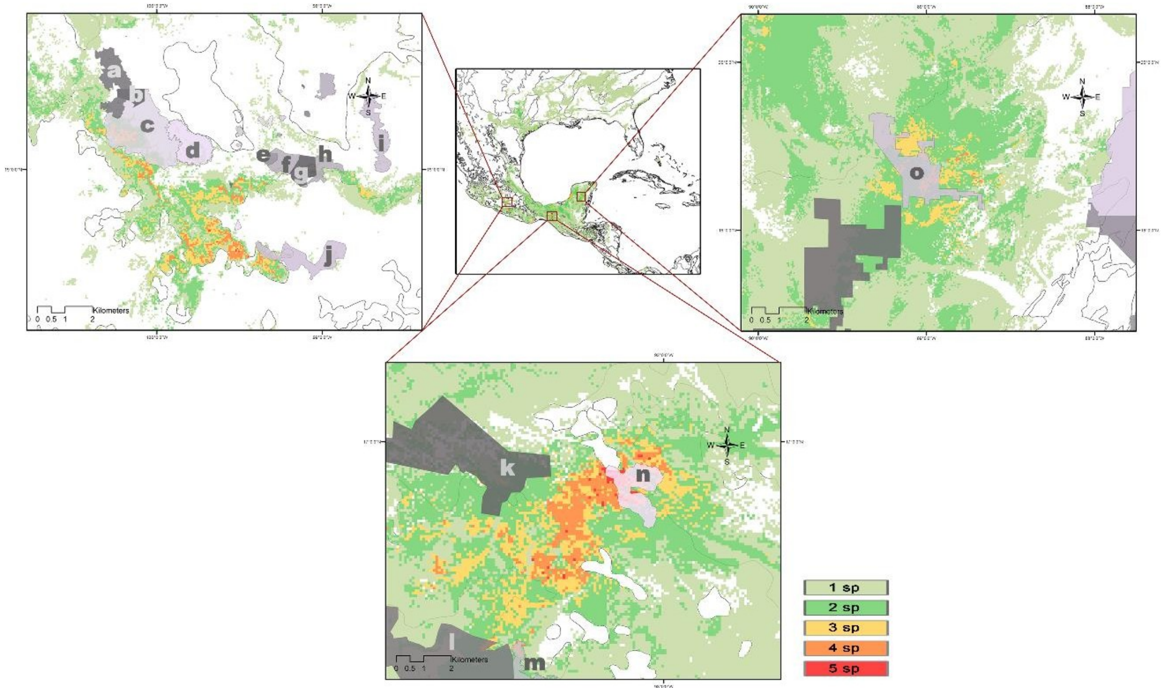


Figura 4. Zonas de mayor riqueza potencial dentro de las áreas naturales protegidas de México. ANP cerca de las zonas de mayor riqueza potencial: a) Mariposa Monarca, b) Bosencheve, c) Z.P.F.T.C.C. de los ríos Valle de Bravo, Malacatepec, Tilostoc y Temascaltepec, d) Nevado de Toluca, e) Lagunas de Zempoala, f) Corredor Biológico Chichinautzin, g) El Tepozteco, h) Corredor Biológico Chichinautzin 2, i) Iztaccíhuatl-Popocatépetl, j) Sierra de Huautla, k) Selva El Ocote, l) La Sepultura, m) Z.P.F. en los terrenos que se encuentran en los municipios de La Concordia, Ángel Albino Corzo, Villa Flores y Jiquipilas, n) Cañón del Sumidero, o) Bala'an K'aax.

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## Appendix 1

Especies presentes por ecorregión en NA.

| Especie | Ecorregiones |
|---|---|
| *Spigelia ambigua* | Cuban dry forests |
| | Cuban pine forests |
| *Spigelia anthelmia* | Bahamian pine mosaic |
| | Bahamian-Antillean mangroves |
| | Central American Atlantic moist forests |
| | Central American dry forests |
| | Central American montane forests |
| | Central American pine-oak forests |
| | Chiapas Depression dry forests |
| | Chocó-Darién moist forests |
| | Costa Rican seasonal moist forests |
| | Hispaniolan moist forests |
| | Isthmian-Atlantic moist forests |
| | Isthmian-Pacific moist forests |
| | Jamaican moist forests |
| | Meseta Central matorral |
| | Mesoamerican Gulf-Caribbean mangroves |
| | Oaxacan montane forests |
| | Panamanian dry forests |
| | Pantanos de Centla |
| | Petén-Veracruz moist forests |
| | Sierra de los Tuxtlas |
| | Sierra Madre de Oaxaca pine-oak forests |
| | Sierra Madre del Sur pine-oak forests |
| | South Florida rocklands |
| | Southern Pacific dry forests |
| | Trans-Mexican Volcanic Belt pine-oak forests |
| | Veracruz dry forests |
| | Veracruz moist forests |
| | Veracruz montane forests |
| | Yucatán dry forests |
| | Yucatán moist forests |
| *Spigelia ayotzinapensis* | Southern Pacific dry forests |
| *Spigelia carnosa* | Central American montane forests |
| | Central American pine-oak forests |
| | Chiapas Depression dry forests |
| | Chiapas montane forests |
| | Petén-Veracruz moist forests |
| *Spigelia chiapensis* | Central American pine-oak forests |
| *Spigelia coelostylioides* | Central American pine-oak forests |
| | Central Mexican matorral |
| | Chiapas Depression dry forests |
| | Oaxacan montane forests |
| | Petén-Veracruz moist forests |
| | Veracruz dry forests |
| | Veracruz moist forests |
| *Spigelia colimensis* | Jalisco dry forests |
| *Spigelia dolichostachya* | Petén-Veracruz moist forests |
| *Spigelia elbakyanieae* | Petén-Veracruz moist forests |
| *Spigelia gentianoides* | Appalachian mixed mesophytic forests |

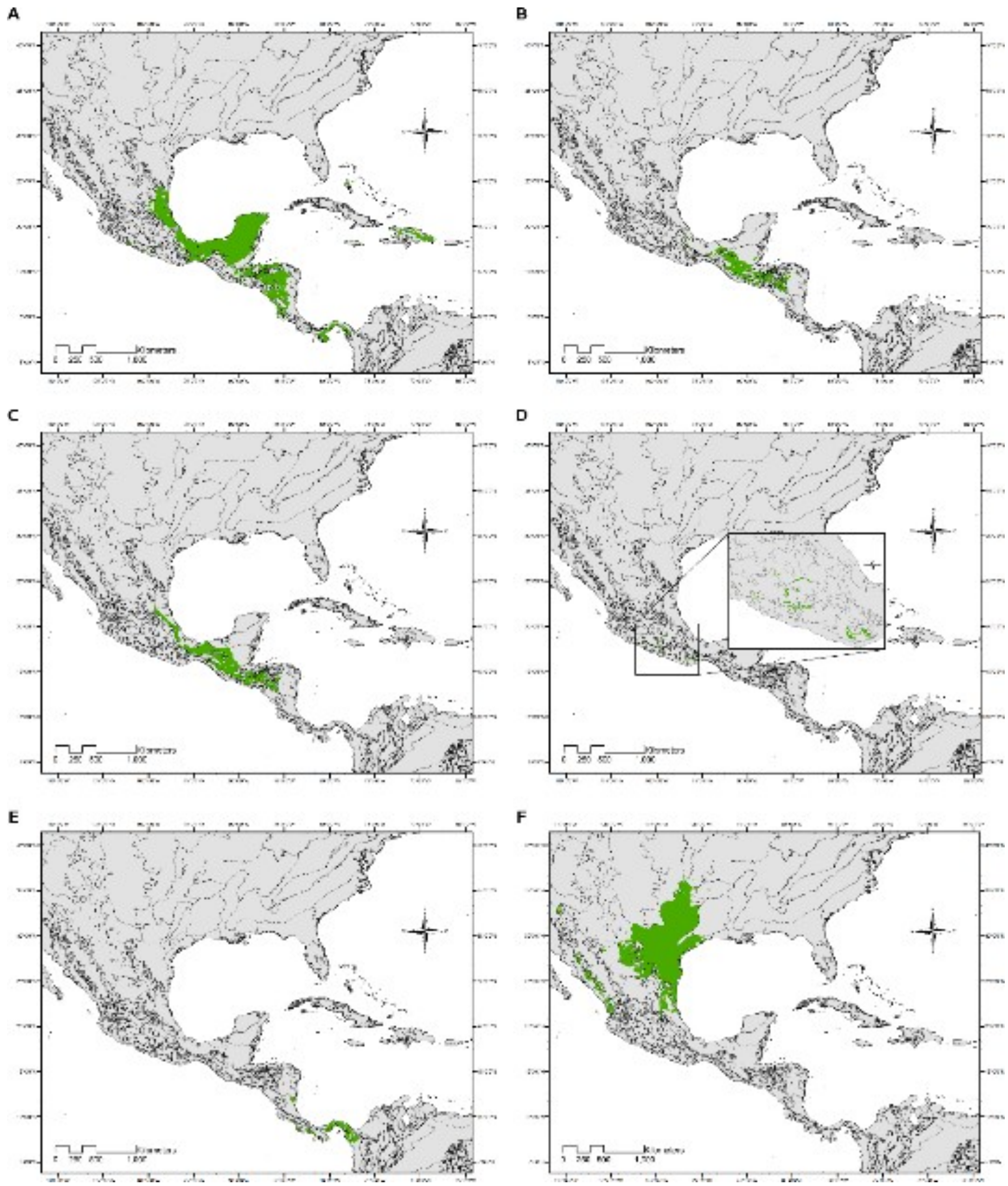
| Especie | Ecorregiones |
|---|---|
| *Spigelia guerrerensis* | Balsas dry forests |
| | Sierra Madre del Sur pine-oak forests |
| | Trans-Mexican Volcanic Belt pine-oak forests |
| *Spigelia hamelioides* | Chocó-Darién moist forests |
| | Isthmian-Atlantic moist forests |
| | Isthmian-Pacific moist forests |
| | Panamanian dry forests |
| *Spigelia hedyotidea* | Central forest-grasslands transition |
| | Chihuahuan desert |
| | East Central Texas forests |
| | Edwards Plateau savanna |
| | Ozark Mountain forests |
| | Sierra Madre Oriental pine-oak forests |
| | Sinaloan dry forests |
| | Tamaulipan mezquital |
| | Texas blackland prairies |
| | Veracruz moist forests |
| | Western Gulf coastal grasslands |
| *Spigelia humboldtiana* | Central American Atlantic moist forests |
| | Central American dry forests |
| | Central American montane forests |
| | Central American pine-oak forests |
| | Chiapas Depression dry forests |
| | Chiapas montane forests |
| | Chimalapas montane forests |
| | Costa Rican seasonal moist forests |
| | Isthmian-Atlantic moist forests |
| | Isthmian-Pacific moist forests |
| | Jalisco dry forests |
| | Meseta Central matorral |
| | Mesoamerican Gulf-Caribbean mangroves |
| | Oaxacan montane forests |
| | Pantanos de Centla |
| | Petén-Veracruz moist forests |
| | Sierra de los Tuxtlas |
| | Sierra Madre de Chiapas moist forests |
| | Sierra Madre de Oaxaca pine-oak forests |
| | Sierra Madre del Sur pine-oak forests |
| | Sierra Madre Oriental pine-oak forests |
| | Southern Mesoamerican Pacific mangroves |
| | Southern Pacific dry forests |
| | Trans-Mexican Volcanic Belt pine-oak forests |
| | Veracruz dry forests |
| | Veracruz moist forests |
| | Veracruz montane forests |
| | Yucatán dry forests |
| | Yucatán moist forests |

| Especie | Ecorregiones |
|---|---|
| *Spigelia loganioides* | Southeastern conifer forests |
| | Southeastern mixed forests |
| | Western Gulf coastal grasslands |
| *Spigelia longiflora* | Central Mexican matorral |
| | Meseta Central matorral |
| | Sierra Madre de Oaxaca pine-oak forests |
| | Sierra Madre Oriental pine-oak forests |
| | Tehuacán Valley matorral |
| | Trans-Mexican Volcanic Belt pine-oak forests |
| | Veracruz moist forests |
| | Veracruz montane forests |
| *Spigelia marilandica* | Appalachian mixed mesophytic forests |
| | Appalachian-Blue Ridge forests |
| | Central forest-grasslands transition |
| | Central U.S. hardwood forests |
| | Edwards Plateau savanna |
| | Middle Atlantic coastal forests |
| | Mississippi lowland forests |
| | Ozark Mountain forests |
| | Piney Woods forests |
| | South Florida rocklands |
| | Southeastern conifer forests |
| | Southeastern mixed forests |
| | Western Gulf coastal grasslands |
| *Spigelia mexicana* | Balsas dry forests |
| | Sierra Madre del Sur pine-oak forests |
| | Trans-Mexican Volcanic Belt pine-oak forests |
| *Spigelia mocinoi* | Trans-Mexican Volcanic Belt pine-oak forests |
| *Spigelia polystachya* | Pantanos de Centla |
| | Petén-Veracruz moist forests |
| | Veracruz dry forests |
| | Yucatán dry forests |
| | Yucatán moist forests |
| *Spigelia pygmaea* | Chiapas Depression dry forests |
| | Petén-Veracruz moist forests |
| | Yucatán dry forests |
| | Yucatán moist forests |

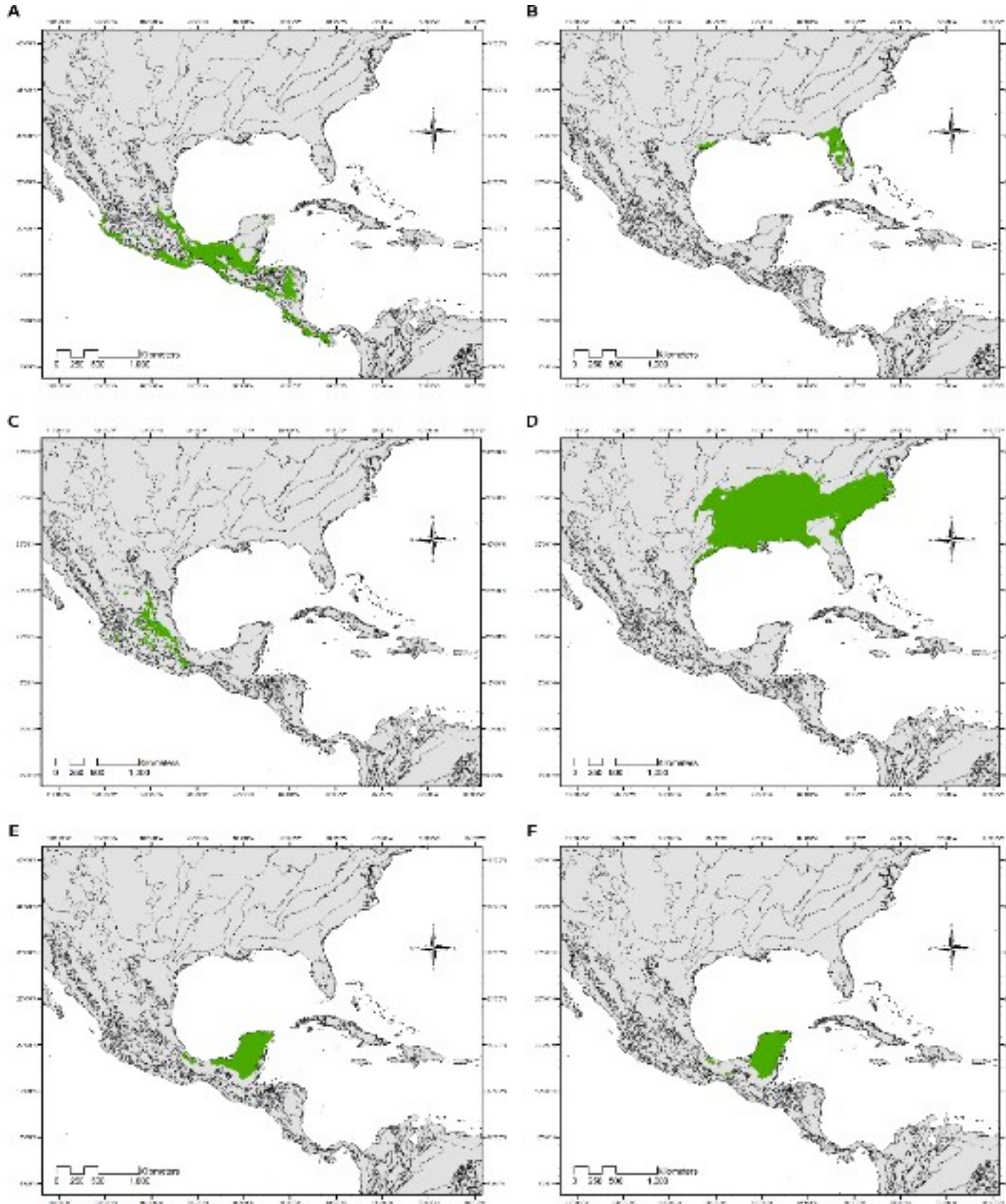
| Especie | Ecorregiones |
|---|---|
| *Spigelia queretarensis* | Sierra Madre Oriental pine-oak forests |
| | Veracruz moist forests |
| *Spigelia scabrella* | Bajío dry forests |
| | Balsas dry forests |
| | Central Mexican matorral |
| | Jalisco dry forests |
| | Sierra Madre del Sur pine-oak forests |
| | Sierra Madre Occidental pine-oak forests |
| | Sierra Madre Oriental pine-oak forests |
| | Sinaloan dry forests |
| | Trans-Mexican Volcanic Belt pine-oak forests |
| *Spigelia speciosa* | Balsas dry forests |
| | Sierra Madre del Sur pine-oak forests |
| | Southern Pacific dry forests |
| | Trans-Mexican Volcanic Belt pine-oak forests |
| *Spigelia sphagnicola* | Cuban pine forests |
| *Spigelia splendens* | Central American pine-oak forests |
| | Chiapas Depression dry forests |
| | Chiapas montane forests |
| | Chimalapas montane forests |
| | Costa Rican seasonal moist forests |
| | Petén-Veracruz moist forests |
| | Sierra Madre del Sur pine-oak forests |
| | Sierra Madre Oriental pine-oak forests |
| *Spigelia texana* | Central and Southern mixed grasslands |
| | East Central Texas forests |
| | Piney Woods forests |
| | Sierra Madre Oriental pine-oak forests |
| | Texas blackland prairies |
| | Western Gulf coastal grasslands |
| *Spigelia trispicata* | Balsas dry forests |
| | Sierra Madre del Sur pine-oak forests |
| *Spigelia xochiquetzalliana* | Balsas dry forests |
| | Jalisco dry forests |
| | Sierra Madre del Sur pine-oak forests |
| | Southern Pacific dry forests |

**Appendix 2**

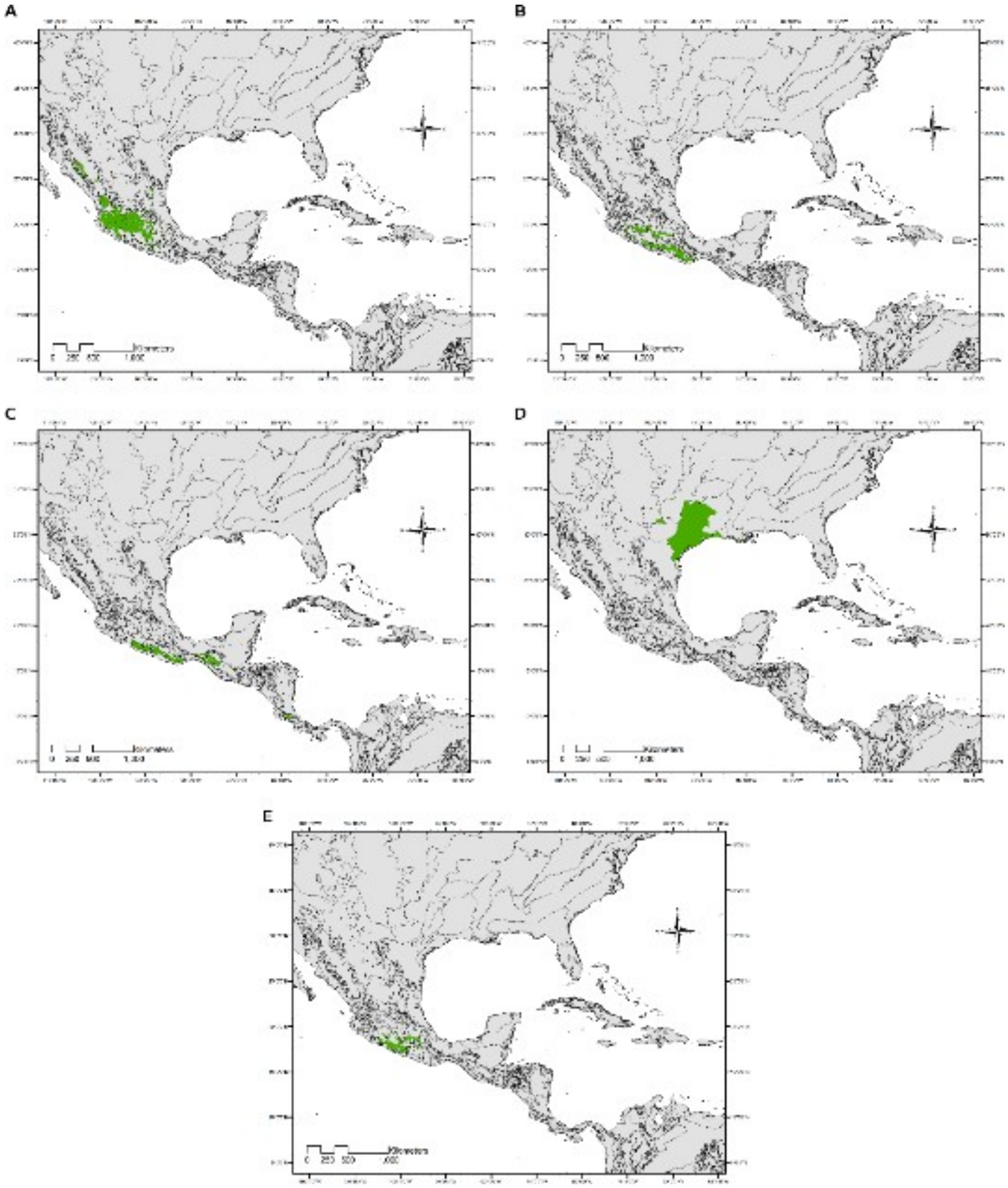
Mapas de distribución potencial de las 17 especies de *Spigelia* presentes en la región de NA que contaron con 5 o más registros de colecta.




A.1-1: A) *Spigelia anthelmia,* B) *S. carnosa,* C) *S. coelostylioides,* D) *S. guerrerensis,* E) *S. hamelioides* y F) *S. hedyotidea*.




A.1-2: A) *Spigelia humbolstiana,* B) *S. loganioides,* C) *S. longiflora,* D) *S. marilandica,* E) *S. polystachya* y F) *S. pygmaea*.




A.1-3: A) *Spigelia scabrella,* B) *S. speciosa,* C) *S. splendens,* D) *S. texana* y E) *S. trispicata*

# DISCUSIÓN Y CONCLUSIÓN

Las zonas tropicales son especialmente llamativas por la alta riqueza de especies que presentan (Dobzhansky, 1950), no solo por unidad de superficie, sino también por su notable diversidad de grupos taxonómicos (Kusneaow, 1957). La información recabada en los capítulos anteriores representa el primer esfuerzo por recopilar y actualizar la información sobre *Spigelia* en las regiones tropicales y subtropicales de Norteamérica, Centroamérica y El Caribe.

El conocimiento sistemático de los taxones resulta de vital importancia, ya que muchos de los grupos distribuidos en las regiones tropicales se encuentran fuertemente amenazados por las acciones del hombre (Gómez-Pompa, 1971; Fernández, 2010). Las especies del género *Spigelia* se han visto desplazadas de su distribución conocida. Esto se pudo reconocer, debido a que, al salir a campo a recolectar las especies para su reconocimiento y estudio morfológico, muchas de las zonas de recolecta registradas en los herbarios, ya no presentaban poblaciones del grupo y tenían un importante cambio de uso de suelo.

El estudio detallado de la morfología nos permite la identificación de las especies a través de claves de identificación. Se observó, a través de diferentes análisis estadísticos de los caracteres carpológicos, que la morfología es útil para la separación de grupos de especies, ya que presentan una importante variación que permite la delimitación de especies para su identificación, incluso si la planta ya no presenta flores ni frutos (Islas-Hernández *et al.*, 2022). Esta información, en conjunto con caracteres vegetales, florales, palinológicos y moleculares, permitirán en un futuro generar análisis filogenéticos combinados (Peterson & Seberg 1998).

Asimismo, la aplicación de herramientas de modelado de nicho nos permitió analizar la distribución de las especies. Los resultados de este trabajo muestran que la diversidad del género se encuentra concentrada en las vertientes del Golfo de México y Océano Pacífico, desde Estados Unidos de América hasta Panamá y en la Península de Yucatán, principalmente en los bosques tropicales y subtropicales. Dentro de la región de NA, México es el país con la mayor riqueza y endemismos de *Spigelia*, y se reconoce como el segundo centro de diversidad para el grupo, solo después de Brasil en la región de SA. Esta información coincide con lo publicado anteriormente, en donde se reconoce a Mesoamérica como un hotspot, debido a que presenta una alta concentración de diversidad de plantas (Sosa & De-Nova, 2012), lo cual se cumple también para el género.

Debido a lo anterior, y considerando que la diversidad del género en NA se encuentra fuertemente amenazada, el conocimiento actualizado sobre su sistemática, distribución y riqueza nos permite generar mapas donde se localicen zonas potenciales que sean una guía para dirigir el trabajo de campo, así como para proponer áreas para la conservación de las especies que se encuentran amenazadas. Asimismo, la información recabada sirve como marco de referencia para trabajos posteriores sobre biogeografíca, ecología y, en conjunto con datos moleculares, permitan esclarecer las relaciones filogenéticas y ajustar la taxonomía del grupo

Derivado de la revisión de ejemplares de diferentes herbarios, se describió y publicó una especie nueva, *Spigelia elbakyaniae* (Phytotaxa 477(2): 277–283), distribuida en el estado de Oaxaca, México. Esta información fue incluida en el trabajo, lo que aumento la diversidad en la región de NA. De igual manera, a partir de la revisión bibliográfica se encontró una especie de *Spigelia* descrita dentro de la familia Rubiaceae, por lo que se publicó un trabajo sobre ajustes taxonómicos en el género, donde se incluye este taxón dentro de la sinonimia de *S. mocinoi*, así como la corrección ortográfica de *S. elbakianiae* (Phytoneuron 23:1–2).

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# ANEXO UNO

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## *Spigelia elbakyanii*, a new species from Oaxaca, Mexico

C. SOFIA ISLAS-HERNÁNDEZ[1,2]* & LEONARDO O. ALVARADO-CÁRDENAS[1,3]
[1] *Departamento de Biología Comparada, Facultad de Ciencias, Universidad Nacional Autónoma de México, Apartado Postal 70-282, 04510, México, D.F. México.*
[2] *sofilasagesse@ciencias.unam.mx; https://orcid.org/0000-0003-4496-3127*
[3] *leonardo.oac77@gmail.com; https://orcid.org/0000-0002-4938-8339*
**Correspondence author: sofilasagesse@ciencias.unam.mx*

### Abstract

A new species of *Spigelia* (Loganiaceae) from Oaxaca, Mexico, is described here. This species is similar to *S. humboldtiana* and *S. anthelmia*, due to its size and white flowers, but the leaf texture, phyllotaxy below the inflorescence, and the style length are characters that allow to recognize it as a new species. With this addition, Mexico reaches a total of 23 species of the genus, of which more than 50% are endemic or microendemic. This places the country as the second area of high diversity after Brazil. A detailed description and illustration of the new species, a dichotomous key and a distribution map of *Spigelia* species in Oaxaca are included.

**Keywords**: Diversity, endemism, restricted, Santa María Chimalapa

### Introduction

*Spigelia* Linnaeus (1753: 149) is a Neotropical genus with around 90 species, belonging to the Loganiaceae family (Fernández-Casas & Huft 2009, Popovkin *et al.* 2011), widely distributed from the warm-temperate southeastern United States of America to the tropical regions of Mexico, Central America, the Caribbean and South America to northern Argentina and Chile.

This taxon has been recovered as monophyletic in molecular phylogenies (Backlund *et al.* 2000, Frasier 2008, Popovkin *et al.* 2011). The genus can be distinguished from the rest of the family by the annual to perennial herbs with opposite leaves, sometimes pseudowhorled below the inflorescences, with interpetiolar stipule; the inflorescences are usually scorpioid cymes with sessile flowers or with short pedicels; the fruits are capsular, sometimes with persistent style and septicidal, loculicidal and circumscissile dehiscence simultaneously (Henrickson 1996, Alvarado-Cárdenas 2007, Fernández-Casas 2009).

During the herbarium review of *Spigelia* in Mexico, we found a specimen collected in Oaxaca whose vegetative and floral features did not correspond to any of the known species for Mexico. Although it shared some floral similarity with *S. humboldtiana* Chamisso & Schlechtendal (1826: 200) and *S. anthelmia* Linnaeus (1753: 149), there were important differences in the shape and texture of the leaves, and the structure of the flower. These features allowed us to suggest a new species, counting thus 23 species of *Spigelia* for Mexico, from which more than 50% are endemic, highlighting it as a center of diversity for the genus. This places the country as the main center of diversity for *Spigelia* in North America, and second in the continent after Brazil, which has nearly 60 species (BFG 2015). In the country, the states of Chiapas, Guerrero, Oaxaca, and Querétaro have the largest species richness, with Oaxaca having a total of eight species distributed within its area (Fig. 1). In this work, we describe the new species, including an illustration of this new taxon and a key for the species distributed in the state of Oaxaca.

### Materials and methods

Herbarium samples from the herbaria ENCB, FCME, FEZA, HGOM, HUAP, IBUG, IEB, MEXU, OAX, SERO, and UAMIZ (Thiers 2019) were analyzed. The description of the new species was based on specimens found during the

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revision of *Spigelia* in several herbaria (OAX, SERO). The leaves were described according to Hickey (1973), the indumentum description was based on Harris and Woolf (1994). Vegetative and reproductive organs were measured with a digital caliper and described with the help of a stereomicroscope. The description of the infundibular corollas was based on Morales (2005), where the lower tube is the portion below the insertion of the stamens. We provide a key to identify the *Spigelia* species present in Oaxaca.

The map was made from a georeferenced database of the species present in Oaxaca using Esri ArcMap 10.1. We followed the species concept of Templeton (1989) to contrast among the similar taxa. This concept has some of the advantages of pluralistic approaches, and we consider it appropriate for the description of the present taxon.

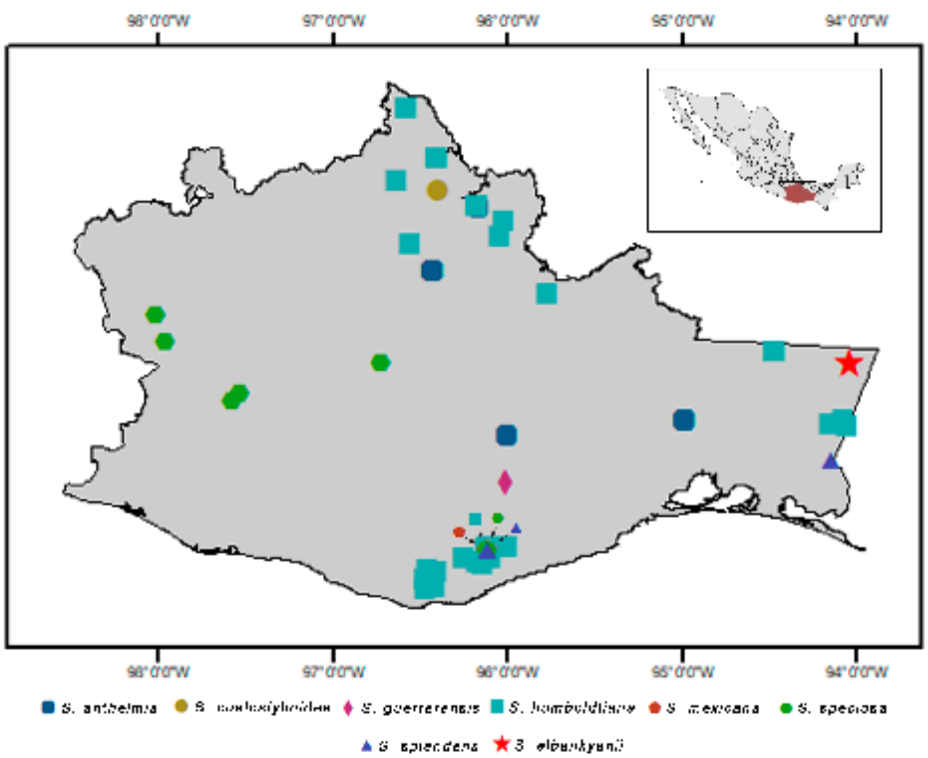


**FIGURE 1.** Map of known distribution of the *Spigelia* species in the state of Oaxaca, Mexico.

## Taxonomic treatment

***Spigelia elbakyanii*** S. Islas & L.O. Alvarado. ***sp. nov.*** (Fig. 2,3)

Type:— MEXICO, Oaxaca, Distrito Juchitán, municipio Santa María Chimalapa. Camino hacia Arroyo San Vicente, 11 km en línea recta al SE de la Gringa, 17°4'0"N, 94°1'32"W, 990 m elevation, 23 March 1995, *E. Torres B. 540* (holotype SERO!, isotype OAX!).

Spigelia elbakyanii *resembles* S. humboldtiana *based on the flower size and color. However,* S. elbakyanii is *distinguished by the opposite leaves below the inflorescence (vs. pseudowhorled leaves), blades chartaceous (vs. membranaceous) and very short style, 1 cm long (vs. 1.5–2 cm long).*

Annual erect herbs, 20 cm tall. Stems quadrangular, pilose, glabrescent when aged, little branched from the base. Leaves opposite on all the stems and below the inflorescence, petiolate; petioles 0.5–1.5 cm long, glabrous; stipules 1.9–3.3 mm long, triangular, shortly papillose to glabrescent; blades 5.7–6.8 × 3.2–4.4 cm, lanceolate, adaxially and abaxially glabrous, chartaceous, base cuneate to rounded, apex acute. Inflorescences terminal, cyme scorpioid; peduncles 1.6 cm long; bracts 1.2 × 0.5 mm, lanceolate, glabrous; flowers per cyme 11; sessile; bracteole 1.2 × 0.5 mm, lanceolate, glabrous. Calyces with lobes 2.0–2.6 × 0.5–0.0 mm, lanceolate, pilose, green. Corolla 1.3–1.6 cm × 7.5 mm, infundibuliform; superior tube 1.05 cm long; lower tube 4.9 mm long, white with purple lines, glabrous; lobes 2.5 × 2.9 mm, deltate, glabrous internally and externally, white inside, white with purple lines outside; stamens included, adnate below the middle of the corolla tube; filaments 0.5 mm long, glabrous; anthers 1.8 mm long, basifixed, lanceolate–sagittate, glabrous; ovary 0.5–1.2 mm in diameter, ovoid; style 10 mm long, glabrous; stigma 1.8 mm long, terete, pilose. Capsules unknown. Seeds unknown.

**Etymology:**—The name *Spigelia elbakyanii* honors Alexandra Elbakyan, founder of Sci–Hub, "a project created to make the knowledge free". Her program has been helpful to access articles, books, and journals, which otherwise would be out of the financial reach for most students.

**Habitat:**—*Spigelia elbakyanii* is distributed in the montane cloud forest, at 990 m elevation, with annual precipitation of 1000–1500 mm and average annual temperature of 12–23° C (Rzedowski 2006).

**Distribution:**—Species endemic to Mexico, restricted to the municipality of Santa María Chimalapa, Oaxaca. This region is part of the biogeographic province of Soconusco that comprises the Sierra Madre of Chiapas and of Guatemala, which holds great diversity and many endemic species (Espinosa *et al.* 2008).

**Phenology:**— Flowering in March. The fruiting period is unknown.

**Conservation:**—*Spigelia elbakyanii* is known from the type locality only. The specimen was collected over 20 years ago in Santa María Chimalapa, Oaxaca. The forest in the Chimalapas region, where the new species was collected, is not exempt from disturbances and it is under deforestation due to timber harvesting and farming (Trejo 2006). The region has also been subject of social and environmental problems such as the fires of 1988, which consumed approximately 80% of the cloud forest (Gallardo-Hernández & Lorea-Hernández 2010). Based on this and because of the very restricted area of distribution and the lack of new records of this species since the type collection, we suggest assigning the category of Critically Endangered (CR) for this taxon (IUCN 2016).

**Taxonomic remarks:**—This species is morphologically similar to *Spigelia humboldtiana* and *S. anthelmia* because of its herbaceous habit and infundibuliform corolla. *Spigelia elbakyanii* can be distinguished by its opposite leaves below the inflorescence (vs. pseudowhorled leaves below the inflorescence of both *S. anthelmia* and *S. humboldtiana*), blades chartaceous (vs. blades membranaceous), inflorescences pedunculate (vs. inflorescences sessile or subsessile) and the style of 1 cm long (vs. style 1.5–2 cm long). The very short style is a character that has not been seen in any other species distributed in Oaxaca (Fig. 3). In *S. humboldtiana* and *S. anthelmia*, the style is more than half as or as long as the corolla. The chartaceous leaves are only known from three other species of the genus (*S. ayotzinapensis* L.O. Alvarado, S. Islas & R. Bustamante (2017: 244), *S. dolichostachya* Fernández-Casas (2005: 123), and *S. hedyotidea* A. De Candolle (1845: 7)), none of them distributed in Oaxaca. In addition, the leaves of *S. elbakyanii* are evidently different from the other species present in the state (Fig. 4). A species key is provided to identify the new taxon from the other species present in Oaxaca.

**Dichotomous key for the identification of species of the genus *Spigelia* in Oaxaca**

1. Leaves opposite below the inflorescence ........ 2
1. Leaves pseudowhorled below the inflorescence ........ 4
2. Stipules triangular ........ 3
2. Stipules linear or absent ........ *Spigelia speciosa*
3. Inflorescences with more than 10 flowers; style 1 cm long, stigma terete ........ *Spigelia elbakyanii*
3. Inflorescences with 1–2 flowers; style 2–3 cm long, stigma capitate ........ *Spigelia guerrerensis*
4. Leaves sessile ........ *Spigelia mexicana*
4. Leaves petiolate ........ 5
5. Inflorescences axillary ........ *Spigelia coelostylioides*
5. Inflorescences terminal ........ 6
6. Capsules papillose at the apex ........ *Spigelia anthelmia*
6. Capsules completely smooth ........ 7
7. Flowers tubular, tube and lobes of the corolla red ........ *Spigelia splendens*
7. Flowers infundibuliform, tube and lobes of the corolla white ........ *Spigelia humboldtiana*


FIGURE 2. Holotype of *Spigelia albakyanii*.

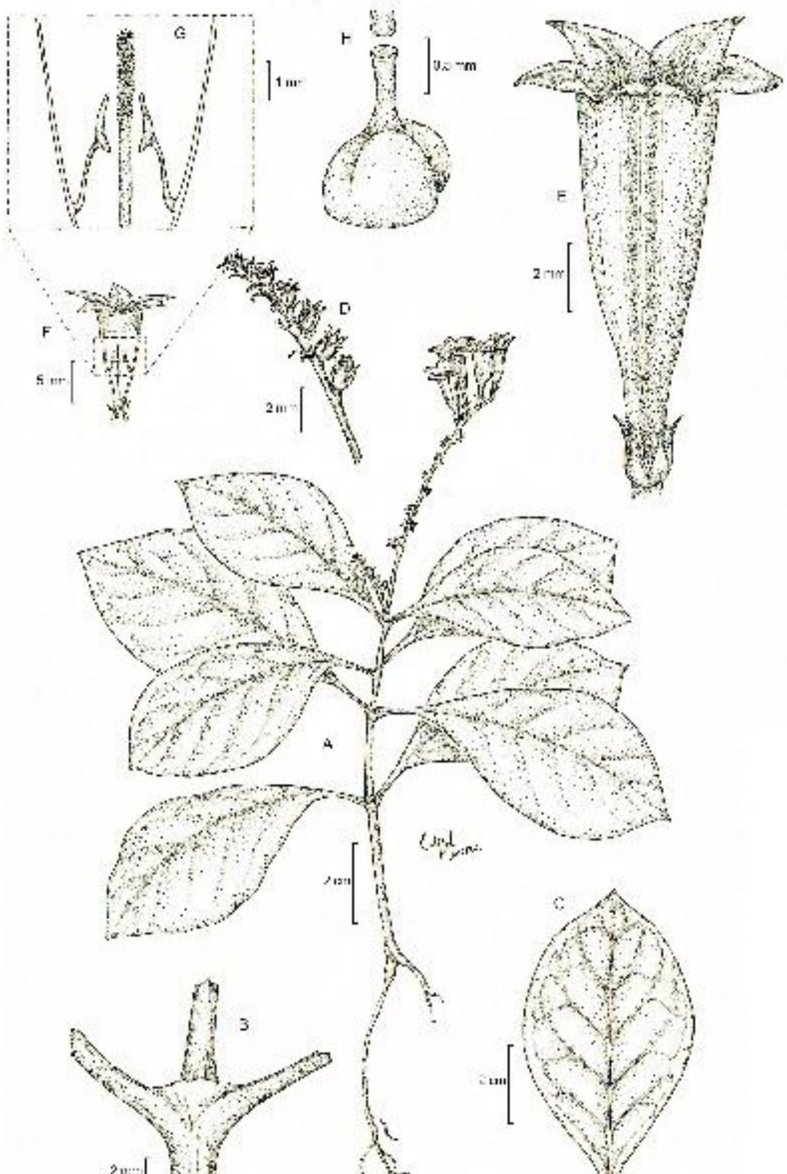

**FIGURE 3.** *Spigelia elbakyanii*. A) Plant habit. B) Detail of the interpetiolar stipule. C) Adaxial surface of the leaf. D) Inflorescence. E) Flower. F) Dissection of the flower showing the style. G) Detail of the style and anthers. H) Ovary with hypostyle. (Illustration made by Belen Cortez)

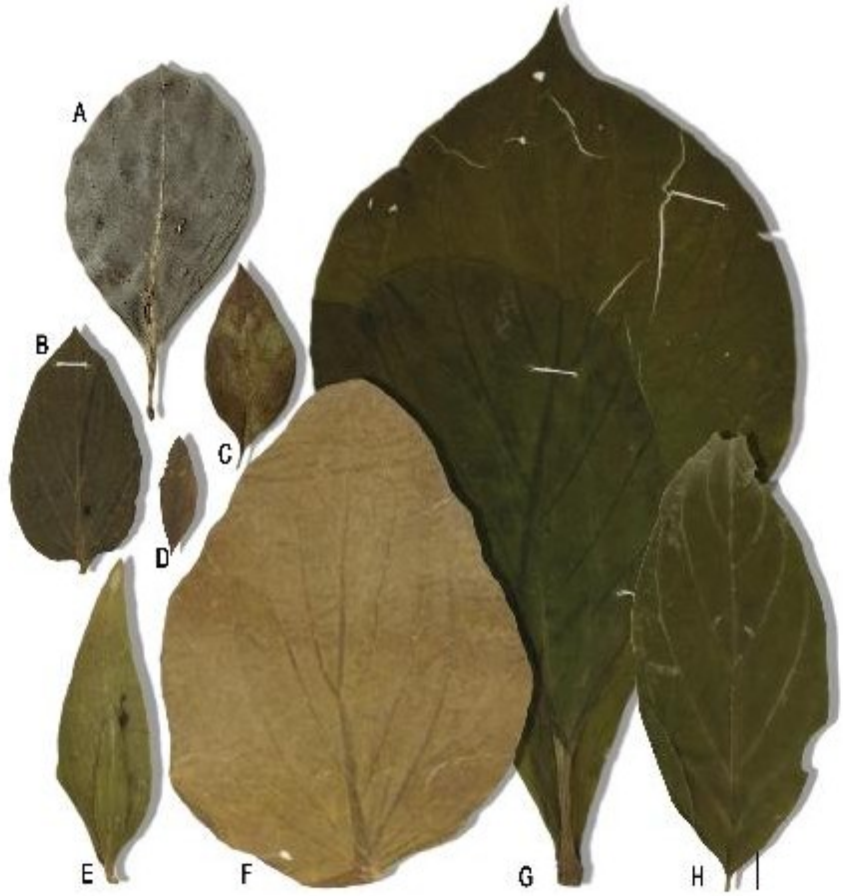


**FIGURE 4.** Comparison of leaves of the *Spigelia* species distributed in Oaxaca, Mexico. A) *S. elbakyanii*, B) *S. guerrerensis*, C) *S. humboldtiana*, D) *S. coelostylioides*, E) *S. anthelmia*, F) *S. speciosa*, G) *S. splendens*, H) *S. mexicana*. Scale bar: 1cm.

**Additional information:**—Mexico is the main center of diversity for *Spigelia* in North America, with 23 species, including the taxon described here, and the second in the Americas, after Brazil (BFG 2015, Islas-Hernández *et al.* 2017a). More than 50% of the species are endemic to the country and show restricted ranges (Gould 1999, Alvarado-Cárdenas & Jiménez 2015, Islas-Hernández *et al.* 2017a, 2017b). The distribution of most endemic species of *Spigelia* is limited to tropical areas in the states of Guerrero, Oaxaca, Querétaro, and Veracruz. These states have been recognized as areas of high diversity for different groups, such as the "La Cuenca del Balsas" in Guerrero (Fernández *et al.* 1998), or the Chimalapas region in Oaxaca (Gallardo-Hernández & Lorea-Hernández 2010), offering particular and isolated habitats for speciation of linages, such as *Spigelia*.

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# ANEXO DOS

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## TAXONOMIC ADJUSTMENTS IN MEXICAN *SPIGELIA* (LOGANIACEAE)

**C. Sofia Islas-Hernández**
Departamento de Biología Comparada
Facultad de Ciencias
Universidad Nacional Autónoma de México
Apartado Postal 70-282, 04510, México, CDMX. México.
sofilasagesse@ciencias.unam.mx

**Leonardo O. Alvarado-Cardenas**
Departamento de Biología Comparada
Facultad de Ciencias
Universidad Nacional Autónoma de México
Apartado Postal 70-282, 04510, México, CDMX. México.
leonardoac@ciencias.unam.mx

### ABSTRACT

A new synonym and an orthographic correction are provided for two species of *Spigelia* L. from Mexico. *Bouvardia amplexicaulis* Borhidi et E. Martínez is placed as synonym of *Spigelia mocinoi* S. Islas & L. O. Alvarado and spelling is corrected for the epithet of *Spigelia elbakyaniae* S. Islas & L.O. Alvarado.

In the preparation of a taxonomic treatment of *Spigelia* in Mexico, we found a type specimen in herbarium MEXU identified as *Bouvardia amplexicaulis* Borhidi et E. Martínez (Rubiaceae) but which is instead a species of *Spigelia*.

**SPIGELIA MOCINOI** S. Islas & L.O. Alvarado, Phytotaxa 331: 247. 2017. **Type: MÉXICO. Estado de México**. Ixtapan, Temascaltepec, 18 Jul 1935, *G.B. Hinton 8063* (holotype: MEXU!; isotype: ENCB!, HUMO!).

*Bouvardia amplexicaulis* Borhidi et E. Martínez (**syn. nov.**). Act. Bot. Hungarica 53: 64. 2011, non *Spigelia amplexicaulis* E.F. Guim. & Fontella 1969. **Type: MÉXICO. Edo. México.** Santiago Amatepec, ladera húmeda, rocosa, barranca, 1300 m, 13 Jul 1970, *E. Matuda 38039* (holotype: MEXU!).

*Bouvardia amplexicaulis* (Rubiaceae) was described based on a collection (*Matuda 38039*) from the state of Mexico and deposited at MEXU but it is actually a member of *Spigelia*. The specimen resembles members of *Bouvardia* such as *B. longifolia* in its white and long salverform corollas, but the sessile leaves, terminal inflorescence in scorpioid cymes, 5-lobed floral whorls, superior ovary, articulated style, and single stigma differ from *Bouvardia* and agree with the attributes of *Spigelia*.

*Bouvardia amplexicaulis* is conspecific with *Spigelia mocinoi*, as indicated by the sessile leaves, the phyllotaxis, and the size and shape of the flowers — the type collections for both were made in close proximity in the state of Mexico. The name *Bouvardia amplexicaulis* has priority over *S. mocinoi* but the epithet *amplexicaulis* is already occupied within *Spigelia* as the correct name for a species of Brazil. A new combination for the Mexican species would be illegitimate (ICN Article 53) and final epithet of the next earliest legitimate name at the same rank is to be used instead (ICN Article 11.4), thus *Spigelia mocinoi* is the correct name, with *B. amplexicaulis* as a synonym.

**Orthography of *Spigelia elbakyaniae***

SPIGELIA ELBAKYANIAE S. Islas & L.O. Alvarado, Phytotaxa 477: 278. 2020 (**orthographic correction**). **Type: MEXICO. Oaxaca.** Distrito Juchitán, Mpio. Santa María Chimalapa: Camino hacia Arroyo San Vicente, 11 km en línea recta al SE de la Gringa, 17°4'0" N, 94°1'32" W, 990 m, 23 Mar 1995, *E. Torres B. 540* (holotype: SERO!, isotype OAX!).

The epithet was published as *Spigelia elbakyanii*. The correct termination, however, for an epithet dedicated to a woman (Alexandra Elbakyan) is *-iae,* instead of *-ii* (Turland et al. 2018) — the error is corrected here without changes in the authorship and date.

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