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ORIGINAL ARTICLE

Systematics, distribution and conservation of *Cascabela* (Apocynaceae: Rauvolfioideae: Plumerieae) in Mexico

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Abstract *Cascabela* is a Neotropical genus of Apocynaceae with six species: *C. balsaensis*, *C. gaumeri*, *C. ovata*, *C. pinifolia*, *C. thevetia* and *C. thevetioides*. Its taxonomic history has long been a subject of controversy, especially due to its circumscription as a genus closely related to *Thevetia.* In this work, we revised the taxonomy of *Cascabela* for Mexico and provide detailed descriptions and illustrations. We also applied species distribution models and geographical information tools to evaluate chorological aspects of the six species occurring in Mexico and provide a conservation category. According to our results, *Cascabela* has a typical tropical distribution within Mexico, and the Balsas basin was identified as an area of diversity and endemism for the genus. The species *C. ovata* and *C. thevetia* have the broadest distribution ranges, and we assigned them the category of least concern. We suggest that the restricted, endemic species *C. balsaensis*, *C. pinifolia* and *C. thevetioides* be considered for protection. The genus was corroborated as an element of deciduous forest, and its cultural importance is highlighted.

Keywords Chorology · Species distribution models · Taxonomy · *Thevetia*

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Introduction

Cascabela Raf. is a Neotropical genus of Apocynaceae. It is included in tribe Plumerieae and subtribe Thevetiinae, together with *Anechites* Griseb., *Cameraria* L., *Cerbera* L., *Cerberiopsis* Viell. ex Pancher & Sébert, *Skytanthus* Meyen, and *Thevetia* L. (Alvarado-Cárdenas and Ochoterena 2007; Endress et al. 2014 as *Thevetia*). The genus has six species distributed mainly in Mexico and Central America, with only one species, *C. thevetia* (L.) Lippold, distributed from Mexico to South America and widely cultivated around the world (Morales 2009a, b). The species are trees or shrubs with showy yellow flowers and are commonly used as ornamentals, although some species present a public health threat because of their highly toxic seeds (González et al. 2003; Escobar et al. 2012).

The most recent evaluation of the genus and its relatives was a morphology-based phylogenetic analysis (Alvarado-Cárdenas and Ochoterena 2007), which suggested that *Cascabela* and *Thevetia* are sister taxa and should remain as separate genera. Based on current information these taxa are recognized in one of two ways; on the one hand, a series of publications (Morales 2009a, b; Shuguftha and Sulthana 2013; Alvarado-Cárdenas and Soto 2014; González-Rocha and Cerros-Tlatilpa 2015) as well as electronic databases (CICY herbarium 2010; The Plant List 2013) recognize *Cascabela* as a separate accepted genus. On the other hand, other sources continue to subordinate it under *Thevetia* (Williams and Stutzman 2008; Zarucchi 2009; Endress et al. 2014; Missouri Botanical Garden 2014). In addition, some works have applied incorrect names to *Cascabela* species (Yepez and Arboleda 2009; Herrera and Rivera 2013; Shuguftha and Sulthana 2013).

In this work, we consider *Cascabela* a distinct, accepted genus supported by characters such as infundibuliform corollas, suprastaminal finger-like appendages, drupes with stony endocarps and non-compressed seeds with reminiscent wings (Fig. 1). In contrast, *Thevetia* has hipocrateriform or infundibuliform corollas, suprastaminal deltoid-like appendages, drupaceous fruits with four fibrous endocarps and compressed seeds with or without reminiscent wings. The incorrect application of the names of *Cascabela* and the new taxon described requires an

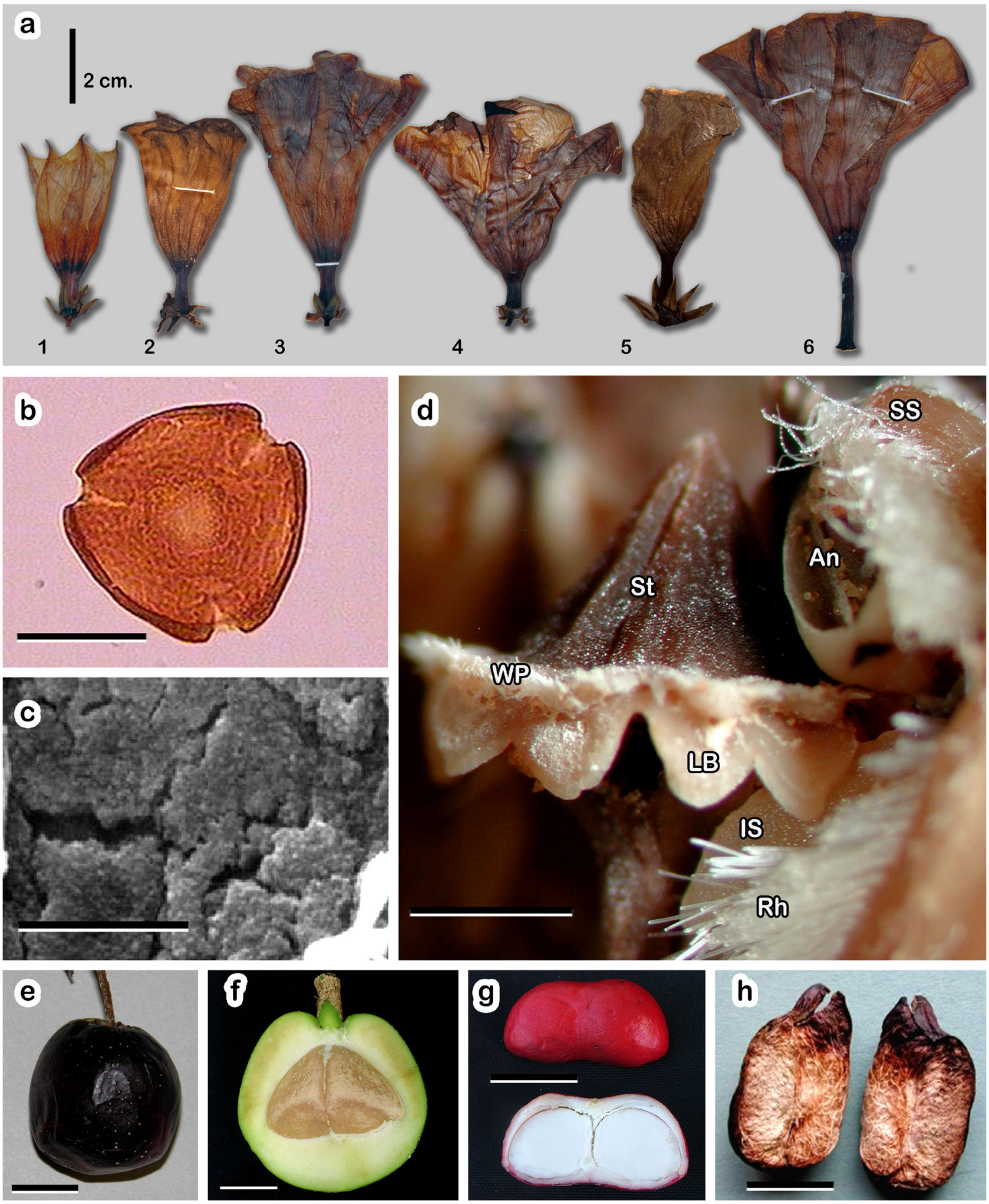


Fig. 1 Morphological attributes of *Cascabela* and *Thevetia*. **a** Flower size comparison between *1 C. balsaensis*, *2 C. gaumeri*, *3 C. pinifolia*, *4 C. ovata*, *5 C. thevetia* and *6 C. thevetioides*, **b** polar view of a pollen grain of *C. thevetia* (*scale bar* 40 μm), **c** internal micrography of pollen grain of *C. pinifolia* showing endofissures (*scale bar* 5 μm), **d** stylar head with anthers, **e** mature fruit of *C. ovata* (*scale bar* 2 cm), **f** fruit with exposed endocarp of *C. thevetioides* (*scale bar* 1 cm), **g** ripe fruit and longitudinal section with exposed endocarp and seeds of *T. ahouai* (*scale bar* 2 cm), **h** dry and segmented fruit of *T. amazonica* (*scale bar* 2 cm). *An* anthers, *IS* infrastaminal appendages, *LB* lobed base, *Rh* Retrorse hairs, *SS* suprastaminal appendages, *St* stigmatae and *WP* equatorial wreath of papillae (*scale bar* 1 mm)

updated taxonomic revision, along with information about the biology of the species. Together with the systematic revision, the knowledge of how genus diversity is distributed is essential for understanding potential biogeographical and evolutionary processes, as well as for highlighting priority areas for conservation and identifying areas of insufficient exploration and collection (Villaseñor 2004; Cruz-Cárdenas et al. 2013).

In order to evaluate the chorology and species richness, numerous quantitative tools have been applied to several taxonomic groups, such as statistical approaches (Villaseñor 2003; Sosa and De-Nova 2012), geo-statistical interpolation methods (Cruz-Cárdenas et al. 2013; Torresín et al. 2013; Villaseñor and Ortiz 2014) or species potential distribution models (Escalante et al. 2009; Villaseñor et al. 2013). This last method seems a viable option to evaluate potential patterns of species richness distribution, since it provides a hypothesis of species distribution and contrasts it with known data-based localities from biological collections. The use of these species distribution modeling tools will be very useful for understanding patterns of species distribution and endemism, as well as to provide a conservation status of each *Cascabela* species.

The genus represents a suitable model because it is a morphologically interesting group, it is a typical element of tropical dry forest (Rzedowski and Calderón de Rzedowski 2013), and it has ecological, economic and public health importance. In this research, we provide an integrative taxonomic update and chorological profile of the six species of *Cascabela* occurring in Mexico. Additionally, we assess the diversity patterns of the genus in the country in order to identify potential sites of high diversity and provide the status of conservation of this plant group.

Methods

Systematics

We performed an exhaustive bibliographical query of systematic works related to *Cascabela* and other Plumerieae genera (Woodson 1937, 1938a, b, 1939; Pichon 1948, 1949, 1950; Veillon 1971; Fallen 1985, 1986; Plumel 1991; Williams 1996a, b; Allorge 1998; Gentry 1998; Rzedowski and Calderón de Rzedowski 1998; Leeuwenberg 1999; Alvarado-Cárdenas 2004; Diego-Pérez 2004; Morales 2005, 2009a, b; Alvarado-Cárdenas and Ochoterena 2007; Simões et al. 2007; Williams and Stutzman 2008; Zarucchi 2009; Alvarado-Cárdenas and Soto 2014; Endress et al. 2014; González-Rocha and Cerros-Tlatilpa 2015). In addition, we carried out an intensive review of specimens, housed at the herbaria ENCB, FCME, G, IEB, INEGI, MEXU, MO, NY, SERO and XAL (Thiers 2016). Supplementary to this work, the first author made a series of field trips to the Mexican states of Guerrero, Mexico, Oaxaca and Puebla to collect and photograph *Cascabela* specimens and preserve flowers and fruits for laboratory studies. The first set of specimens collected was deposited at MEXU, and duplicate specimens were sent to IEB and MO.

For each species, we provide a list of synonyms, taxonomic descriptions complementing previous descriptions of the taxa and integrating new information, common names and uses taken from the specimen label or based on bibliography. We also listed a general and contrasted description of the characters useful for the taxonomy of the group. The description of the infundibular corollas was based on the work of Morales (2005), where the lower tube is the portion of the corolla below the point of insertion of the stamens and upper tube is the portion above the insertion of the stamens. We included only selected specimens, with one specimen per municipality (Mun) from each Mexican state. A complete list of specimens is available upon request. We took information on phenology, habitat and distribution from the specimen labels and supplemented with information gathered from the field trips. Similarly, we gathered information about common names and uses from the specimen labels and the literature (cited in the text when used).

Species distribution modeling and richness analysis

Distribution data

To evaluate the patterns of species richness and endemism of the *Cascabela* species, we first generated a database of the six species known in Mexico with more than 800 geo-referenced locations from the taxonomic inventory of the Mexican Apocynaceae (Alvarado-Cárdenas et al. in preparation). This information was compiled through an intensive review of herbaria as well as bibliographical searches. From the total locality data, we used 667 geo-referenced and unique records to calculate the most appropriate square size for the analysis, following recommendations of the International Union for the Conservation of Nature (IUCN 2001). Thus, the area of occupancy (AOO) of a species was determined considering a selected grid square size based on 10% of the distance between the two most distant geo-referenced collection points (Suárez-Mota and Villaseñor 2011). We then used the “Conservation Assessment Tools” (Moat 2007) extension for Arcview to calculate grid size. The width of the optimal cell for each species was averaged to obtain a size applicable to all species, resulting in a grid square network of 304 cells, each measuring 0.91° per side.

Species distribution modeling

Before performing the species distribution models (SDMs), we evaluated the quality of the data. The number of locality records for each of the six species varied from three to more than 100. When a species had 10 (minimum number of records considered to carry out the models) or more occurrence records, we applied a test of randomness to evaluate whether the species point records were randomly distributed (Bivand et al. 2008), i.e., there was little spatial autocorrelation. When the records of a species showed a random distribution, we used 75% of the records for model trials and 25% for model validation. When the species records were not randomly distributed, we applied a spatial pattern analysis using ILWIS 3.4 software (ITC 52° North 2007), to calculate the distance with the highest probability of finding a record. We used the resulting distance value as the side length for a grid of square cells using Quantum Gis 1.7.4 (QGIS Development Team 2012). Then, one locality record was selected randomly from each cell to test the model, and 25% of the remaining records in each cell were used for model validation. The species *C. balsaensis* and *C. pinifolia* each had fewer than 10 records, so we could not perform the randomness test. For *C. balsaensis* all records were used to generate models, and for *C. pinifolia*, 50% of the records were used for trials and the remaining 50% were used to validate the model.

To select the model that best fits the data, we carried out modifications to the regularization (beta) parameter in the "settings" module of MaxEnt. We adjusted the beta using four values: the standard values of 1, 0.5 and 0.25, and the value based on the beta formula (linear quadratic + square root of the number of records used for modeling). The selection of beta values followed recommendations from the help menu in MaxEnt. We selected the raw output for model generation. Finally, we analyzed the models obtained using the tool "Model selection" in the program ENMTools (Warren et al. 2009), which applied an Akaike test to assess which of the models fit best.

We used seven climatic layers, selected from a principal components analysis performed on 20 variables (for details on the methodology see Cruz-Cárdenas et al. 2013; these authors kindly provided the climatic layers). The pixel's resolution size was 1 km^2. The layers of bioclimatic information summarize the uncorrelated variables that model the potential conditions the species may require. We used records for trial and validation to model the potential distribution of the species, using the software MaxEnt (Phillips et al. 2006). This program uses an algorithm that requires only the presence of species records and a set of environmental layers as predictors; absence records are generated by creating random background data from the selected region. This program seems to perform better than other methods of species distribution modeling that use only presence data (Elith et al. 2006). Additionally, the program provides well-supported models even when only three to five records are available, which is the minimum data to perform the analysis (Phillips et al. 2006). Default MaxEnt configurations were used (Phillips and Dudik 2008), except that the "Extrapolate" and "Do clamping" modules were disabled and the output format of the model was logistical.

The resulting potential distributions were transformed to Boolean (presence–absence) layers using ArcMap 9.3.1 (Esri Inc. 2009) and edited by selecting a threshold of 10% of omission errors (Pearson et al. 2007). Finally, validation was performed using a binomial test, in order to assess whether it was better than randomly obtained models ($p = 0.5$). Positive validation was obtained to quantify the number of records with logistical values above the selected threshold (Cruz-Cárdenas et al. 2013). To draw the areas of prediction from each model, we used the species points of occurrence and selected the morphotectonic provinces (Ferrusquía-Villafranca 1990) where the points occurred. The maps obtained are considered hypotheses of geographical distribution (Soberón 2010). Thus, we had a map of potential distribution for each species, indicating suitability areas where the models predicted their occurrence.

In addition, we compared the vegetation type preferences of species of *Cascabela*. We cross-examined the distribution models of every species with Rzedowski's (1990) vegetation map. The overlap between the models and vegetation map allowed us to observe the pattern of vegetation type preferences for each species.

Species richness analysis

The locality data of *Cascabela* in Mexico were assessed on a grid of 304 cells of 0.91° per side. The analysis aimed to obtain the number of species in each geographical unit (grid cell or square). With this information, we generated a map of known species richness. Similarly, the potential distribution models of the six species were crossed on this grid square network, assigning their presence in each grid cell, according to their occurrence as indicated by the models. This information generated a map of potential richness that we contrasted with the pattern of known species diversity.

Classifying species risk of extinction

To suggest the conservation status of the species of *Cascabela*, we used the Geospatial Conservation Assessment Tool (GeoCAT) (Bachman et al. 2011), http://geocat.kew.org/. This program considers extent of occurrence [EOO, "the area contained within the shortest continuous imaginary boundary, which can be drawn to encompass all the known, inferred or projected sites of present occurrences of a taxon, excluding cases of vagrancy" (IUCN 2013) and area of occupancy (AOO, "the area within its 'extent of occurrence', which is occupied by a taxon, excluding cases of vagrancy" (IUCN 2013)] to classify the species risk. Furthermore, we evaluated the extent of the projected and edited niche models and compared the results. We provide additional information about the biology of the species to adjust and suggest the final risk categories.

In addition to the assignment of risk categories, we summed the models of endemic species to get the overlapping areas or center of richness for the genus. These species and areas are sensitive to habitat perturbations and vulnerable to extinction, representing a guideline for the conservation status of the areas (Brooks et al. 2002; Solano and Feria 2007). We cross-referenced the identified richness centers with Mexican natural protected areas (Instituto Nacional de Ecología 1999) to assess the potential risk status of the group.

Sampling effort

We used collection records to generate the presence/absence data matrix of species richness for *Cascabela* (Gotelli and Colwell 2001). The 92 cells that record species occurrences were used to generate a species accumulation curve, using the program Estimates, version 8.2.0 (Colwell 2009). The asymptote of the accumulation curve is related to the number of species that should be found in the study area (Jiménez-Valverde and Hortal 2003). The curve was fit using the Clench equation (Soberón and Llorente 1993; Colwell and Coddington 1994), using the Simplex and Quasi-Newton methods in the program STATISTICA (StatSoft Inc 2011).

Results

Potential species distribution models and richness

Species distribution models of the Mexican species of *Cascabela* showed good area under the curve (AUC) values and significant results in the validation tests (Table 1). Potential models were generated using default regularization values ($\beta = 1$) for *C. gaumeri* (Hemsl.) Lippold, *C. ovata*, *C. thevetia* and *C. thevetioides*, and regularization values of 0.27 and 0.39 were applied to *C. balsaensis* L.O.Alvarado & J.C.Soto and *C. pinifolia* (Standl. & Steyerm.) L.O.Alvarado & Ochot.-Booth, respectively. Regularization values were obtained with the "Model selection" test. Models based on these regularizations showed suitability areas congruent with the empirical evidence.

Model predictions revealed greater areas of extension than those using only occurrence data, suggesting new potential areas in which to look for the species. The discussion of the distribution models is provided after the taxonomic descriptions of each species. The distribution of *Cascabela* is mostly limited to the tropical slopes of the Pacific Ocean and the lowlands around the Gulf of Mexico, as well as to the central and southeastern portion of the country (Figs. 2, 3). There was no predicted presence of the genus in the northern portions, corresponding to the Holarctic region.

There were important differences between the real and potential species richness distributions. We recorded species occurrence in only 92 grid squares, out of the 304 into which Mexico was divided. Most of them recorded a single species, and only one grid square recorded the largest number of species (5, Fig. 3). *Cascabela ovata* and *C. thevetia* were recorded in the highest number of grid squares (50 and 40, respectively), while *C. balsaensis* presented the lowest, with only 2 (Table 2). On the other hand, potential distribution models increase the richness distribution to 147 grid squares, 41 of them recording a single species (Table 2) and 27 including greater species richness (Table 2; Fig. 3).

The richness centers identified for the genus (Fig. 3) are located in the Balsas River Depression morphotectonic province. Both real and potential richnesses identified portions of the states of Guerrero, Mexico, Michoacán, Morelos, Oaxaca and Puebla as the most important due to their number of species. However, the potential distribution analyses identified additional zones on the Pacific lowlands, especially along the states of Colima, Jalisco, Guerrero, Michoacán and Oaxaca, as well as portions of southwestern Chiapas as potential richness areas for the genus. The northern part of the country is considered unimportant for the genus, since most of the empty cells were located there (Fig. 3). The models and the locality points corroborate the presence of these species, mainly in the tropical dry forest, which is the vegetation type with the highest diversity for the genus (Fig. 4). However, *C. thevetia* and *C. gaumeri* may also grow in more mesic environments.

The values of EOO, AOO and extent of the species distribution models (ESDM) are contrasting (Table 3). The EOO and ESDM had higher values compared to AOO and were the most similar to each other. Based on the ESDM and the biology data of the species, we assigned the Mexican endemic species *C. balsaensis*, *C. pinifolia* and *C. thevetioides* under some risk category, whereas the remaining species were designated as least concern.

The area with the largest number of endemic species is located in the western portion of the Balsas basin (Fig. 5). This area is not included in any of the decreed natural protected areas. Efforts for its inclusion in the system of

Table 1 MaxEnt modeling and validation results for the species of *Cascabela*

Species	Points unbiased and non-duplicated	AUC training/test	Logistic threshold at 10 percentile	Validation test $p = 0.5$
C. balsaensis	3	0.970	0.588	$p = -$
C. gaumeri	27	0.806/0.632	0.304	$p = 0.059$
C. ovata	73	0.902/0.779	0.330	$p = 0.074$
C. pinifolia	12	0.903/0.804	0.494	$p = 0.3$
C. thevetia	56	0.749/0.586	0.374	$p = 0.06$
C. thevetioides	41	0.862/0.826	0.380	$p < 0.001$

The validation test of *C. balsaensis* was not calculated due to the small number of records

Fig. 2 Distribution map of *Cascabela* in Mexico. Known distribution based on 800 species records (*white circles*). Potential distribution (*green*) based on the sum of the six species models

protected areas must be encouraged, especially because it represents a small part of the full potential distribution of the genus *Cascabela* in Mexico (Fig. 5).

The analysis of the species sampling effort indicated that *Cascabela* species accumulation curves reached 96% of completeness, practically the asymptote of the curve (Fig. 6). Therefore, we can assume that the genus is well sampled in Mexico and that the addition of new species is not expected.

Morphological attributes of *Cascabela*

The following section provides more detailed morphological observations of *Cascabela*, as well as a comparison of *Cascabela* with its related genera in the tribe Plumerieae.

Leaves

All species have alternate leaves, with entire and revolute margins. The lamina is variable in shape (elliptic, linear, lanceolate to obovate), membranaceous to subcoriaceous and glabrous to pubescent, with colleters at the base of the petioles. According to the classification of Hickey and Wolfe (1975), the venation is pinnate camptodromous, with secondary venation brochidodromus with an intra-marginal vein evident in *C. ovata* (Cav.) Lippold and *C. thevetioides* (Kunth) Lippold. Secondary venation can be conspicuous or not evident; when conspicuous, the number of secondary vein pairs is around (15–) 30–46. Both leaf shape and venation are useful taxonomic traits (Williams 1996a; Morales 2009a, b).

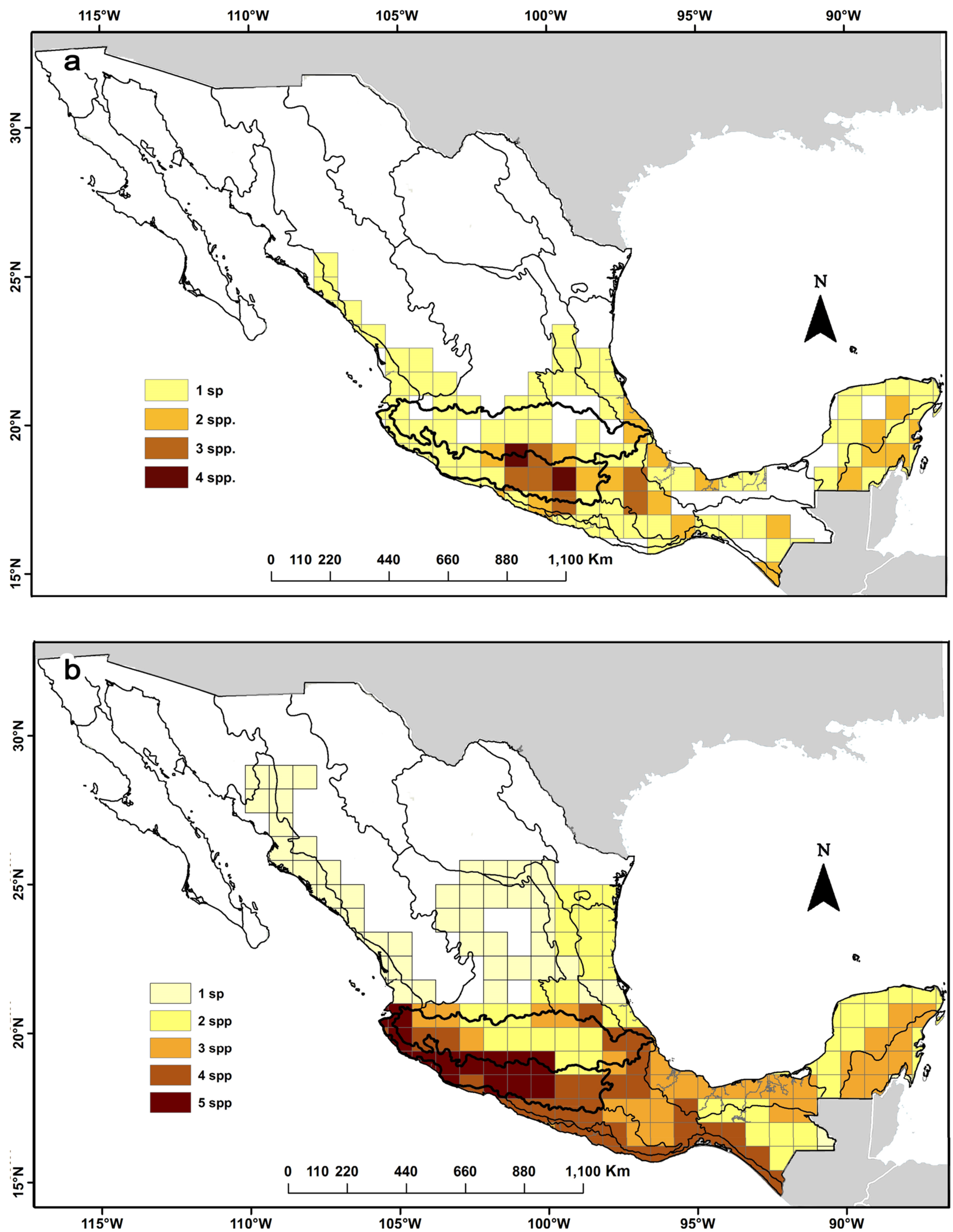


Fig. 3 **a** Known species richness of *Cascabela* in Mexico ($N = 6$ species), **b** predicted species richness of *Cascabela* in Mexico, based on the sum of the species distribution models ($N = 6$ species). The *different colors* indicate the number of species registered in each square ($0.91° \times 0.91°$)

Inflorescence

The inflorescence is a corymb-like dichasium, sometimes branched. The peduncles are usually evident or sometimes reduced. This floral arrangement contrasts with those of other genera in Plumerieae, such as *Cerbera*, *Cerberiopsis*, *Himatanthus* Willd. ex Roem. & Schult., *Mortoniella* Woodson, *Plumeria* L., and *Skytanthus* with long

Table 2 Number of species and species of *Cascabela* recorded per grid square

Species number	Squares of known species richness	Squares of predicted species richness	Species	Squares of known distribution	Squares of predicted distribution
1	60	41	*C. balsaensis*	2	13
2	24	50	*C. gaumeri*	19	46
3	4	29	*C. ovata*	50	96
4	4	27	*C. pinifolia*	7	41
			C. thevetia	40	107
			C. thevetioides	19	60

Known species richness and known distribution refer to the number based on herbaria specimens and predicted species richness and predicted distribution based on species distribution models (Fig. 3)

pedunculate thyrses; *Anechites* with racemes and *Cameraria* with dichasia (Veillon 1971; Fallen 1983; Morales 2005, 2009a).

Flowers

The calyx is pentamerous, strongly divided, with numerous colleters in one or two rows on the internal surface of each sepal. The sepals are equal to subequal in size, ovate, foliaceous and usually extended. The shape and dimensions of the sepals for each species are similar to the subtending bracts. The corolla is infundibuliform (Fig. 1a), and the tube is glabrous outside but internally pubescent, yellow to yellowish-green. The size of the corolla is a useful trait to distinguish several species (Morales 2009a, b; Alvarado-Cárdenas and Soto 2014). The shape and color of the corolla are important traits to distinguish between some of the genera in Plumerieae; for example, *Anechites* (yellow), *Cameraria* (white), *Cerbera* (white or yellowish tingled with purple or pink at base of corolla lobes), *Himatanthus* (white), *Mortoniella* (white), *Plumeria* (white, yellow, pink), *Skytanthus* (yellow and salveform) and *Allamanda* L. (yellow and purple) and some species of *Thevetia* (yellow with infundibuliform corollas) (Leeuwenberg 1999; Morales 2005, 2009a).

The corolla has two different kinds of appendages or coronas (Fig. 1d), five suprastaminal appendages with digitiform shape, covered with dense tomentose pubescence, and five infrastaminal appendages, triangular, and fused with the base of the stigmatic head. The structure of the corona is similar in *Cerbera* and *Thevetia*, but it is absent in practically all the other taxa in Plumerieae. The estivation is sinistrorse. The corolla lobes are obliquely obovate to oblong, obtuse to truncate at the apex. The lobes are expanded or partially erect.

The anthers have latrorse dehiscence and are supported by a short and thick filament or rib. Their shape is ovoid and apically acuminate; usually the connective apex is fused with the other apices. The members of *Cerbera* and *Thevetia* are the only ones with fused connective apices. Species of *Cameraria* and *Skytanthus* possess free and long linear connective apices. The genera *Allamanda*, *Himatanthus*, *Mortoniella* and *Plumeria*, on the other hand, show longitudinal anther dehiscence and cylindrical or flat filaments. In members of the Plumeriineae Pichon ex Leeuwenb. and Allamandinae A.DC., the connective apices are short acuminate and free from each other. The pollen grains are tricolporate, with internal fissures or endofissures (Fig. 1b, c). The other genera also have tricolporate pollen grains, but without fissures. The only taxa where pollen fissures have been reported are *Thevetia* (Plumerieae) and *Carissa* L. (Carisseae).

The ovary is superior and partially syncarpous, basally fused, glabrous, with two ovules per carpel. The style head is massive, typical of the subtribe Thevetiineae A.DC. (Pichon 1948; Leeuwenberg 1999; Alvarado-Cárdenas and Ochoterena 2007), with a longitudinal differentiated structure (Fallen 1986). The apex has two conical appendages called stigmatae (Pichon 1948), the middle area has a wreath of hairs, and the basal section is a 10-lobed basal part, which acts as a pollen-collecting apparatus. A nectar disk is present and evident. The genera in subtribe Plumeriineae show half-inferior and apocarpic ovaries with numerous ovules and no differentiated style head (Fallen 1986; Plumel 1991). In *Allamanda,* the ovary is superior and postgenitally syncarpous with numerous seeds and style head differentiated (Fallen 1985).

The pollination system showed by Thevetiineae could be one of the most complex in Plumerieae. The synorganization of anthers, style head and corolline appendages in *Cascabela* (Fig. 1d), as well as in *Thevetia*, suggests a system that would favor cross-fertilization and avoid self-fertilization. The presence of suprastaminal appendages pressing the anthers against the style head apex, the fusion of the anther connective apices and the infrastaminal appendages, adnate to the style head base, force the pollinator's mouth to pass only through the space between the anthers. The stigmatae and the equatorial wreath of hairs receive and keep the pollen grains wet, shed by their own anthers, blocking their

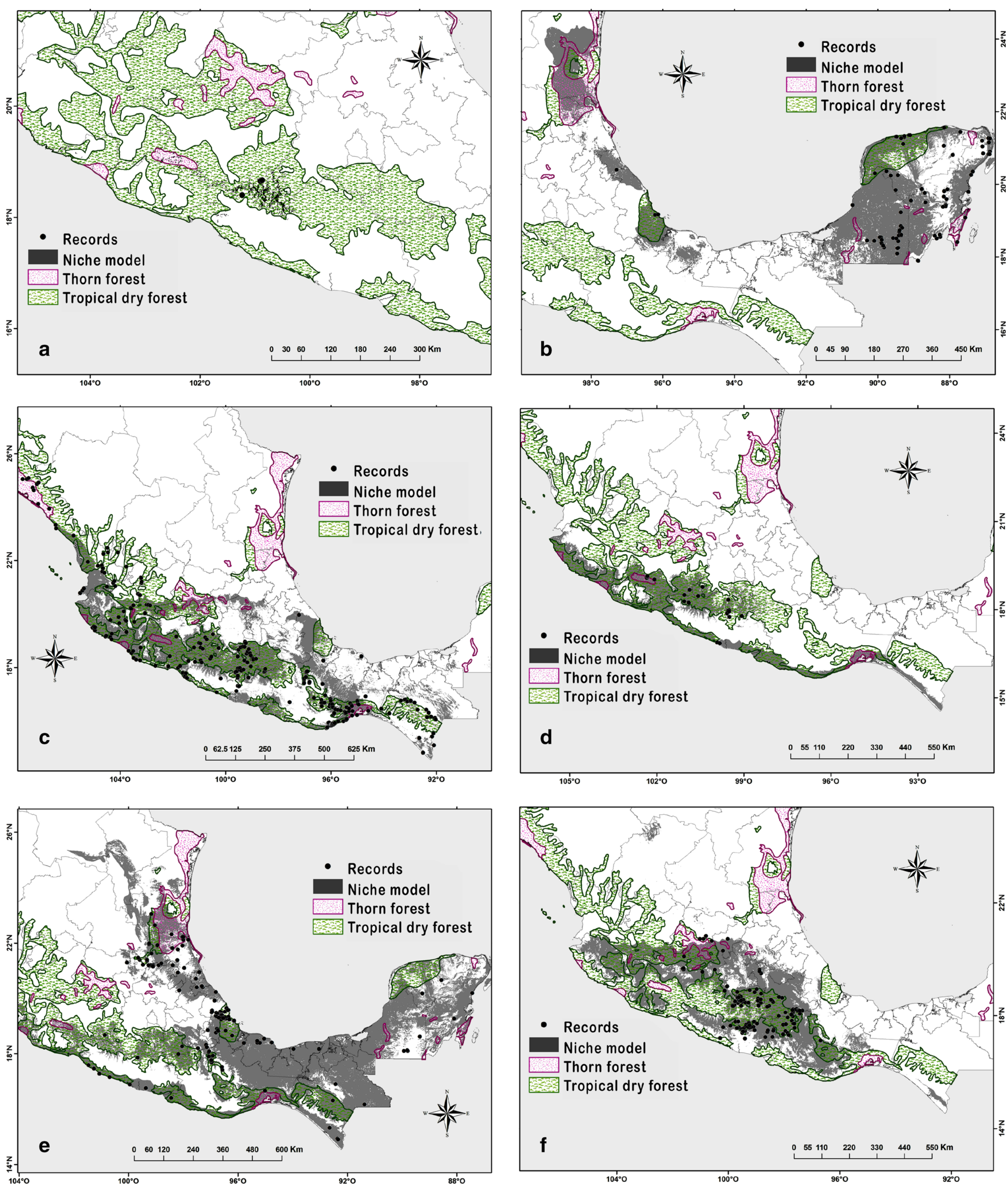


Fig. 4 Comparison between distribution in the tropical dry forest and thorn forest, and the modeled and known distribution of the species of *Cascabela* in Mexico. **a** *C. balsaensis*, **b** *C. gaumeri*, **c** *C. pinifolia*, **d** *C. ovata*, **e** *C. thevetia* and **f** *C. thevetioides*

passage to the lower section (Fallen 1986). In addition, the system ensures the release of foreign pollen below the style head, helped by its 10-lobed base and a group of retrorse hairs in the corolla tube, and the collection of pollen from the apex of the style head, when the proboscis is removed.

Table 3 Distribution and IUCN risk categories for each species of *Cascabela*

Species	EOO	%AM	Category EOO	AOO	%AM	Category AOO	ESDM	%AM	Category suggested
C. balsensis	23.98	0.001	CR	12	0.0006	EN	25.103	0.001	CR
C. gaumeri	390, 233	19.865	LC	324	0.016	EN	208,969	10.637	LC
C. ovata	252, 038	12.830	LC	984	0.050	VU	264,725	13.476	LC
C. pinifolia	35, 319	1.797	NT	80	0.004	EN	58,068	2.959	VU
C. thevetia	821, 907	41.840	LC	524	0.026	VU	494,000	25.147	LC
C. thevetioides	121, 062	6.162	LC	504	0.025	VU	250,383	12.746	NT

All values obtained are in km^2

EOO extent of occurrence, *AOO* area of occupancy, *ESDM* extension of species distribution models, *EN* endangered, *CR* critically endangered, *NT* near threatened, *VU* vulnerable, *LC* least concern, *%AM* percentage of the total area of Mexico

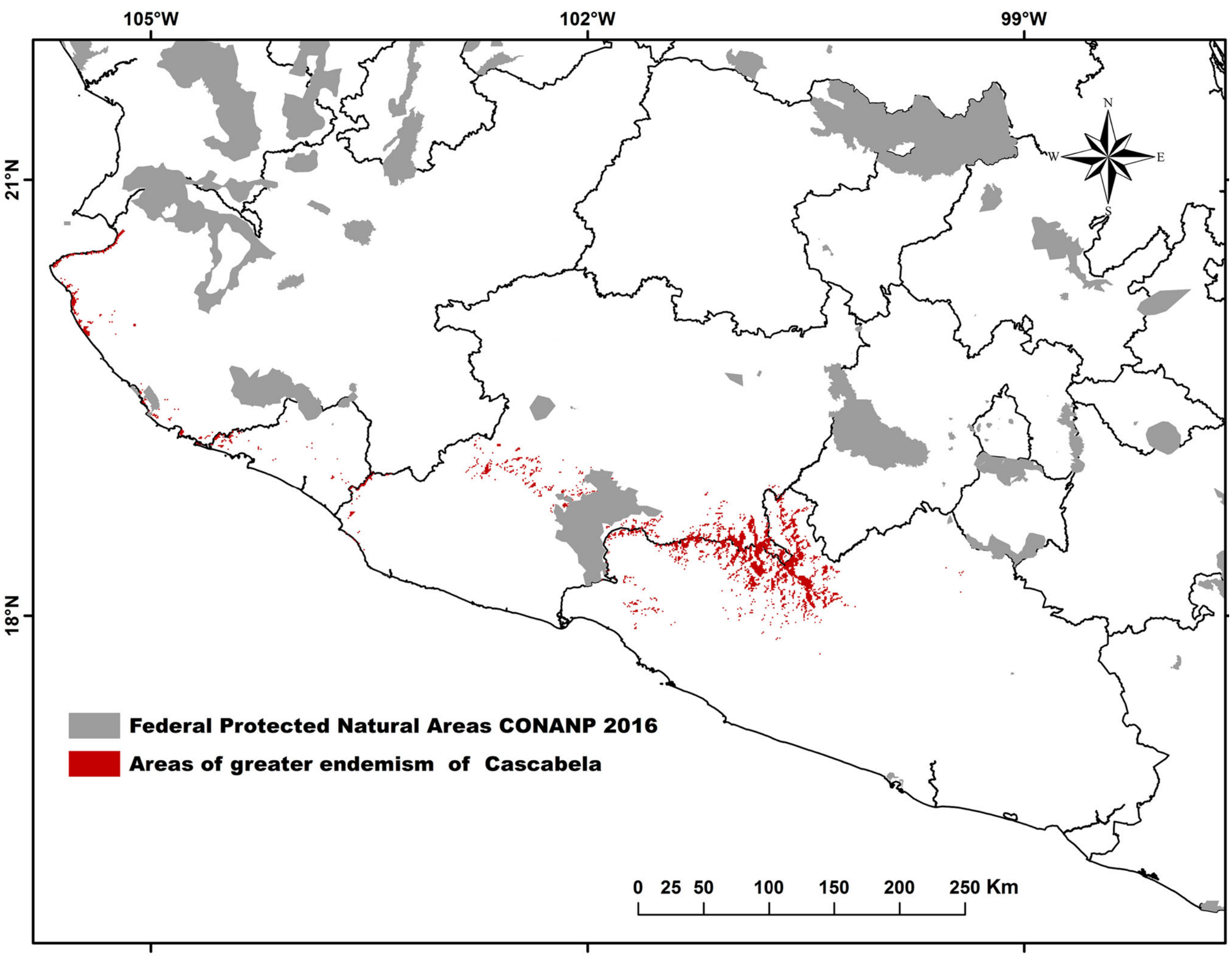


Fig. 5 Placement of the area of endemic species concentration of *Cascabela*, based on the species distribution models, and the Natural Protected Areas of Mexico

Fruit

The fruits are subglobose to pear-shaped black drupes (Fig. 1e, f). The exocarp is formed by a very thin layer with or without lenticels. The mesocarp is a very conspicuous fleshy layer; both the exocarp and the endocarp turn black when ripe. The endocarp is an inverted deltoid to sub-pyramidal stone (Fig. 1f), very hard when dry, but permeable to water. When fully hydrated, it becomes soft and easy to rip, allowing seed germination. Inside, the placentas

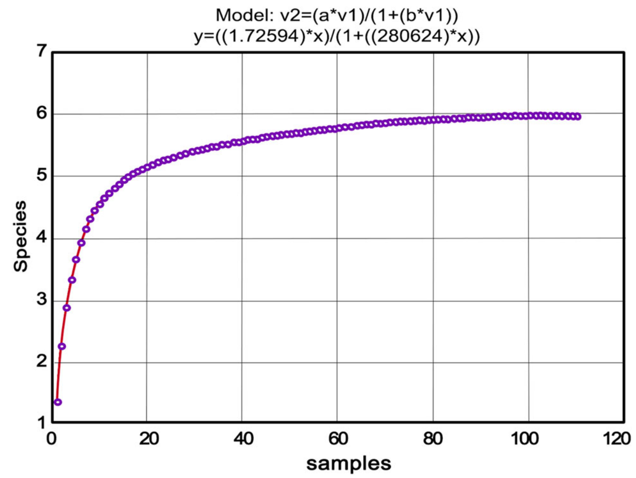


Fig. 6 Species accumulation curve for *Cascabela* in Mexico. The *circles* represent sampling units (*squares* of 0.91° per side). The asymptote is reached at six species, indicating a satisfactory level of completeness

are lignified and form a wall separating both locules; they are also joined with the seeds. In the case of *Thevetia*, the fruits are reniform red pseudodrupes, sometimes called mericarps (Fig. 1g, h). The exocarp is formed by a very thin layer without lenticels. The mesocarp is a very conspicuous white and fleshy layer. The endocarp is divided in four fibrous and ovoidal elements, fused with the lignified placenta. The fruit divides in four when dried. The fruit in *Cascabela* is very distinct from the other taxa in Plumerieae; in *Anechites*, *Himatanthus*, *Mortoniella*, *Plumeria* and *Skytanthus* they are follicles; in *Allamanda* are capsules, and *Cameraria* and *Cerberiopsis* are samaras (Veillon 1971; Plumel 1991; Morales 2005).

Seeds

There are four or fewer seeds per fruit due to abortion; they are subglobose to slightly angulated, with a papery testa and a reminiscent and fimbriate wing. In contrast, the seeds of *Thevetia* are flat in one face and only in *T. ahouai* the testa is papery with a reminiscent and fimbriate wing; in the other species the testa is coriaceous and wingless. The seeds in the tribe are mainly flat and winged, though *Skytanthus acutus* and *Anechites* have wingless seeds (Pichon 1948; Fallen 1983; Morales 2009b).

Discussion

The species of *Cascabela* grow in contrasting habitats, especially those at lower elevations, such as dry tropical forests. The distribution patterns obtained from current known distributions and potential distribution models are congruent, suggesting the genus is mainly distributed at the transition zone of the Neotropical and the Nearctic realms (Figs. 3, 4).

The potential distribution models agree with known collection localities (Figs. 3, 7, 8, 9, 10, 11, 12), though with some differences. The most important difference is the larger predicted areas generated by the SDM for practically all species. Undoubtedly, those areas with potential environmental conditions suitable for the presence of the species should be considered in future exploratory work (Table 2). These contrasts may be related to several factors, including different collecting efforts and field exploration strategies. Another factor may be the effect of soil and land use changes where the species could be present; anthropogenic activities may affect the primary vegetation, preventing collecting activities from finding the species.

The SDM and point localities found a center of richness for the genus in part of the Balsas River basin, where four species are present (Fig. 4), *C. balsaensis*, *C. pinifolia*, *C. thevetioides* and *C. ovata*, the first three of which are endemic to Mexico. These results support earlier observations of the Balsas basin as a very rich and important floristic area for many genera (Sousa and Soto 1987; Fernández et al. 1998), including those of the Apocynaceae (Williams 1996a; Alvarado-Cárdenas and Soto 2014). Our results identify the Balsas basin as either a center of richness or endemism for *Cascabela*, since four of the six of species (three endemic) occur in the area. In addition, the results of the SDMs may turn out to be complementary evidence to suggest sisterhood between some of the species, based on the idea of niche conservatism (Wiens et al. 2010). One pair is *C. gaumeri* and *C. thevetia*, whose distribution models overlap along the Atlantic coast and the Yucatan Peninsula, suggesting a potential environmental similarity that complements their similar morphology and potential sisterhood. The remaining species share morphological attributes and their SDMs overlap in the Pacific Coast, mainly in the Balsas basin where all the species occur. The use of systematic tools to evaluate similarities and differences between species, including phylogenetics, may help to corroborate the hypothesis of close relationship among these species of *Cascabela*.

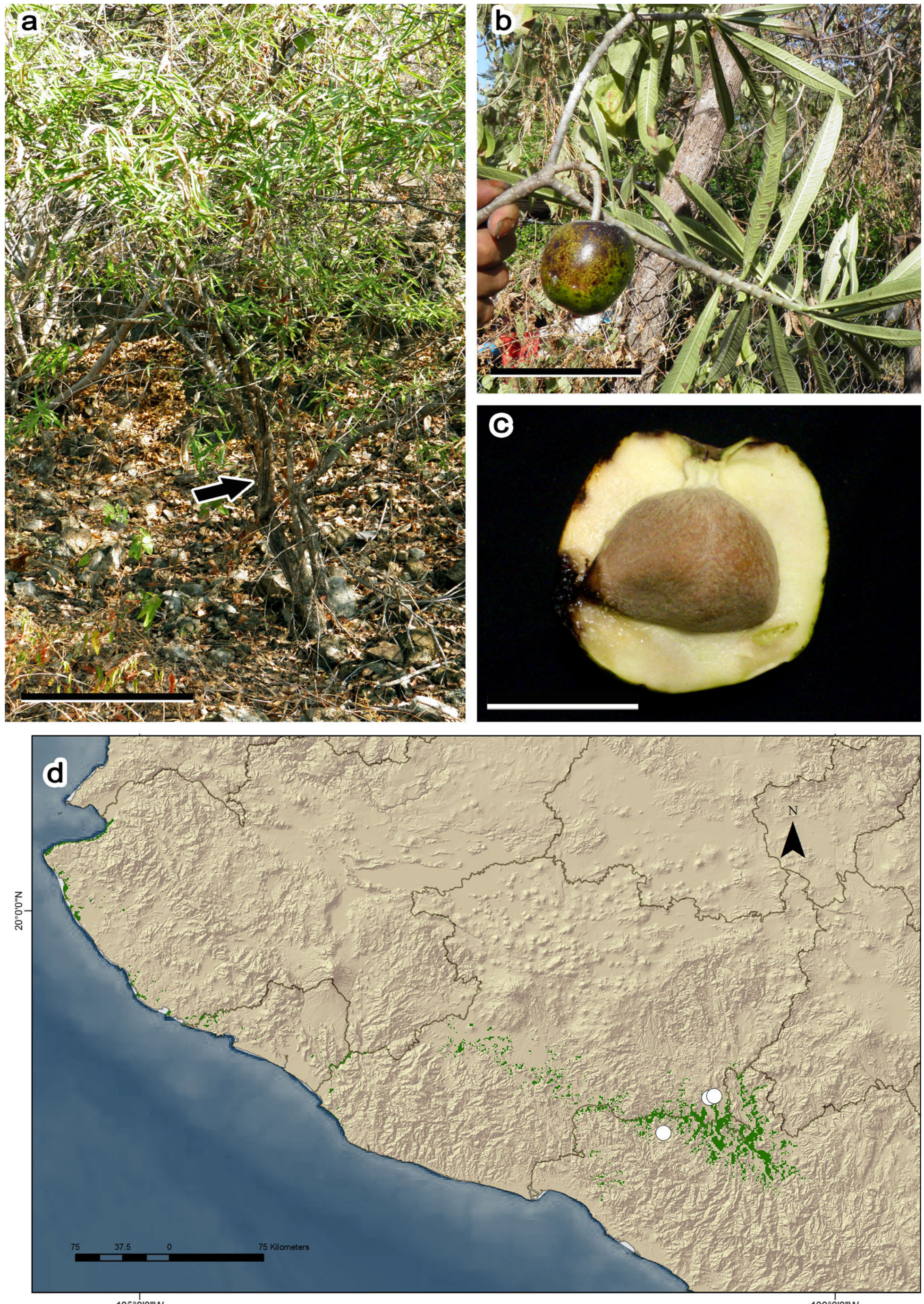
The SDMs also suggest that the Pacific slope, the southwestern portion of the Yucatan Peninsula, and some portions of Veracruz, Oaxaca and Puebla, may be regarded as secondary richness centers for the genus. The distribution and richness patterns show a south-to-north gradient of temperature humidity, where dry conditions increase and water availability decreases. In addition, species of *Cascabela* are better represented in areas below 1500 m a. s. l. (with the exception of *C. ovata*, *C. thevetia* and *C. thevetioides,* which can grow above to 2000 m a. s. l.). The elevation limit agrees with the SDMs, since the diversity

Fig. 7 Uses of the species of *Cascabela* in Mexico. **a** *C. balsaensis,* cultivated as a live fence, Michoacán, **b** *C. pinifolia,* cultivated in a graveyard, Michoacán, **c** *C. thevetioides* cultivated in a front yard, state of Mexico, **d** a cultivar of *C. thevetia* with salmon corolla cultivated in a garden, Oaxaca. **e–f** Handcrafts with endocarp, probably of *C. thevetia*, **g–h** folk musical instruments with endocarp, probably of C. *thevetioides* and *C. thevetia*, **i** anklets with endocarps of *C. thevetioides*, **j** folk dancer wearing anklets with endocarps of *C. thevetioides* (*red circles*)

areas are below 1500 m a. s. l., such as the Pacific and Gulf slopes, the Balsas River basin and the Yucatan Peninsula, where the environmental conditions are warmer and more favorable, or at least not as extreme as those found in the northernmost areas of Mexico.

Some of the members of Apocynaceae are regarded as typical elements of tropical dry forest (Juárez-Jaimes et al. 2007; Rzedowski and Calderón de Rzedowski 2013). Our results support this observation for *Cascabela*, which is mainly restricted to this vegetation type (Fig. 4), although

Fig. 8 *Cascabela balsaensis*. **a** Habit (*scale bar* 1 m), **b** fruiting branch (*scale bar* 10 cm), **c** leaves (*scale bar* 10 cm), **d** fruit (*scale bar* 5 cm), **e** known distribution (*white circles*) and potential distribution model in Mexico



its species may grow under even drier vegetation, such as xeric scrubs or thorn forests, as well as moister vegetation types, such as tropical subperennial forests. Morphological attributes in *Cascabela* suggest adaptation to dry environments; for instance, several species have dense pubescence that reduces desiccation, as in *C. balsaensis*, *C. ovata* and *C. thevetioides* (Alvarado-Cárdenas and Soto 2014), whereas *C. pinifolia* shows a reduced laminar surface (Fig. 10) compared to other species. In addition, *Cascabela thevetia* seems to have higher physiological tolerance, growing in both humid and dry environments (Figs. 6, 11). The study of physiological responses and the potential adaptive value of the morphological characters in this group may help to identify which attributes contributed more to its diversification in dry environments.

The SDMs suggest that future work is needed to better understand the genus distribution and its richness patterns. For instance, fieldwork is desirable to validate the areas predicted by the models as potential richness areas for the genus. *Cascabela thevetioides* has not yet been collected in

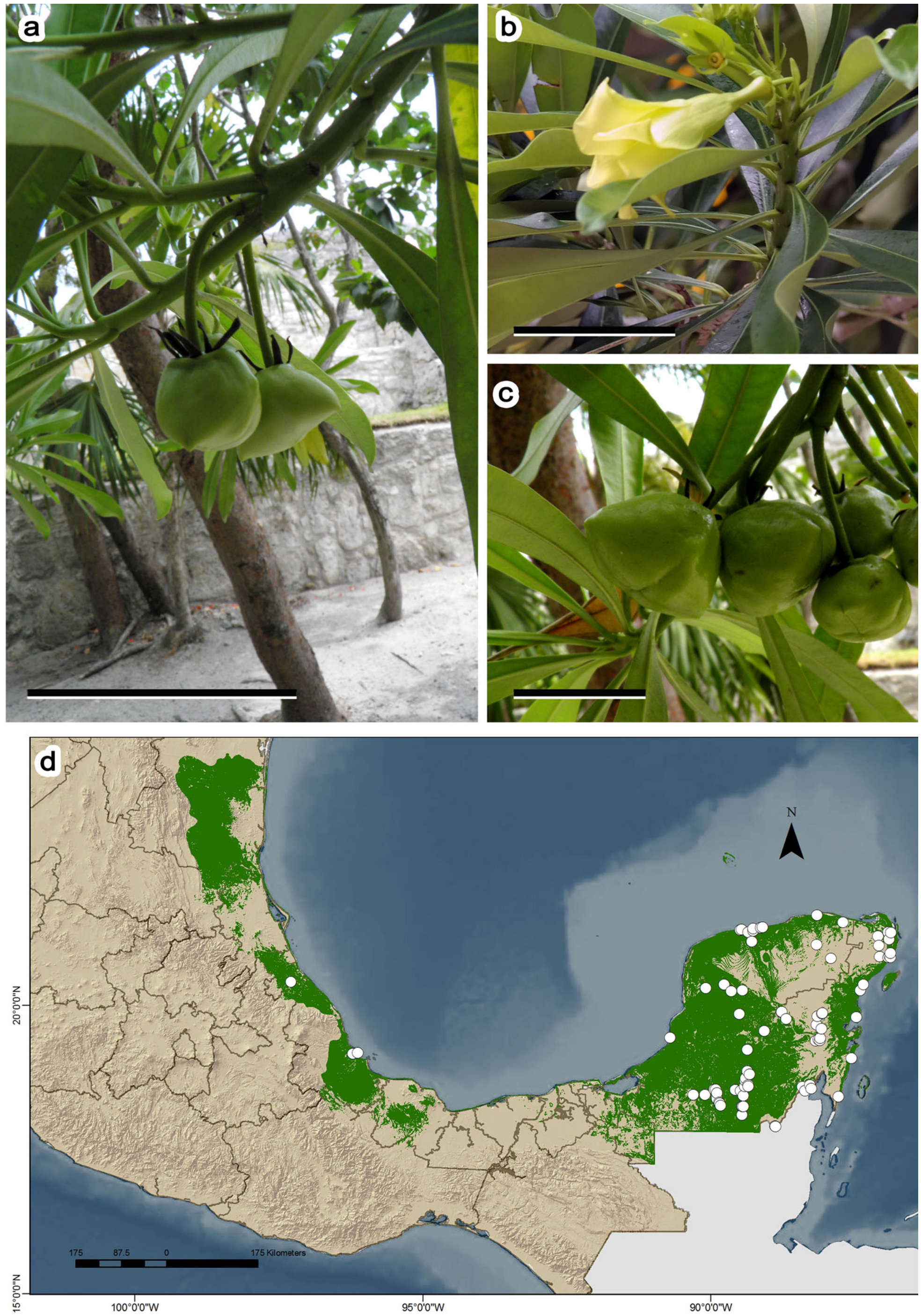


Fig. 9 *Cascabela gaumeri*. **a** Habit (*scale bar* 1 m), **b** flowering branch (*scale bar* 5 cm), **c** leaves and fruits (*scale bar* 4 cm), **d** known distribution (*white circles*) and potential distribution model in Mexico

Veracruz (Fig. 13), and the SDM of *C. thevetia* predicts its presence in the northern states of Chihuahua, Nuevo Leon and Coahuila (Fig. 12). Moreover, it would be interesting to explore the predicted diversity areas along the southern coast of Chiapas and the Pacific slope in the states of Colima, Guerrero, Jalisco, Michoacán and Oaxaca (Fig. 3). Even if the genus were not found in these states, there is a probability of finding new species or new records from other taxa in such unexplored areas, a situation previously reported for other groups (Raxworthy et al. 2003).

The status of conservation of *Cascabela* is the first approach for the family Apocynaceae in Mexico, combining both distribution analysis and observations in the field. The EOO, AOO and ESDM values for each species are contrasting, due to the different measures of the distribution data (Arroyo et al. 2009). The AOO showed that

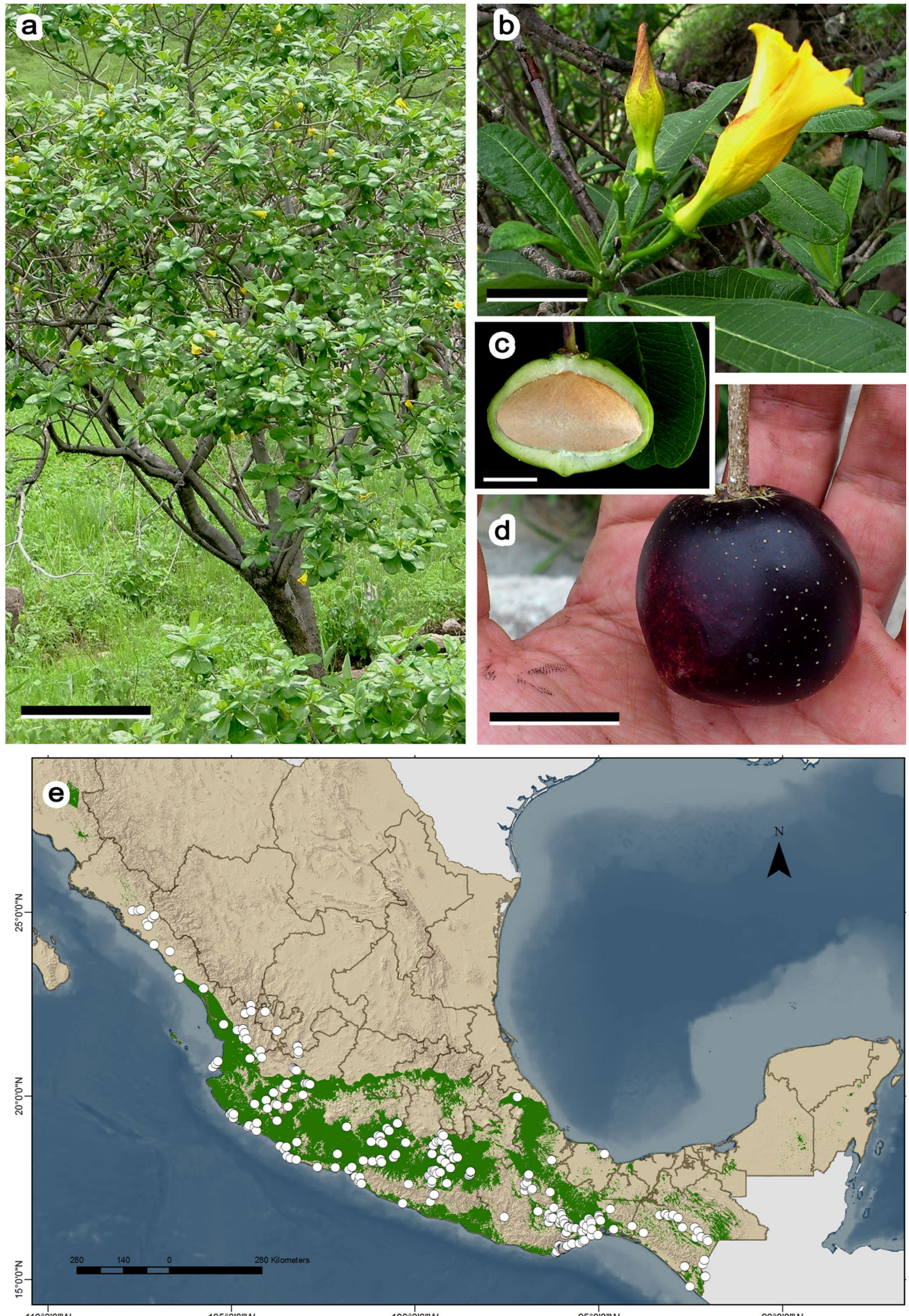


Fig. 10 *Cascabela ovata*. **a** Habit (*scale bar* 1 m), **b** flowering branch (*scale bar* 2 cm), **c** fruit with exposed endocarp (*scale bar* 1 cm), **d** mature fruit (*scale bar* 2 cm), **e** known distribution (*white circles*) and potential distribution model in Mexico

all the species are under some risk, because it used specific extent of occurrence; the EOO showed two species under some risk, based on polygonal extent, and our results, based on the comparison of the ESDM and the observations of the species, we placed three species under a risk category (Table 3). All the measures have their pros and cons, but the SDM has been considered a better approach to estimate the extent of distribution because models include the current species distribution as well as ecological and geographical information (Anderson and Martínez-Meyer 2004; Ortega-Huerta and Peterson 2004; Solano and Feria 2007; Arroyo et al. 2009). In our results, the ESDM showed relatively similar values to the EOO, and we agreed with some of the categories suggested, such as least concern for *C. gaumeri*, *C. ovata* and *C. thevetia* because of their larger extent values, and

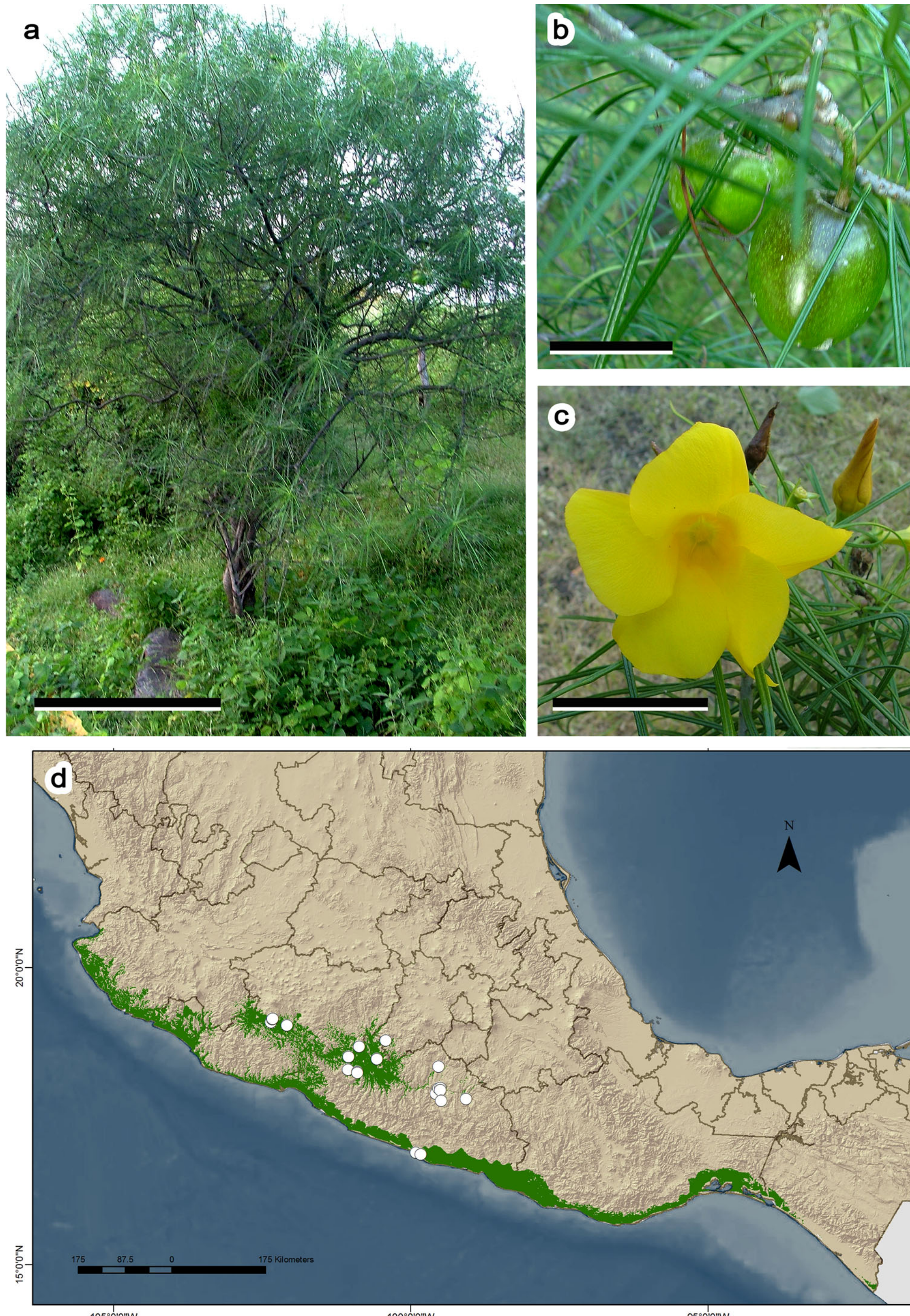


Fig. 11 *Cascabela pinifolia*. **a** Habit (*scale bar* 1 m), **b** fruiting branch (*scale bar* 2 cm), **c** leaves and flowers (*scale bar* 3 cm), **d** known distribution (*white circles*) and potential distribution model in Mexico

critically endangered for *C. balsaensis*, a highly restricted endemic.

The SDM of *C. pinifolia* overestimates its distribution, extending the prediction through the Pacific coast. We decided to be conservative and follow the area of the EOO, which showed a more restricted area, and together with our observations of few individuals per population assigned the category of vulnerable (VU). A similar case is *C. thevetioides,* with a model of higher area than the EOO, and we regard that this species should be placed, temporarily, in the near threatened category. Even though it is not a geographically restricted species, the different uses of its fruits and seeds could affect the natural populations. The comparison among different tools for calculating the extent of distribution complemented with field observations offers stronger support of the risk categories.

The area where most endemic species of *Cascabela* are concentrated, based on the predictive models, is a small

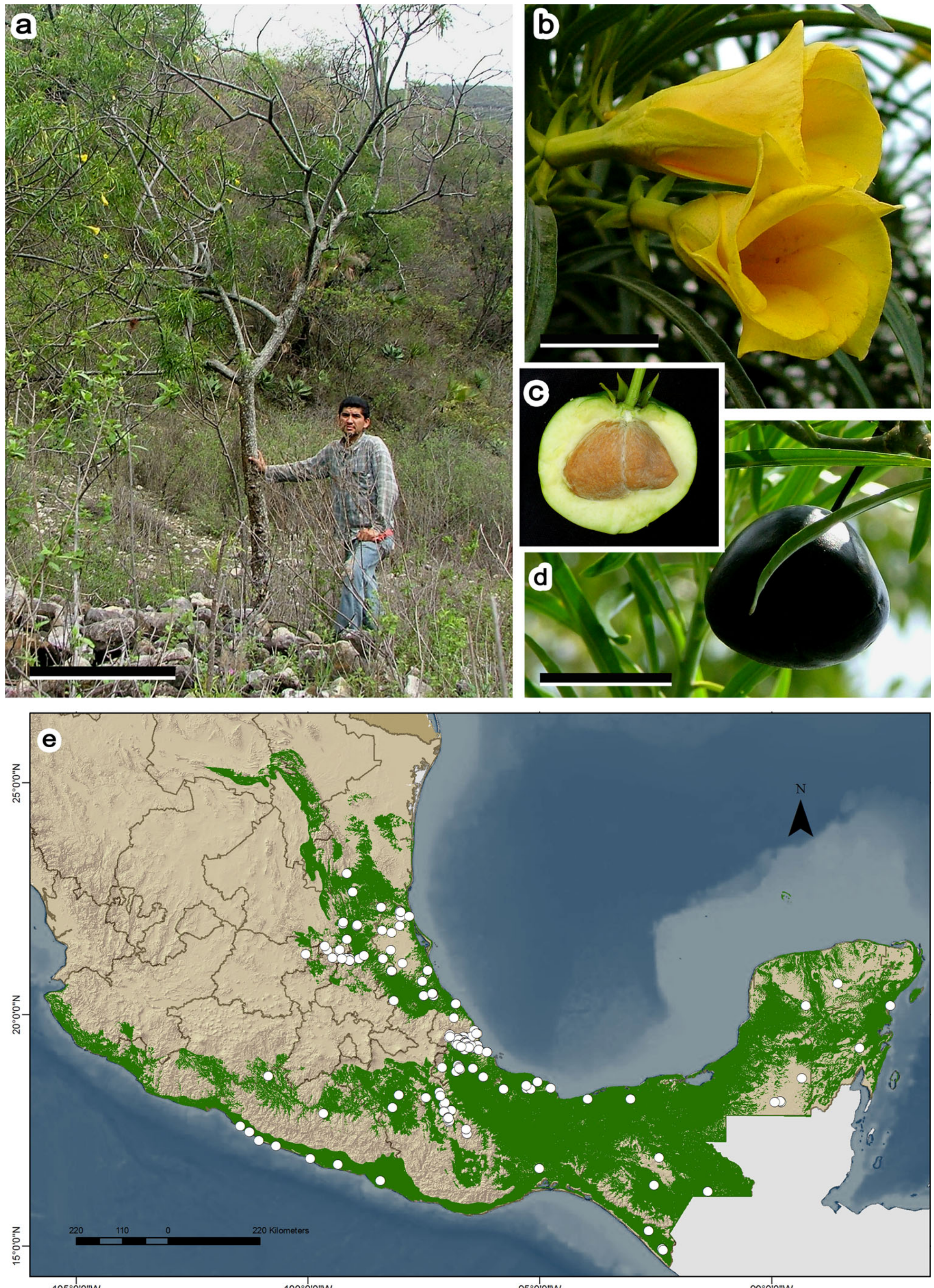


Fig. 12 *Cascabela thevetia*. **a** Habit (*scale bar* 1 m), **b** flowering branch (*scale bar* 2 cm), **c** fruit with exposed endocarp (*scale bar* 1 cm), **d** mature fruit (*scale bar* 2 cm), **e** known distribution (*white circles*) and potential distribution model in Mexico

western portion of the Balsas basin (Fig. 5) that is not included in any natural protected area. The only endemic species recorded inside a protected area was *C. thevetioides*, which would imply that the other two highly restricted species have a high risk of extinction. Our analysis could be used as a reference to reevaluate the present protected area systems, as well as to propose in the Mexican Official Norm the inclusion of these three endemic species under a category of special protection.

The species accumulation curve suggests a satisfactory collecting effort (Fig. 6) and therefore does not predict additional species of the genus in Mexico. The last species described is *C. balsaensis* (Alvarado-Cárdenas and Soto 2014), more than 50 years after the description of the previous last known species (Leavenworth 1946). Although we do not expect to find new species based on morphological attributes, the application of different analytical tools (molecular markers or geometric morphometrics)

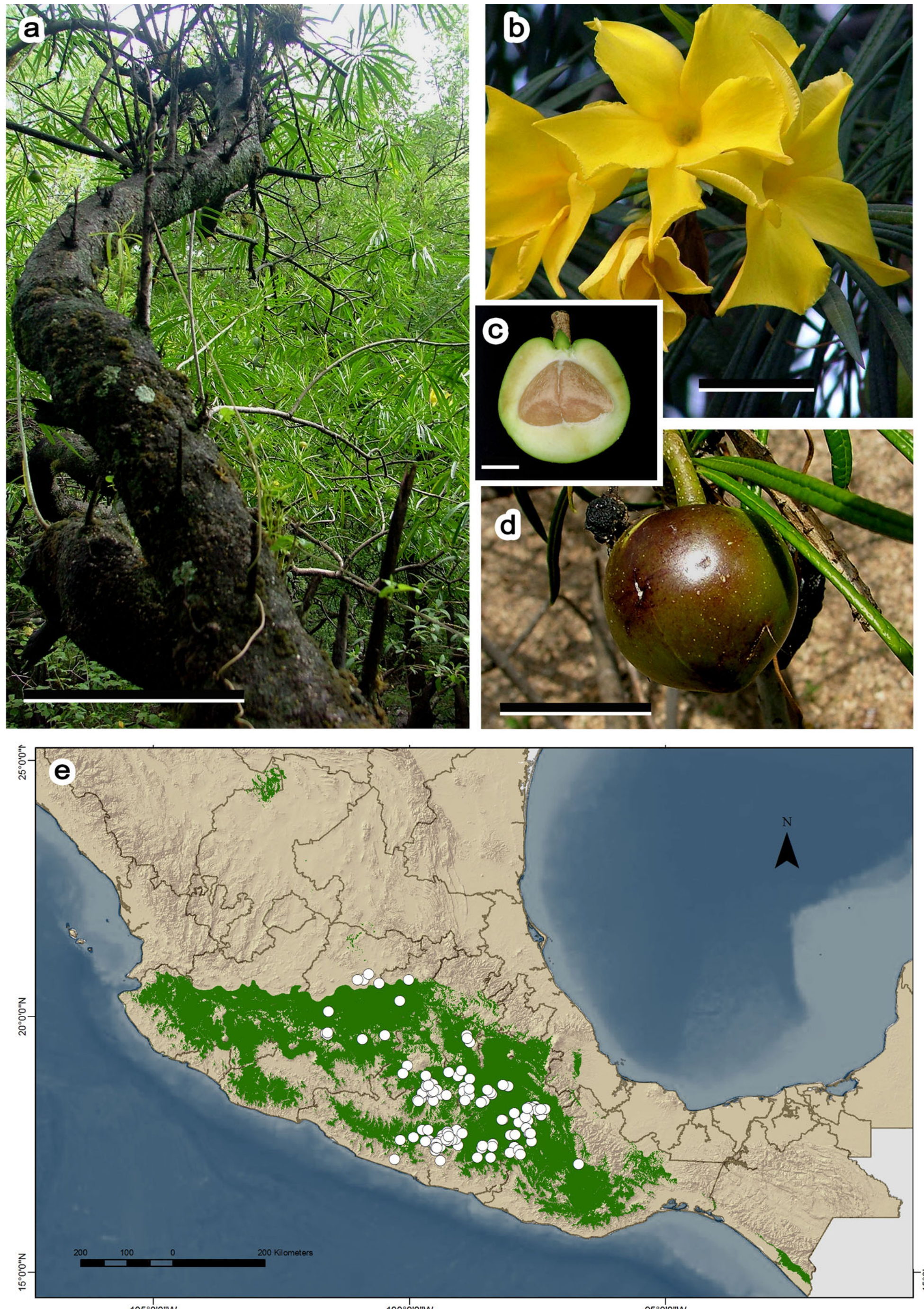


Fig. 13 *Cascabela thevetioides*. **a** Habit (*scale bar* 1 m), **b** flowering branch (*scale bar* 5 cm), **c** fruit with exposed endocarp (*scale bar* 1 cm), **d** mature fruit (*scale bar* 5 cm), **e** known distribution (*white circles*) and potential distribution model in Mexico

could provide evidence of other specific taxa. The use of these tools in species like *C. ovata* or *C. thevetia* may provide evidence of the occurrence of species complexes in the genus.

The use of species distribution models complements taxonomic information, giving rise to new perspectives about species distribution and conservation (Palmas-Pérez et al. 2013; Villaseñor et al. 2013). These models also help to identify and test some traits of species complexes. The present approach provides novel information about distribution, conservation and uses, leading to new questions about the biogeography of *Cascabela*. This work points out the importance of well-curated botanical collections to build potential distribution models, and it provides a reference source for understanding species distribution patterns in this genus.

Taxonomic treatment

Cascabela Raf., Sylva Tellur. 162. 1838. ≡ *Thevetia* Adans., Fam. Pl. 2: 171. 1763, non-*Thevetia* L., 1758. ≡ *Thevetia* section *Euthevetia* K.Schum. in Engler & Prantl, Nat. Pflanzenfam. 4(2): 159. 1895. ≡ *Thevetia* section *Yccotli* Kuntze in Post & Kuntze, Lex. Gen. Phan. 558. 1904.—TYPE: *Cascabela peruviana* (Pers.) Raf., Sylva Tellur. 162. 1838. [≡ *Cascabela thevetia* (L.) Lippold].

Trees or shrubs with smooth, woody stems; young branches glabrous to sparsely pubescent, old branches glabrous. Leaves simple, alternate, petiolate or sessile, with intrapetiolar colleters, conic to subulate; lamina elliptic-lanceolate to lanceolate, linear, linear-elliptic, obovate or spathulate, entire, membranaceous, firmly membranaceous to subcoriaceous, secondary venation conspicuous or inconspicuous, when conspicuous (15–)30–46 pairs of veins, glabrous to densely pubescent in both surfaces. Inflorescences corymbose, simple or branched. Calyx with five sepals connate at the base; sepals subequal, usually foliaceous, 10–nerved, glabrous or pubescent on both surfaces, with colleters on the adaxial base, in one or two rows or rarely absent. Corolla infundibuliform, yellow to yellowish green, lower tube cylindrical, upper tube campanulate, limb lobes dextrose contorted, obliquely obovate to oblongate, apex truncate to slightly rounded, extended to partially erect. Stamens subsessile, inserted in the apex of the lower tube; anthers ovoid, apically acuminate and usually fused, with latrorse dehiscence; suprastaminal appendages densely tomentose, digitiform, infrastaminal glabrous appendages, deltoid. Pollen grains subglobose to suboblated, tricolporate, 60–80 μm in polar view, 60–90 μm in equatorial view, with internal fissures or endofissures, tectum heterofoveolate to microreticulate. Ovary superior, carpel 2, partially syncarpic, glabrous, ovules 2 per carpel, placentation marginal; style head umbraculiform, with two massive conical tips, papillate, and a 10-lobed base; nectar disk completely fused, lobed at apex. Drupe pear-shaped to subglobose, exocarp with or without lenticels, turning purple to black, mesocarp fleshy, glabrous, black when mature, stony endocarp, irregularly deltoid to ellipsoid. Seeds joined to the lignified placenta, subglobose, with a papyraceous testa and a marginal fimbriate wing.

Cascabela includes six species, distributed from northern Mexico to Colombia and Venezuela. Mexico constitutes its main center of richness and endemism, with all the species recorded in its territory and three of them endemic to the country (*C. balsaensis*, *C. pinifolia* and *C. thevetioides*). In Mexico, the genus occurs in both the Pacific and Atlantic slopes, as well as in the central and southeastern parts of the country (Fig. 2).

Cascabela and *Thevetia* share a complicated taxonomic history. Following Rafinesque-Schmaltz's (1838) description, the taxonomy of *Cascabela* has long been controversial, especially due to its circumscription as a genus closely related to *Thevetia* L. See Gensel (1969) and Lippold (1980) for a detailed taxonomic history of *Cascabela*. The sister relationship of the genera is supported by a morphology-based phylogenetic analysis (Alvarado-Cárdenas and Ochoterena 2007). This phylogeny recovered two distinct clades, one including *Cascabela* and the other *Thevetia*, both sharing important similarities, such as style head shape, pollen grains size and shape (except in *T. ahouai*), and chromosome number $2n = 22$ (Williams and Stutzman 2008). According to these results, the selection of the alternative proposals *Thevetia* s.l. or *Thevetia* s.s. + *Cascabela* is both acceptable from a phylogenetic perspective, due to the sister relationship of the genera.

Notwithstanding these similarities, we consider that the two genera show important morphological differences. Species of the *Cascabela* clade show a morphological cohesion with constant infundibuliform flowers, drupaceous fruits and subglobose seeds with papyraceous testas (Fig. 1). Although fruit types have been regarded as homoplasic because of their evolutionary link with their dispersers (Simões et al. 2007), our examination of the fruits revealed important and consistent differences between the genera. Other authors, who have regarded these two taxa as different genera (Woodson 1937; Pichon 1948, 1950; Morales 2009a, b), have also pointed out these observations. The fruits in *Cascabela* are pyriform to globular in shape, with a thin exocarp and a thick mesocarp, purple to black in color when mature, and a stony and single endocarp with an apical dehiscence line. These features contrast with those of *Thevetia*, which include hipocrateriform (two species) and infundibuliform (one species) flowers, bilobed fruits, with red exocarp, white mesocarp, and a segmented and fibrous endocarp (Fig. 1g, h). The use of molecular markers to test the relationships within Apocynaceae has improved our knowledge of the group (Simões et al. 2004, 2006; Fishbein et al. 2011) and could provide new evidence to corroborate the hypothesis of sisterhood between *Cascabela* and *Thevetia*.

Distribution area: The distribution of both genera showed some differences; *Cascabela* includes three species endemic to Mexico, two restricted to Central America and one widespread (*C. thevetia*). On the other hand, the three known species of *Thevetia* are distributed in South America, with only *T. ahouai* reaching southern Mexico. The distribution and diversity of both taxa suggest that *Cascabela* and *Thevetia* originated in different areas and under different climatic conditions. Evaluating this biogeographical hypothesis requires methods such as phylogeography or niche tests (Warren et al. 2009). However, morphological attributes and geographical patterns support our suggestion that the two taxa are distinct genera.

Uses: Species of *Cascabela* have a long history of traditional uses (Fig. 7). Their wood is used to make musical instruments and handcrafts; their leaves, fruits and seeds are used in traditional medicine or as a poison. The genus is also important as an ornamental, with *C. thevetia* cultivated around the world (Allorge 1998). The showy and sweet-scented flower of the genus is one of the reasons why some of its species are tolerated in crops or cultivated in yards and public gardens (Fig. 7a–d). The uses of some species have been reported since pre-hispanic times. For example, an endocarp of *C. thevetia* was found in the caves of Tehuacán, Puebla, and was dated to be more than 10,000 years old, together with other important plants such as maize or cucumber (Smith 1967). Members of *Cascabela* are considered very poisonous; they produce numerous secondary metabolites, such as cerberine and thevetine cardenolid glycosides (Sowjanya et al. 2013). Similarly, the leaves, bark and mainly the seeds are applied in several traditional medical treatments against skin diseases, tooth infections or hemorrhoids (Alvarado-Cárdenas 2004; Diego-Pérez 2004). The seeds are reputedly poisonous, and the consumption of only a few seeds may be lethal for humans (Gensel 1969; García and Luna 2013; Diego-Pérez 2004). Recently, the extracts of some species have been used as antibiotics (Reddy 2009). Both fruits and seeds have a long history of traditional uses in medicinal practices and the construction of folk musical instruments (Fig. 7g–j).

Key to species of *Cascabela*

1a. Lamina obovate to oblanceolate 2
1b. Lamina linear, linear-elliptic, elliptic-lanceolate to lanceolate 3
2a. Lamina firmly membranaceous, glabrous, secondary venation inconspicuous; bracts glabrous; drupes not lenticellate .... ***C. gaumeri***
2b. Lamina coriaceous, sparsely to densely pubescent, secondary venation conspicuous; bracts pubescent on both surfaces; drupes lenticellate .... ***C. ovata***
3a. Lamina with inconspicuous secondary venation 4
3b. Lamina with conspicuous secondary venation 5
4a. Lamina 5–14 mm wide, lanceolate to linear-elliptic; bracts glabrous. Drupes not lenticellate .... ***C. thevetia***
4b. Lamina 1–3 mm wide, linear; bracts pubescent on both surfaces. Drupes lenticellate .... ***C. pinifolia***
5a. Lamina densely pubescent on both sides; corolla lower tube 8–12 mm long .... ***C. balsaensis***
5b. Lamina abaxially sparsely tomentulose and adaxially glabrous; corolla lower tube 20–35 mm long … ***C. thevetioides***

Cascabela balsaensis L.O.Alvarado & J.C.Soto, Phytotaxa 177(3): 164. 2014.—TYPE: Mexico. Michoacán: Municipality of Huetamo de Núñez. En la subida al Cerro Dolores, aprox. 4.5 km al NE de La Parota y a 10.5 km al NE de Huetamo, por la brecha a La Estancia. 18°40′0.61″N, 100°51′56.95″W, 600 m a. s. l., 22 Jun 2009, *Soto 15792* (holotype: MEXU!; isotypes: FCME!, MO!) (Fig. 8).

Description: Trees or shrubs 2.5–5 m tall, young branches sparsely pubescent. Leaves petiolate, petioles 1–3 mm long, pubescent; lamina 5.5–12 × 4–11 mm, elliptic-lanceolate to lanceolate, base and apex acute, firmly membranaceous to subcoriaceous, densely pubescent on both sides, secondary venation conspicuous, 34–46 pairs of veins. Inflorescences, 8–12 cm long, 4–6-flowered; peduncles 3–5(–13) mm long, pubescent; bracts 3–8 mm long, ovate-lanceolate to oblong-lanceolate, foliaceous, pubescent on both surfaces, with colleters on the adaxial base; pedicels 17–38 mm long, pubescent. Sepals (4–) 6–11 × 3–4 mm, ovate-lanceolate to oblong-ovate, foliaceous, pubescent on both surfaces, with (0–)4–6 small colleters in one or two rows, sometimes with irregular distribution. Corolla 45–52 mm long, yellow; lower tube 8–12 × 3.5–6 mm, glabrous outside, with internal retrorse hairs, upper tube 8–15 × 15–18 mm, glabrous, limb lobes 23–26 × (13–)18–20 mm long, obliquely oblong-ovate, spreading, margin ciliate, sparsely puberulent abaxially. Anthers 5–6 mm long, pollen grains 59–68 µm in polar view, 73.6–80.0 µm in equatorial view, suboblate to oblate–spheroidal, heterofoveolate to microreticulate. Pistil 14–16 mm long; ovary 3.0–3.5 mm long; style head 3.0–3.5 mm long; nectar disk 2–3 mm, lobed at apex. Drupe 35–40 × 35–45 mm, subglobose, glabrous, black, not lenticellate, endocarp deltoid; seeds oblongate, 11–14 × 10 mm, white to yellowish.

Phenology: Flowering from March to June, fruiting from March to September.

Habitat and ecology: *Cascabela balsaensis* is restricted to dry tropical forests (Fig. 4), and the SDM supported its distribution in this vegetation type, on rocky limestone hills, at elevations of 350–800 m.

Distribution area: The species is a narrowly distributed Mexican endemic, known only from a small area in the states of Michoacán and Guerrero, forming part of the Balsas River basin (Fig. 8). The known populations are scarce, and the individuals are dispersed. The potential distribution model is congruent with its known restricted distribution; however, predictions suggest a few additional areas in the western portion of the basin, in the states of Jalisco and Colima (Figs. 4, 8). These suitable areas could represent additional sites in which to look for new localities of the species. Its SDM suggests an area of occupancy of

25 km^2 (EOO 23.98 km^2 and AOO 12 km^2), which represents a small percentage of the country's area (Table 3). This species requires better sampling to improve the models, but we consider it appropriate to search in the not yet explored places predicted by the model, especially those located inside the Balsas River basin.

Conservation status: Critically endangered (CR). This species grows naturally in few localities in Michoacán and Guerrero (Fig. 8), with dispersed individuals. In both states, *Cascabela balsaensis* is sometimes used for living fences and seems to tolerate some degree of disturbance. The species is found in a small area of the Balsas River basin and its SDM suggests an area of occupancy of 25 km^2 (EOO: 23.98 km^2 and AOO: 12 km^2), which represent a small percentage of the country area (Table 3). Notwithstanding, its restricted distribution and grazing activities may significantly reduce the number of individuals in the future. We suggest changing its previous conservation status from vulnerable (Alvarado-Cárdenas and Soto 2014) to critically endangered.

Additional specimens examined: **Guerrero**: Mun Eduardo Neri, Ameyaltepec, 23 Apr 1994, *Villa 706* (MEXU!); Mun Zirándaro, en Carechurio, 20.43 km al SO de la Parota, carretera La Parota-Guayameo, 358 m a. s. l., 15 Jun 2014, *Soto 21418* (MEXU!). **Michoacán**: Mun Huetamo de Núñez, en la subida al Cerro Dolores, aprox. 4.5 km al NE de La Parota y a 10.5 km al NE de Huetamo, por la brecha a La Estancia, 600 m a. s. l., 22 Jun 2009, *Soto 15792* (MEXU!).

Common names and uses: "camé", "camín". This species is sometimes used as an ornamental, cultivated in yards or as living fences around houses. Local people sometimes eat the ripe fruits of *C. balsaensis*.

Cascabela gaumeri (Hemsl.) Lippold, Feddes Repert. 91: 53. 1980. ≡ *Thevetia gaumeri* Hemsl., Hooker's Icon. Pl. 1517. 1886.—TYPE: Mexico. Quintana Roo: Cozumel Island, 1885, *Gaumer 7* (holotype: F barcode F0044763F [web!]) (Fig. 9).

= *Thevetia spathulata* Millsp., Publ. Field Columbian Mus., Bot. Ser. 1: 383. 1898.—TYPE: Mexico. Yucatan: Yucatan, common at the port of Silam, Apr 1895, *Gaumer 678* (lectotype: MO barcode MO-022209!, designed by Morales (2005); isotypes: F barcodes F0048408 [web!], F0048409 [web!]).

= *Thevetia steerei* Woodson, Amer. J. Bot. 22: 685. 1935.—TYPE: Mexico. Yucatan: in low forest, Progreso, 11–15 Aug 1932, *Steere 3056* (holotype: MO barcode MO-022210!; isotypes: MICH barcode MICH1111576 [web!], NY, barcode 00318419!, [photo!]).

Description: Trees 2–13 m tall; young branches glabrous. Leaves petiolate, petioles 1–3 mm long, glabrous; lamina 7–16 × 1.5–3 cm, oblanceolate, base and apex acute, firmly membranaceous, glabrous on both sides, secondary venation inconspicuous. Inflorescences 8–10 cm long, 4–6-flowered; peduncles 2–5 cm long, glabrous; bracts 4–6 mm long, ovate-lanceolate, foliaceous, glabrous, with colleters on the adaxial base; pedicels 17–35(–42) mm long, glabrous. Sepals 5–13 × 3–4 mm, ovate-lanceolate, foliaceous, glabrous on both surfaces, with 6–10 colleters in a row. Corolla 48–65 mm long, greenish yellow; lower tube 15–17 × 3–4 mm, glabrous on both surfaces, upper tube 11–13 × 15–17 mm, glabrous, limb lobes 25–30 × 18–20 mm long, obliquely oblong to oblong–ovate, erect, glabrous on both surfaces. Anthers 2–3 mm long, pollen grains 59–64 µm in polar view, (69–)71–81.6 µm in equatorial view, subprolate to oblate–spheroidal, foveolate to microreticulate. Pistil 14–18 mm long; ovary 1.6–2 mm long; style 11–15 mm long, style head 2.0–2.5 mm long; nectar disk 1.7–2.0 mm, lobed at apex. Drupe 20–28 × 25–35 mm, subglobose, glabrous, black, not lenticellate, endocarp deltoid to irregularly deltoid; seeds oblong, 14–20 × 10–15 mm, white to yellowish.

Phenology: Flowering and fruiting year-round.

Habitat and ecology: This species grows in tropical dry forests, evergreen forests and mangroves, as well as in disturbed vegetation (Fig. 4) at elevations between 0 and 500 m. The fruits are consumed by birds, wild turkeys, rats and opossums (Rodríguez et al. 2003).

Distribution area: Mexico (Campeche, Quintana Roo, Veracruz, and Yucatan) and Central America (Guatemala, Belize, Nicaragua, and cultivated in Costa Rica). In Mexico, the species has also been recorded in the state of Guerrero (Diego-Pérez 2004, Alvarado-Cárdenas and Ochoterena 2007). Although we have seen the specimens supporting such distribution, we did not include them in the potential distribution analysis because the localities recorded are near human settlements, suggesting that the plants were cultivated or have escaped from cultivation. There are no additional records along the Pacific slopes that may suggest the occurrence of this species on this side of the country (Fig. 9). The potential distribution model (SDM) suggests that some portions of the states of Chiapas, Oaxaca, Puebla, San Luis Potosí, Tabasco and Tamaulipas have suitable climatic conditions for this species (Fig. 9). The predicted regions are limited by the Eastern Sierra Madre, the Trans-Mexican Volcanic Belt and the Southern Sierra Madre, agreeing with the known localities. All these mountain barriers support the idea that *C. gaumeri* is not naturally distributed on the Pacific slopes. In addition, the areas predicted by the SDM on the Mexican Gulf slopes are plausible areas to find additional populations, since they have similar environmental conditions to those where the species is currently known.

Conservation status: Least concern (LC). *Cascabela gaumeri* is widely distributed from eastern-southeastern Mexico to Nicaragua and Costa Rica. It grows in different vegetation types and in various protected areas. It is also cultivated in parks, houses backyards, as living fences, and in museum gardens because of its tolerance to environmental perturbation. The potential distribution model suggests an area of occupancy of about 208,969 km^2 (EOO 390, 233 km^2 and AOO 324 km^2); this represents a large area of the Mexican Gulf plains and the Peninsula of Yucatan, and more than the 10% of the Mexican territory (Fig. 9; Table 3). The species has tolerance to some anthropogenic disturbance; its occurrence in several protected areas, relatively high population density, and its fruit and seed production throughout the year suggest that the species is under least concern.

Additional specimens examined: **Campeche**: Mun Calakmul, 1 km N del poblado Narciso Mendoza, 240 m a. s. l., 26 Jun 1997, *Álvarez 63* (MEXU!); Mun Champotón, 8.5 km del entroque hacia Calakmul, 2 Dec 1996, *Durán 2833* (NY!); Mun Hecelchacán, Ruinas de Chicana, 100 m a. s. l., 21 Oct 1981, *Chan 989* (MEXU!); Mun Hopelchén, a 1.19 km al E de X-Mejía, 160 m a. s. l., 31 May 2004, *Álvarez 8634* (MEXU!). **Quintana Roo**: Mun Adolfo de la Huerta, 0.7 km N del poblado Sabana de San Francisco, 90 m a. s. l., 19 Jun 2004, *Álvarez 9426* (MEXU!); Mun Benito Juárez, 18 km N del km 29 de la carretera Cancún-Leona Vicario, 4 Jul 1991, *Simá 1249* (MEXU!, MO!); Mun Cobá, Sacbé No. 8, 20 m a. s. l., 19 Aug 1976, *López 592* (MEXU!); Mun Chetumal, 10–15 km N de Chetumal, sobre camino a Laguna Guerrero, 5 Sep 1984, *Cabrera 7223* (MEXU!); Mun Felipe Carrillo Puerto, 2 km antes de Punta Pulticub, 45 km NE de Majahual, 0 m a. s. l., 17 Jan 2003, *Tapia 1404* (MEXU!, MO!); Mun Isla Mujeres, 500 m al N de la Playa Lancheros, sobre el camino al restaurante Hacienda Gomar, 6 Jan 1988, *Cabrera 15442* (MEXU!); Mun José María Morelos, Laguna Chichankanab, 3.5 km al E de Dziuché, 4 Dec 1996, *Durán 2853* (NY!); Mun Othon P. Blanco, La Unión, 2 km al NW de Othon P. Blanco, 29 Sep 1992, *Campos 2868* (MEXU!); Mun San Felipe Bacalar, Centro Experimental Forestal INIF, San Felipe Bacalar, 23 Aug 1979, *Pérez 432* (MEXU!); Mun Solidaridad. Xcacel-Xcacelito, aprox. 13 km N de Tulum, sobre la carretera Fed. 307 Chetumal-Puerto Juárez, 14 Jun 1998, *Gallardo 2226* (MEXU!, MO!). **Veracruz**: Mun Papantla, Cerro de Carbón, 200 m a. s. l., 10 Sep 1982, *Cortés 412* (MEXU!); Mun Veracruz, 5 km al Poniente del Puerto, Paso del Jobo, 23 Jun 1990, *García 531* (MEXU!). **Yucatan**: Mun Chema, en el ejido de Sisbichen, el cual se encuentra a 15 km del Municipio, 20 Aug 1986, *Aguilar 301* (MEXU!); Mun Chicxulub, 1 km después de Uaymitun-Telchac, 1 m a. s. l., 20 Jul 1985, *Ayora 45* (MEXU!); Mun Dzemul, 8 km al S de Xtampú, camino a Dzemul, 8 Sep 1993, *Simá 1668* (MEXU!); Mun Felipe Carrillo Puerto, aprox. 5 km W de Señor, entrando 2 km al NW, Jul 2001, *Correa 10* (MEXU!, MO!); Mun Ixil, a 25 km al W de Telchac camino de terracería a Progreso Uaymitun, 0 m a. s. l., 23 Jul 1981, *Espejel 242* (MEXU!); Mun Motul, 6 km S de Telchak Pueblo, sobre la carretera Motul-Telchak Puerto, 24 Jul 1986, *Cabrera 11696* (IEB!, MEXU!, MO!); Mun Oxkutzcab, Loltun, 20 Jun 1982, *Xelhuantzi s.n.* (IEB!); Mun Progreso, whitout locality, 10 Oct 1999, *Peña-Chocarro 571* (MEXU!); Mun Telchac, en el poblado del Puerto de Telchac, 6 Nov 1980, *Calzada 6586* (MEXU!); Mun Tizimín, 10 km al E de Telchak Puerto, sobre la carretera A Puerto Progreso-Dzilam de Bravo, 23 Jan 1986, *Cabrera 10747* (MEXU!, NY!).

Common names and uses: "aak'its", "ac'itch", "acitz", "aiquitz", "campanilla", "cojón de gato", "cojón de perro", "cojón de venado", "good luck seed", "huevo de rey", "sac-itza". This species is widely cultivated as an ornamental in Veracruz and the Yucatan Peninsula. In Campeche, it is used in traditional medicine as a relaxant for tooth infections and its stony endocarp is used as a lucky charm, which is carried in pockets or worn as a necklace (CYCI herbarium 2016).

Notes: *Cascabela gaumeri* and *C. thevetia* are morphologically very similar, having obscured secondary venation, flowers with erect petals and fruits without lenticels (Fig. 1a). In addition, the distribution models of both species overlap along the Pacific coast and the Yucatan Peninsula (Figs. 9, 12). The models may suggest, together with species morphology, the possible sisterhood of these two species due to the shared climatic conditions, probably suggesting niche conservatism (Wiens et al. 2010). Nevertheless, a resolved phylogeny and ecological tests are necessary to corroborate this hypothesis. The two species can be easily distinguished by the shape of the laminae (oblanceolate in *C. gaumeri* vs. lanceolate to elliptic in *C. thevetia*), the hairs on the corolla tube (absent in *C. gaumeri* vs. present in *C. thevetia*) and flower (yellowish green in *C. gaumeri* vs. yellow or orange in *C. thevetia*).

Cascabela ovata (Cav.) Lippold, Feddes Repert. 91: 53. 1980. ≡ *Cerbera ovata* Cav., Icon. 3: 35, pl. 270. 1796. ≡ *Thevetia ovata* (Cav.) A.DC., Prodr. 8: 344. 1844. —TYPE: Mexico. Nueva España, *s. loc. et coll.* (holotype: MA barcode MA475509 [web!]) (Fig. 10).

= *Cerbera alliodora* Roem. & Schult., Syst. Veg. 4: 798. 1819. ≡ *Cascabela alliodora* (Roem. & Schult.) Lippold, Feddes Repert. 91: 53. 1980. ≡ *Thevetia alliodora* (Roem. & Schult.) L.Allorge, Succulentes 21: 27. 1998. —TYPE: Mexico. Guerrero: ''inter Zumpango et Mescalam, in convalli Zopilote'' Apr 1803, *Humboldt* and *Bonpland s.n.* (holotype: P [n.v.], NY [photo!]).
= *Cerbera cuneifolia* Kunth, Nov. Gen. Sp. 3: 224. 1818 [1819]. ≡ *Thevetia cuneifolia* (Kunth) A.DC., Prodr. 8: 344. 1844. —TYPE: Mexico. Guerrero: ''inter Zumpango et Mescalam, in convalli Zopilote, Apr 1803, *Humboldt* and *Bonpland s.n.* (holotype: P barcode P00670865 [web!], MEXU [photo!]).
= *Thevetia cuneifolia* (Kunth) A.DC. var. *andrieuxii* A.DC., Prodr. 8: 344. 1844. —TYPE: Mexico. [Mexico-Morelos]: in Mexico ad Gonacatepec, *Andrieux 254* (holotype: G-DC!; isotypes: K barcode K000587612 [web!], P barcode P00649936 [web!]).
= *Thevetia plumeriifolia* Benth., Bot. Voy. Sulfur 124, t. 43. 1845. ≡ *Cascabela plumeriifolia* (Benth.) Lippold, Feddes Repert. 91: 53. 1980. —LECTOTYPE: Honduras. Gulf of Fonseca, *Sinclair s.n.*, (lectotype: K barcode K000195450 [web!], designed by Nelson (1996); isolectotype: K barcode K000195451 [web!]).

Description: Trees 2–10 m tall, young branches sparsely pubescent. Leaves petiolate, petioles 5–15 mm long, pubescent; lamina 5.5–18.5 × 2.5–12 cm, obovate to oblanceolate, base acute, apex obtuse, coriaceous, sparsely pubescent adaxially and densely to sparsely pubescent abaxially, secondary venation conspicuous, 15–30 pairs of veins. Inflorescences (8–) 10–15 cm long, 5–10-flowered; peduncles 10–50 mm long, pubescent; bracts 3–8 mm long, ovate to broadly ovate, foliaceous, pubescent on both surfaces, with colleters on the adaxial base; pedicels 2.4–7.0 cm long, pubescent to glabrate. Sepals 5–12 × 3–4 mm, ovate-lanceolate, foliaceous, pubescent on both surfaces, with 6–8 colleters in one or two rows. Corolla 45–52 mm long, yellow; lower tube 10–25 × 3.5–6.0 mm, glabrous outside, with retrorse hairs internally, upper tube (9–)13–20 × 20–25 mm, glabrous, limb lobes (12–)24–40 × (1–)20–25 mm long, obliquely oblong-ovate, spreading, margin ciliate, sparsely puberulent to glabrous on both surfaces. Anthers 2–3 mm long, pollen grains (49–)52–59 μm in polar view, 67–72 μm in equatorial view, suboblate to oblate spheroidal, heterofoveolate. Pistil 14–25 mm long; ovary 1.9–4.0 mm long; style 12–15 mm long, style head 1–2 × 2.5 mm; nectar disk 2–3 mm, apex lobed. Drupe 20–40 × 28–55 mm, subglobose, glabrous, black, lenticellate, endocarp irregularly deltoid to ellipsoid; seeds oblongate to deltoid, 18–20 × 18 mm, white to yellowish.

Phenology: Flowering between February and August, fruiting between May and January.

Habitat and ecology: The species grows in tropical dry forests (Fig. 4), desert thorn scrubs, riparian vegetation, *Pinus–Quercus*, *Quercus* forests, and secondary vegetation, at elevations usually 0–2000 (–2500) m a. s. l.

Distribution area: Mexico (Chiapas, Colima, Durango, Guerrero, Jalisco, Mexico, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, Sinaloa, Veracruz, and Zacatecas), Guatemala, El Salvador, Honduras, Nicaragua and Costa Rica. The species is distributed mainly in the center of Mexico and the Pacific slopes, but with some localities in Gulf of Mexico states, such as Veracruz (Fig. 10). The SDM agrees with the current known distribution, but suggests additional places where the environmental conditions are appropriate for the species. The model predicts its potential distribution in practically all the states adjacent to the Trans-Mexican Volcanic Belt, suggesting additional small areas in Campeche, Quintana Roo, Tabasco and Sonora, with high probability of finding new populations of *C. ovata* (Fig. 10).

Conservation status: Least concern (LC). *Cascabela ovata* is widely distributed from western-southeastern Mexico to Costa Rica. In Mexico, it grows in different vegetation types, elevations and numerous protected areas and individuals yield fruits year-round. Its potential distribution area comprises 264,725 km^2 (EOO: 252,038 km^2 and AOO: 984 km^2), which is one of the greatest predicted areas among the species analyzed (Table 3). We conclude that this species is not under threat.

Additional specimens examined: **Chiapas**: Mun Arriaga, Poza Galana, 400 m a. s. l., 12 Aug 2002, *Reyes-García 5362* (MEXU!); Mun Chiapa de Corzo, 3 km E de Chiapa de Corzo, sobre la carretera A Tuxtla Tuxtla Gutiérrez-San Cristóbal Casas, 6 Oct 1983, *Cabrera 5933* (MEXU!); Mun Cintalapa, carretera Mex. 190, km 29 al N del mirador Iris, al S de Rizo de Oro, 710 m a. s. l., 14 Oct 2003, *Flores 5243* (MEXU!); Mun Comalapa, 15 km S de Amatenango, 1230 m a. s. l., 24 Apr 1987, *Reyes-García 48* (MEXU!); Mun Comitán, 1 km SE del entroque Tzimol-Uninajab, camino Uninajab, 1110 m a. s. l., 6 Nov 1988, *Reyes-García 1118* (MEXU!); Mun Escuintla, Escuintla, Ovando, 4 Nov 1939, *Matuda 6129* (MEXU!); Mun La Trinitaria, 13 km S-SE de la Trinitaria, 1050 m a. s. l., 27 Jul 1983, *Grether 1727* (MEXU!); Mun Male, Porvenir, 3200 m a. s. l., 6 Jul 1941, *Matuda 4659* (MEXU!); Mun Mazapa, 10 km E de Motozintla, carretera Mex. 190, 1110 m a. s. l., 5 Feb 1990, *Reyes-García 1524* (MEXU!, MO!); Mun Ocozocuautla, 1 km NW del entronque aeropuerto-Ocozocuautla, sobre la carretera 190, 940 m a. s. l., 19 Sep 1988, *Reyes-García 1020* (MEXU!); Mun Suchiate, Región Soconusco, 27 May 1992, *Aquino 170AA* (MEXU!); Mun Tuxtla Gutiérrez, 8 km W de Tuxtla Gutiérrez, al W de la colonia Juan Crispín, 700 m a. s. l., 17 Jul 1990, *Reyes-García 1955* (MEXU!); Mun Tzimol, 15 km S of Comitán on road to Tuxtla Gutiérrez, 1200 m a. s. l., 18 Jul 1981, *Breedlove 51620* (MEXU!); Mun Venustiano Carranza, Near Rancho Carmen along the road from Acala to Venustiano Carranza, 2500 m a. s. l., 25 Oct 1966, *Laughlin 2667* (MEXU!). **Colima**: Mun Comala, Comala, 15 Jan 1991, *Salcedo* (IEB!); Mun Manzanillo, 15 mi W of Manzanillo, side road to Playa de Oro, 27 Aug 1970, *Spetzman 1426* (MEXU!). **Durango**: El Mezquital, 6 km S de Huazamota, 700 m a. s. l., 7 May 1983, *González 2403* (MEXU!). **Estado de México**: Mun Amatepec, Dolores, 850 m a. s. l., 25 Aug 1954, *Matuda 31264* (MEXU!, MO!). **Guerrero**: Mun Acapulco, La Venta, falda E del Cerro El Peregrino, 280 m a. s. l., 18 Jun 1968, *Kruse 1803* (MEXU!); Mun Ahuacuotzingo, 4 km de Ahuacuotzingo rumbo a Ajuatetla, 6 Sep 2002, *Diego 9475* (FCME!); Mun Atenango del Río, 2 km S de Tuzantlán, camino Iguala-Tulimán, 1090 m a. s. l., 5 May 1982, *Rodríguez 6* (NY!); Mun Buenavista de Cuéllar, 8 km NW de Iguala, camino Iguala-Taxco, 800 m a. s. l., 6 Jul 1982, *Martínez 1201* (MEXU!, MO!); Mun Chilpancingo de los Bravo, 3.5 km al SE de Soyatepec por el camino al Cerro El Toro, 1000 m a. s. l., *Rodríguez 308* (FCME!); Mun Eduardo Neri, 11 km S de Mezcala, 600 m a. s. l., 5 Jul 1994, *Monroy de la Rosa 313* (IEB!, MEXU!); Mun Copalillo, Copalillo, 875 m a. s. l., 30 Apr 2012, *Lozada 1649* (FCME!); Mun Coyuca de Benítez, El Pozuelo, laguna de Mitla, 5 m a. s. l., 31 Aug 1984, *Lozada 74* (MEXU!); Mun Coyuca de Catalán, Placeres-Camarón, 400 m a. s. l., 8 Jan 1936, *Hinton 9190* (MO!, NY!); Mun General Heliodoro Castillo, Campo Morado Otatlán, 1000 m a. s. l., 5 Nov 1939, *Hinton 14251* (MEXU!, MO!, NY!); Mun Huamuxtitlán, 2 km N de Huamuxtitlán, en el camino Tlapa-Tecomatlán, 900 m a. s. l., 8 Dec 1982, *Martínez 2889* (MEXU!, MO!); Mun Huitzuco de los Figueroa, 2 km E de San Francisco Ozomatlán, 540 m a. s. l., *Vargas-Pérez 328* (MEXU!); Mun Iguala de la Independencia, carretera Iguala-Taxco, en un lugar llamado Mexicaltepec, 8 km NE de Iguala, 970 m a. s. l., 14 Oct 1981, *Soto 3339* (MEXU!); Mun La Unión, 6 km N de la Juntas de los Ríos, 310 m a. s. l., 22 Jul 1985, *Soto 9633* (MEXU!); Mun Mártir de Cuilapan, San Marcos Oacotzingo, Cerro de la Cruz, 972 m a. s. l., 21 Oct 2003, *Lozada 542* (FCME!); Mun Pilcaya Cacahuamilpa, 23 Jun 1940, *Miranda 424* (MEXU!); Mun Tepecoacuilco de Trujano, de Trujano Barranca de Amoloncán a 150 m de la orilla del río, 740 m a. s. l., 29 Sep 2001, *Diego 166* (FCME!); Mun Xochihuehuetlán, 2 km S de Xilotepec carretera a Huamoxtitlán, 1090 m a. s. l., 25 Aug 1999, *Fragoso 1431* (MEXU!); Mun Zirándaro, Los Parajes, 22 Jul 1999, *Calonico* (IEB!). **Jalisco**: Mun Autlán de Navarro, Autlán de Navarro, 2 Aug 1985, *Díaz-Luna* (IEB!); Mun Bolaños, Camino a Rancho El Platanal, sobre el arroyo Cantaranas, 950 m a. s. l., 20 Oct 1983, *Lott 2089* (MEXU!); Mun Chapala. Chapala, Oct 1886, *Palmer 306* (NY!); Mun Chiquilistlán, Chiquilistlán, 15 Nov 1987, *Cházaro* (IEB!); Mun El Limón, Rancho El Recodo, 2 km E de San Miguel Hidalgo, 850 m a. s. l., 1 Sep 1987, *Santana 2956* (MEXU!); Mun Guadalajara, Barranca Colimilla, about 4 mi NE of Guadalajara, 1200 m a. s. l., 19 Jul 1951, *Gentry 10899* (MEXU!); Mun Hostotipaquillo, Canyon W of La Venta de Mochititle (Mochitiltic), 28 Jun 1959, *College of Idaho* (MEXU!); Mun La Huerta, Cumbres de Cuixmala, el 45, camino a Cumbres, 50 m a. s. l., 25 Aug 1988, *Acevedo 953* (MEXU!); Mun Mezcala, Brecha Mezcala-Poncitlán, 1590 m a. s. l., 14 Sep 1974, *Villareal 6755* (MEXU!); Mun Tuxcacuesco, 400 m al E de El Rancho El Acoste, 820 m a. s. l., 8 Aug 1988, *Robles 571* (MEXU!); Mun Venustiano Carranza, 7 km N de Venustiano Carranza, camino a Tapalpa, 1230 m a. s. l., 30 Jun 1981, *Lott 430* (MEXU!, MO!); Mun Zacoalco de Torres, 3 km al S de Zacoalco de Torres, 2100 m a. s. l., 24 Aug 1996, *Pérez 3* (INEGI, MEXU!). **Michoacán**: Mun Aquila, 3 km S de la Cruz Cachán, 90 m a. s. l., 29 Sep 1980, *Guerrero 1017* (IEB!, MEXU!); Mun Arteaga, Along Mex 37, ca. 0.5 km NE of Puerto San Salvador, 950 m a. s. l., 23 Oct 2000, *Steinmann 2170* (IEB!, MEXU!); Mun Huetamo de Núñez, en Chihuero a 10 km NE de Huetamo, 455 m a. s. l., 20 Jul 1982, *Martínez 1473* (MEXU!, MO!); Mun Lázaro Cárdenas, 1 km W de Mexcalhuacán, o 45 km al W de Playa Azul, camino a Caleta de Campos, 5 m a. s. l., 27 Sep 1983, *Martínez 4588* (MEXU!); Mun Nuevo Urecho, El Encinar, 800 m a. s. l., 20 Feb 1997, *Gómez* (MEXU!); Mun Parícuaro, 3 km SW de Parícuaro, carretera Zitácuaro-Huetamo, 1400 m a. s. l., 19 Jun 1983, *Soto 5316* (MEXU!, MO!); Mun Tuzantla, entre El Quedable y Arturo Benítez, 910 m a. s. l., 29 Dec 1972, *González 5068* (MEXU!); Mun Tzenzéncuaro, Tzenzéncuaro, 26 km N de Tiquícheo, 780 m a. s. l., 10 Oct 1981, *Soto 3286* (MEXU!). **Morelos**: Mun Coatlán del Río, Coatlán del Río, 30 Oct 1976, *Torres 429* (MEXU!); Mun Cuernavaca, Lava beds near Cuernavaca, 1500 m a. s. l., 23 Jun 1896, *Pringle 6332* (MO!, NY!); Mun Jojutla, Cerro Grande, 15 Apr 1955, *Becerra* (MEXU!); Mun Tlaquiltenango, Brecha Xicatlán a Xicatlacotla, 900 m a. s. l., 1 Jul 1987, *Quezada 1699* (MEXU!). **Nayarit**: Mun Ahuacatlán, 4 km al sur de Ahuacatlán, camino a Amatlán de Cañas, 19 Oct 1986, *Téllez 9959* (MEXU!, MO!); Mun Compostela, En la Playa Venado a 2 km al S de Los Marcos, 30 Jul 1990, *Tellez 12729* (IEB!, MEXU!, MO!); Mun Islas Marías, Parte E de la Isla María Magdalena en campo de fútbol abandonado, 24 Nov 1986, *Chiang 1021* (IEB!, MEXU!, MO!); Mun Nayar, La Nopalera aprox 11 km E de la Cortina de la P.

H. Aguamilpa, 170 m a. s. l., 21 Aug 1993, *Flores 2801* (MEXU!); Mun Santa María del Oro, El Cajón, Río Santiago, 2 km Río arriba de donde desemboca el Arroyo Palmillas, 230 m a. s. l., 7 Nov 1991, *Acevedo 1029* (MEXU!); Mun Tepic, 9.4 km NE de Jesús María, Camino a Huejuquilla, 775 m a. s. l., *Flores 1077* (IEB!, MEXU!, MO!). **Oaxaca**: Mun Juchitán, Ruta 185, 10 km N de la Ventosa al S de Matías Romero, 200 m a. s. l., 10 Dec 1980, *Cedillo 490* (NY!); Mun Magdalena Tlacotepec, 8 km de la desviación a Tlacotepec, en el entronque a Ojo de Agua, 200 m a. s. l., 26 Sep 1984, *Cabrera 7370* (MEXU!); Mun Matías Romero, Sobre la carretera entre-Matías Romero-Tehuantepec, 180 m a. s. l., 17 Sep 1967, *Pennington 9211* (NY!); Mun Miahuatlán, San Miguel Suchixtepec, Carrizal al N de San Miguel Suchixtepec, 1100 m a. s. l., 21 Sep 1992, *Tenorio 18385* (MEXU!); Mun Nejapa de Madero, Paraje El Agua del Cuajilote, 115 m a. s. l., 15 Jun 2009, *Martínez 43* (MEXU!, SERO!); Mun Pochutla, San Miguel del Puerto, Majahual, Puente 0.5 km S de la carretera costera, 50 m a. s. l., 20 Aug 1998, *Misael 646* (MEXU!); Mun San Jerónimo Sosola, Barranca Ceniza, NO de El Parián, cerca de La Calera, 1500 m a. s. l., 30 May 1992, *Salinas 6905* (MEXU!, MO!); Mun San Juan Bautista Cuicatlán, 14 km NE de San Juan Bautista Cuicatlán, carretera a Concepción Pápalo, 1140 m a. s. l., 22 Apr 1983, *Cedillo 2230* (MEXU!, MO!); Mun San Juan Bautista Jayacatlán, 8 km al N camino a San Juan Bautista Atatlahuaca, 1380 m a. s. l., 13 Jul 2002, *Alvarado 176* (MEXU!); Mun San Mateo del Mar, Water hole W of San Mateo del Mar, 3 Jan 1945, *Alexander 249* (NY!); Mun San Pedro Jaltepetongo, Cañada SW de la estación de ferrocarril, El Venado, 1500 m a. s. l., 11 Jun 2002, *Medina 1090* (MEXU!); Mun San Pedro Quiatoni, Quiatoni, 3 km NW de Unión Juárez, camino de Río Minas a Peña Colorada, 1300 m a. s. l., 4 Nov 1987, *Acosta 806* (MEXU!); Mun Santa Ana Tavela, Paraje Los Mangos de tío Genaro, a 100 m a. s. l., 627 m a. s. l., 17 May 2009, *Reyes 47* (MEXU!, SERO!); Mun Santa Cruz Itundujia a 300 m en LR (N) de la colonia Agua del Platanal, Agencia Iturbide, 968 m a. s. l., 18 Jun 2008, *Velasco 2736* (MEXU!, MO!, SERO!); Mun Santa María Chimalapa, 8 km al NW de El Mezquite, 200 m a. s. l., 23 Feb 1982, *Torres 69* (MEXU!); Mun Santa María Huatulco, Santa María Huatulco, Playa Bocana, S de la Bahía Tangoluda, 25 m a. s. l., 15 Aug 1994, *Reyes-García 2671* (IEB!, MEXU!, MO!); Mun Santiago Astata, Barra de la Cruz, 3 km E de la desviación de la carretera vereda la Vaquita, 65 m a. s. l., 11 Jun 1998 *Elorsa 255* (NY!); Mun Santo Domingo Tehuantepec, Km 140 carretera Oax-Tehuantepec, 7 Dec 1980, *Cedillo 449* (MEXU!, NY!); Mun Tlacolula, Km 636 Totoloapan, 1230 m a. s. l., 28 May 1961, *Boone 1205* (MEXU!); Mun Yautepec, En la subida de la estación de microondas de San Cristóbal, 12.6 km SE del Camarón, 31 Aug 1985, *Torres 6948* (MEXU!, MO!, NY!). **Puebla**: Mun Jolalpan, El Salado, 1 Sep 1985, *Vidaña* (IEB!). **Sinaloa**: Mun Culiacán, Near Culiacán, 23 Nov 1939, *Howard 5028* (MEXU!, MO!, NY!); Mun Mazatlán, Cerro de la Nevería, 50 m a. s. l., *González 203* (MEXU!); Mun Sinaloa, Las Palmas, *González 733* (MEXU!). **Veracruz**: Mun Soteapan, Ejido Emiliano Zapata, 500 m a. s. l., 21 Oct 1979, *Ramírez 481* (XAL!); Mun Tlapacoyan, Tlapacoyan, 10 Aug 1981, *Ventura* (IEB!). **Zacatecas**: Mun Juchipila, 1500 m a. s. l., 11 Nov 1992, *Enríquez 374* (MEXU!); Mun Moyahua, San Lorenzo Cerro de Las Anonas, 4 Aug 1992, *Enríquez 44* (MEXU!).

Common names and uses: Chiapas: "cascabel de lacandón". Guerrero: "bolas de Borrego", "bolón", "codo de fraile", "huevo de toro", "kochiyoyohtle de sisiwatl", "okichyoyotli", "tepecicle", "torito", "venenillo", "yoyote", "yoyotliokixtli", "yuyoteokichyo yotli de susuwatl". Jalisco: "cabrito", "ortiguillo". Michoacán: "cames", "chiquilillo". Morelos: "berraco", "chiclillo", "habilla", "tapaco", "ayoyote". Nayarit: "árbol de Villa". Oaxaca-Puebla: "chancule", "liv", "yoyote". The species is cultivated in backyards or living fences. The seeds mixed with food are used as poison to kill dogs and rats (Diego-Pérez 2004).

Notes: *Cascabela ovata* is easily recognized by its subcoriaceous obovate to oblanceolate leaves, tomentose indumentum on the abaxial side, and conspicuous secondary venation. The leaf morphology of the species is variable in size and shape, as well as in pubescence density and venation pattern (Gensel 1969; Morales 2009a, b). As Gensel (1969) has pointed out, its wide distribution along a temperature/humidity gradient could be the factor in these differences. The use of molecular techniques and wide sampling, including members from the different populations along its distribution, would be desirable to determine whether there is more than one species within the current circumscription of *C. ovata*.

Cascabela pinifolia (Standl. & Steyerm.) L.O.Alvarado & Ochot.-Booth, Ann. Missouri Bot. 94: 320. 2007. ≡ *Thevetia peruviana* K.Schum. var. *pinifolia* Standl. & Steyerm., Amer. Midl. Naturalist 36: 185. 1946. ≡ *Thevetia pinifolia* (Standl. & Steyerm.) J.K.Williams, Sida 17: 187. 1996. —TYPE: Mexico. Michoacán: trail from Apatzingan to Tancitaro, 7 Aug 1940, *Leavenworth 505* (holotype: F barcode F0044762 [web!]; isotypes: GH barcode GH00217709 [web!], MICH barcode MICH1111575 [web!], NY 00318420!) (Fig. 11).

Description: Trees or shrubs 1.8–5 m tall, young branches sparsely pubescent. Leaves petiolate or sessile, petioles when present 1–2 mm long, sparsely pubescent; lamina 7–20 × 1–3 mm, linear, base and apex acute, membranaceous, sparsely puberulent to glabrous on both sides, secondary venation inconspicuous. Inflorescences 6–10 cm long, 3–6(–10)-flowered; peduncles 10–30 mm long, pubescent to glabrate; bracts 3–6 mm long, ovate to ovate-lanceolate, foliaceous, pubescent on both surfaces, with colleters on the adaxial base; pedicels 8–30 mm long, pubescent to glabrous. Sepals 5–11 × 3–4 mm, ovate-lanceolate, foliaceous, pubescent on both surfaces, with 6–10 colleters in one row, on the adaxial base. Corolla 42–55 mm long, yellow; lower tube 10–18 × 3–4 mm, glabrous outside, with retrorse hairs internally, upper tube 8–11 × 15–20 mm, glabrous, limb lobes 24–37 × 18–20 mm, obliquely oblong-ovate, spreading, margin ciliate, sparsely puberulent abaxially. Anthers 2–3 mm long, pollen grains 59–68 μm in polar view, 73.6–80 μm in equatorial view, suboblate, heterofoveolate. Pistil 18–20 mm long; ovary 2.5–3.2 × 3.0 mm; style 12–15 mm long; style head 2.0–2.4 mm long; nectar disk 2–3 mm, lobed at apex. Drupe 25–30 × 40–50 mm, subglobose, glabrous, black, lenticellate, endocarp irregularly deltoid; seeds oblongate, 10–18 × 10 mm, white to yellowish.

Phenology: Flowering and fruiting occur from May to October.

Habitat and ecology: This species grows in tropical dry forests and tropical scrub forests (Fig. 4), riparian vegetation and disturbed vegetation, at elevations of 250–1560 m. The potential distribution model supports the affinity of this species to dry environments, mainly to the tropical dry forests (Fig. 4), highlighting its preference for these environmental conditions.

Distribution area: *Cascabela pinifolia* is endemic to southwestern Mexico, in the states of Guerrero, Mexico, Michoacán and Puebla (Fig. 11). The locality data agree with the SDM, which suggests its likely occurrence also in Chiapas, Colima, Jalisco and Oaxaca, where suitable climatic conditions were recorded.

Conservation status: Vulnerable (VU). The species is restricted to few known localities in five states, with a SDM extending its distribution along the Pacific Slope, from Jalisco to Chiapas (Fig. 11). The area predicted by the model has 112,000 km^2 (EOO 35,319 km^2 and AOO 80 km^2), suggesting additional places of distribution. However, the area is restricted to <6% of Mexico' surface (Table 3); its populations are scarce, and grazing and building activities may significantly reduce the number of individuals in the future.

Additional specimens examined: **Estado de México**: Mun Temascaltepec. Bejucos, 610 m a. s. l., 18 Apr 1933, *Hinton 3792* (NY!). **Guerrero**: Mun Acapulco de Juárez. Mirador del Coloso, 400 m a. s. l., 16 Apr 2009, *Lozada 183* (FCME!); Mun Ahuacuotzingo, Ajuatetla (Reserva campesina), 1560 m a. s. l., 13 Oct 1999, *Diego 9162* (FCME!); Mun Coyuca de Catalán. Cutzamala, 3 Apr 1935, *Hinton 7579* (MEXU!, NY!); Mun Eduardo Neri. Zoquiapan, Cerro Cacalotepec, Ameyaltepec. 828 m a. s. l., 22 Feb 2004, *Alvarado 524* (FCME!); Mun General Heliodo Castillo. Placeres, 350 m a. s. l., 2 Aug 1937, *Hinton 10532* (NY!); Mun Iguala de Independencia. South of Iguala, 11 Aug 1945, *Alexander 152* (MEXU!); Mun Tepecoacuilco de Trujano. 7 km de la desviación a San Juan Tetelcingo, 730 m a. s. l., *Lozada 403* (FCME!); Mun Zirándaro. 29 km SW de Zirándaro, cam. Guayameo, 430 m a. s. l., 13 Jun 1982, *Martínez 1336* (NY!). **Michoacán**: Mun Apatzingán. Apatzingán, 300 m a. s. l., 15 Aug 1938, *Hinton 12018* (NY!); Mun Múgica. Alrededores de la Presa Gral. Francisco J. Múgica. Cerro de Nueva Italia, 519 m a. s. l., 13 Apr 2011, *Cortés 147* (MEXU!). **Puebla.** Paraje Cerro Gordo, 1 km NE de la cabecera Municipal, *Castañeda 41* (MEXU!).

Common names and uses: "came", "camín", "kochyoyohtle de tlatlakatl", "okichyoyotli de tlatlakatl", "yoyomaté pitsák". In Michoacán, this species is sometimes used as an ornamental, cultivated in yards around houses, gardens, or graveyards (Gensel 1998).

Notes: *Cascabela pinifolia* is commonly incorrectly determined as *C. thevetia* due to their morphological similarity; however, the former species can be easily differentiated by their linear lamina (vs. lanceolate linear-elliptic in *C. thevetia*) and the indumentum on the bracts (hirsutulous vs. glabrous in *C. thevetia*). In addition, its fruits are lenticellate (vs. not lenticellate in *C. thevetia*) and its distribution is restricted to the Balsas River basin (vs. practically all of the Pacific and Atlantic slopes and the center of the country in *C. thevetia*).

Cascabela thevetia (L.) Lippold, Feddes Repert. 91(1–2): 52. 1980. ≡ *Cerbera thevetia* L., Sp. Pl. 1: 209. 1753. ≡ *Cerbera peruviana* Pers., Syn. Pl. 1: 267. 1805. ≡ *Thevetia neriifolia* Juss. ex Steud., Nomencl. Bot. (ed. 2). 180. 1821. ≡ *Cascabela peruviana* (Pers.) Raf., Sylva Tellur. 162. 1838. ≡ *Thevetia linearis* Raf., Sylva Tellur. 91. 1838. ≡ *Thevetia thevetia* (L.) H.Karst., Deut. Fl., ed. 2, 2: 613. 1894. ≡ *Thevetia peruviana* K.Schum. in Engler and Prantl, Nat. Pflanzenfam. 4: 159. 1895. ≡ *Ahouai thevetia* (L.) M.Gómez, Fl. Habanera. 357. 1897. ≡ *Thevetia thevetia* (L.) Millsp., Publ. Field Columb. Mus., Bot. Ser. 2: 83. 1900. —LECTOTYPE: America. *s. loc. et coll.* (lectotype: LINN. 296.4 [web!], designed by Lippold (1980)) (Fig. 12).
= *Thevetia yccotli* var. *glabra* A.DC., Prodr. 8: 343. 1844.—TYPE: Mexico. Tamaulipas: Tampico, 1827,

Berlandier 189 (holotype: G-DC!; isotype: P [n.v.], MEXU [photo!]).

Description: Trees 2–8(10) m tall, young branches glabrous. Leaves petiolate, petioles 1–5 mm long, glabrous; lamina 70–170 × 5–14 mm, lanceolate to linear-elliptic, base and apex acute, firmly membranaceous, glabrous on both sides, secondary venation inconspicuous. Inflorescences 8–10 cm long, 5–8-flowered; peduncles (5–) 10–35(–50) mm long, glabrous; bracts 1.8–4.0 mm long, ovate-lanceolate, foliaceous, glabrous on both surfaces, with colleters on the adaxial base; pedicels 25–30 mm long, glabrous. Sepals 5–13 × 2–4 mm, ovate-lanceolate, foliaceous, glabrous on both surfaces, with (0–) 4–10 colleters in one row. Corolla 45–65 mm long, yellow to orange; lower tube 12–20 × 2–5 mm, with internal retrorse hairs, upper tube 8–15 × 12–15 mm, glabrous, limb lobes 25–35 × 17–25 mm, obliquely oblong to oblong–ovate, erect, glabrous on both surfaces. Anthers 2–3 mm long, pollen grains 59–69 μm in polar view, 68–76(–80) μm in equatorial view, oblate–spheroidal to prolate–spheroidal, foveolate to microreticulate. Pistil 14–18 mm long, glabrous; ovary 4.0 × 3.0 mm, glabrous; style 1.0–1.2 cm long, style head 2.0–3.0 × 2.5–3.0 mm long; nectar disk 3–3.5 mm, completely fused, lobed at apex. Drupe 25–35 × 20–45 mm, subglobose, glabrous, black, endocarp stony, irregularly deltoid, not lenticellate; seeds oblongate, 10–12 × 10 mm, white to yellowish.

Phenology: The species flowers and fruits year-round.

Habitat and ecology: *Cascabela thevetia* grows in tropical dry forests (Fig. 4), scrublands, oak forests, cloud forests, tropical subperennial forests and secondary vegetation, at elevations 0–1500 (–2100) m. The SDM indicates that the species mainly thrives in humid environments, such as those found along the Atlantic coast, but it can also explore a mosaic of additional climatic conditions. The fruits of this species are consumed by birds, rats and bats (Rodríguez et al. 2003).

Distribution area: Mexico, Central America (Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama), South America (Colombia, Venezuela, British Guiana, Brazil, Ecuador, Peru, and Bolivia) and cultivated in the Antilles (Bahamas, Cuba, Haiti, Jamaica, Puerto Rico, and Dominican Republic). Today it is cultivated in the tropics around the world. In Mexico, the species occurs in Campeche, Chiapas, Guanajuato, Guerrero, Hidalgo, Michoacán, Nayarit, Oaxaca, Puebla, Querétaro, Quintana Roo, San Luis Potosí, Tabasco, Tamaulipas, Veracruz and Yucatán (Fig. 12). The species was also reported in Chihuahua and Sinaloa (Gensel 1969; Rzedowski and Calderon de Rzedowski 1998). We did not include the data from these states in the models because the available information is not clear about the collection sites.

The SDM is supported by the locality data, and additional locations are predicted in the states of Coahuila, Colima, Jalisco and Nuevo León; however, it failed to predict its occurrence in Sinaloa and Chihuahua, where it has been reported. The model suggests that in the northwest, dry climatic conditions play an important role in restricting its natural distribution (Fig. 12).

Conservation status: Least concern (LC). This species has a wide distribution in Mexico (Fig. 12; Table 3), with an estimated SDM area of occupancy of 494,000 km^2 (EOO 821,907 km^2 and AOO 524 km^2). It grows in a variety of vegetation types, elevations and climatic conditions. In addition, it flowers and yields fruits throughout year, and its cultivation and tolerance to anthropic disturbances suggest that the species easily adapts to harsh conditions. We consider that the species is not under any kind of threat.

Additional specimens examined: **Campeche**: Mun Calakmul, La Aguada, a 2 km al W de Calakmul, 150 m a. s. l., 17 Oct 1997, *Martínez 29004* (MEXU!, NY!); Mun Champotón, 120 km al SW de Xpujil, en los alrededores de la zona arqueológica de Calakmul, 150 m a. s. l., 13 Aug 1996, *Pascual 491* (MEXU!). **Chiapas**: Mun Esperanza, Escuintla, 1947, *Matuda 16715* (MEXU!); Mun Las Margaritas, Río Jabalí, 45 km E de Tziscao, camino a Ixcán, sobre la carretera Fronteriza del Sur, 300 m a. s. l., 12 May 1984, *Martínez 6324* (MEXU!); Mun Tapachula, Región Soconusco, Álvaro Obregón, 18 Mar 1992, *Vázquez 98AA* (MEXU!); Mun Tenejapa, Salida del Río Cruz Pilal, 21 Jun 1984, *Méndez 7701* (MEXU!); Mun Venustiano Carranza, 5 km W de Venustiano Carranza, sobre el camino a Pujiltic, 4 Apr 1985, *Cabrera 8036* (MEXU!). **Guanajuato**: Mun Xichú, Las Adjuntas, 1000 m a. s. l., 18 Oct 1990, *Ventura 8984* (IEB!, MEXU!). **Guerrero**: Mun Acapulco, Barra de Coyuca, NW de Acapulco, 1 Aug 1971, *Boege 1912* (MEXU!); Mun Eduardo Neri, 10 km después de Mezcala, al Oeste, 1150 m a. s. l., 7 Dec 1994, *Diego 378-a* (FCME!); Mun Zihuatanejo de Azueta, Laguna Playa Blanca, 5 m a. s. l., 11 Jul 1990, *Diego 6107* (FCME!); Mun Petatlán, Estación de Microondas Las Rocas, Costa Grande, 3 m a. s. l., *Diego 378* (FCME!); Mun San Marcos, 1 km camino a Pesquería, laguna de Tecomate, 15 m a. s. l., 26 Sep 1990, *Lozada 1397* (MEXU!); Mun Tecpan de Galeana, aprox. 0.5 km NW de la Vinata, márgenes de la laguna El Plan, 2 May 1990, *Lorea 5100* (IEB!, MEXU!); Mun Zirándaro, En La Parota 37 km SW de Zirándaro, camino Zirándaro-Guayameo, 330 m a. s. l., 20 Mar 1983, *Martínez 3588* (MEXU!). **Hidalgo**: Límites de Hidalgo-San Luis Potosí, hacia Tamazuchale, 700 m a. s. l., 7 Nov 1979, *Hernández 3922* (MEXU!). **Michoacán**: Mun Huetamo, Tuzantla, carretera Zitácuaro, 700 m a. s. l., 27 Jun 1983, *Soto 5349* (MEXU!).

Nayarit: Mun Isla María Madre, La Quita La Concordia, en el campamento Balleto, 9 Jan 1981, *Téllez 4139* (MEXU!). **Oaxaca**: Mun Ixtlán de Juarez, San Juan Atepec, 8 km de la terracería al poblado, hacia Abejones, en el Puente de Río Grande, 17 Apr 2002, *Alvarado 38* (MEXU!); Mun Jamiltepec, San Pedro Tutultepec, 4 km E del Agua Zarca, 15 Jun 1985, *López 684* (MEXU!); Mun Juchitán, Asunción Ixtaltepec, cercano a Nizanda, 180 m a. s. l., 3 Feb 1996, *Pérez-García 943* (MEXU!); Mun San Juan Bautista Cuicatlán, Cuesta de Quiotepec, 650 m a. s. l., 25 Mar 1920, *Conzatti 3917* (MEXU!); Mun San Juan de Los Cues, 2 km E de Los Cues, 1000 m a. s. l., 29 Jun 1987, *García-Mendoza 3376* (IEB!, MEXU!); Mun San Martín Toxpalapan, La Loma of San Martín Toxpalapan, 2.5 km from San Martín Toxpalapan on the track at 1.5 km from the Teotitlán del Camino-Oaxaca road, 980 m a. s. l., 17 Jun 2002, *Calzada 23207* (MEXU!); Mun Santa María Ixcatlán, Río Seco, SW de Tecomavaca, brecha a Ixcatlán, 1150 m a. s. l., 4 Dec 1991, *Salinas 6461* (MEXU!); Mun Santo Domingo Tehuantepec, Santo Domingo Petapa, camino del pueblo, 4 Sep 1992, *Frei FREI019* (MEXU!); Mun Valerio Trujano, 3 km de Valerio Trujano, orillas del Río Apoala, 692 m a. s. l., 16 Oct 2004, *Juárez 609* (MEXU!). **Puebla**: Mun Acatlán, Población de las Nieves, 7 Dec 1996, *Guízar 3655* (MEXU!); Mun Caltepec, El Tambor, 2122 m a. s. l., 8 Dec 2001, *Tenorio 21606* (MEXU!); Mun Coxcatlán, Near Coxcatlán on Cerro Ajuereado and in the adjacent valley, 1000 m a. s. l., 21 Jul 1961, *Smith 3640* (MEXU!, NY!); Mun Guadalupe Santana, Paraje Río Grande (Río Mixteco) a 3 km al SW de Chiltepec, 1220 m a. s. l., 15 Jul 1999, *Castañeda 479* (MEXU!); Mun Pahuatlán, El Río a 3 km N de Pahuatlán, carretera San Pablito, 850 m a. s. l., 4 May 1989, *Tenorio 15726* (MEXU!). **Querétaro**: Mun Arroyo Seco, Orilla del Río Santa María, 4 km de las mesas de Agua Fría, 650 m a. s. l., 16 May 1988, *Herrera 128* (IEB!, MEXU!); Mun Jalpan de Serra, 5 km SE de Tancoyol, 860 m a. s. l., 10 Jun 1998, *Carranza 585* (IEB!, MEXU!); Mun Landa de Matamoros, Rincón de la Chirimoya, 2.5 km SE de Acatitlán de Zaragoza, 1250 m a. s. l., 5 Jun 1989, *González 692* (IEB!, MEXU!); Mun Landa de Morelos, 11 km W de Tilaco, 900 m a. s. l., 9 Jun 1986, *Fernández 3428* (IEB!, NY!). **Quintana Roo**: Mun Felipe Carrillo Puerto, Rancho Las Palmas, km 160 carretera Felipe Carrillo Puerto-Chetumal, 19 Nov 1987, *Mata 87-103* (MEXU!). **San Luis Potosí**: Mun Ciudad Valles, Rancho Tinaja, 5.5 mi S of Cd. Valles, 130 m a. s. l., 22 Mar 1981, *Fryxell 3543* (NY!); Mun Tamazunchale, Tamanzunchale, 70 m a. s. l., 5 Aug 1937, *Fisher* (NY!). **Tabasco**: Mun Balancán, Por la carretera W–O, en el aserradero Quemado, 100 m a. s. l., 9 Apr 1976, *Calzada 2375* (MEXU!); Mun Comalcalco, Wolter finca, 6 Jun 1962, *Barlow 29-10B* (MEXU!); Mun Guatacalca, Nacajuca, 25 m a. s. l., 7 Oct 1978, *Ortega 915* (MEXU!); Mun Heróica Cárdenas, Campo Rodador, en camino a cinco Presidentes, 20 m Rodador, en camino a cinco Presidentes, 8 Oct 1996, *Tenorio 19507* (MEXU!). **Tamaulipas**: Mun Gómez Farias, Sierra Guatemala, a mile airline N of the square at GómezFarias on road to Rancho del Cielo, 228 m a. s. l., 24 Jun 1971, *Sullivan 683* (NY!); Mun Mante, Along route 85, ca. 4-5 mi S of Cd. Mante, 18 Feb 1961, *Merril 3804* (NY!); Mun Tampico, Tampico, 15 m a. s. l., 27 Apr 1910, *Palmer 339* (NY!). **Veracruz**: Mun Plan Dos Ríos, Jalapa-Veracruz hwy, 11 Jul 1974, *Sohmer 9381* (MEXU!); Mun Actopan, Laguna de la Macha, borde SE del Manglar, 0 m a. s. l., 10 Jun 1977, *Novelo 344* (MEXU!, NY!, XAL!); Mun Apazapan, 2 km NE of Emiliano Zapata (Carrizal), 1 km S of hwy Mex. 140, 400 m a. s. l., 27 Jun 1980, *Hansen 7518* (NY!); Mun Atoyac, Atoyac, 550 m a. s. l., 19 Jul 1985, *Acevedo 392* (IEB!, MEXU!, XAL!); Mun Axocoapan, Monterrey, Ejido Coetzalan, 500 m a. s. l., 25 May 1983, *Robles 189* (MEXU!); Mun Catemaco, Catemaco, 200 m a. s. l., 10 May 1974, *Vázquez 658* (XAL!); Mun Coatepec, Desviación a Jalcomulco, 500 m a. s. l., 8 Dec 1993, *Luna 893* (XAL!); Mun Chalma, 6.5 km N of Huejutla on the road to Platón Sánchez, 250 m a. s. l., 22 Jun 1980, *Née 18464* (MEXU!); Mun Chicontepec, En el Poblado de Tlacolula, 270 m a. s. l., 29 Aug 1979, *Calzada 5644* (MEXU!, XAL!); Mun Coatzintla, Palmar de Zapata, 110 m a. s. l., 25 Jan 1982, *Cortés 105* (XAL!); Mun Cuitláhuac, 3 km NW of Cuitláhuc on small dirty road, 350 m a. s. l., 3 Jul 1980, *Hansen 7557* (NY!); Mun Emiliano Zapata, Entre Cerro Gordo y Plan del Río, 8 Apr 1982, *Castillo 2595* (MEXU!); Mun Orizaba, Orizaba, 1200 m a. s. l., Feb 1885, *Gray* (XAL!); Mun Pánuco, Poblado de Tamos, 10 m a. s. l., 12 Jul 1978, *Calzada 4518* (MEXU!); Mun Papantla, Predio Escolín, 12 km al NE de Papantla, 370 m a. s. l., 22 Jun 1987, *García-Mendoza 3221* (MEXU!, IEB!, XAL!); Mun Paso de Ovejas, Salmoral, alrededores, 28 m a. s. l., 6 Jun 1987, *Torres 116* (MEXU!, XAL!); Mun Puente Nacional, Barranca de Pachuquilla, 2 km al SW de dicha población, 260 m a. s. l., 26 Aug 1985, *Medina 427* (MEXU!, XAL!); Mun San Andres Tuxtla, Salto de Eyipantla, 12 km al W de Catemaco, 5 km by air S of San Andrés Tuxtla, 230 m a. s. l., 28 Jun 1975, *Sousa 4667* (MEXU!, XAL!); Mun Tampico el Alto, La River, entrada por Tampico El Alto a Laguna de Tamiahua, 30 m a. s. l., 10 Sep 1980, *Calzada 6326* (MEXU!, XAL!); Mun Tepetlán, Cerca de Almolonga, en el Malpaís, 900 m a. s. l., Nov 1979, *Cházaro 1269* (MEXU!, XAL!); Mun Tuxpan, En la Ciudad de Tuxpan, antes de entrar al puente del Río Tuxpan, 50 m a. s. l., 10 Sep 1980, *Calzada 6335* (IEB!, MEXU!, XAL!); Mun Veracruz, Playa Norte de Veracruz, al S de la planta de tratamiento de aguas negras, 29 Apr 1996, *Castillo-Campos 14696* (IEB!, XAL!). **Yucatan**: Mun Cozumel, 1 km al SE de Tecax, sobre la carretera a

Chetumal, 20 Apr 1986, *Cabrera 11328* (MEXU!); Mun Tinum Valladolid, (Chichen Itzá), 30 Jun 1932, *Steere 1686* (MO!); Mun Tizimín, En Tizimín, 17 Jul 1985, *Cabrera 8919* (NY!).

Common names and uses: Yucatan Peninsula: "aak'its", "sak iits'", "k'an lool". Jalisco: "campanilla", "campanita", "flor de San Pedro", "naranjo amarillo", "narciso amarillo". Michoacán: "came", "solimán". Mexico-Guerrero-Veracruz: "came", "rosa amarilla", "yoyote", "yoyotli". *Cascabela thevetia* is widely cultivated in Mexico. The fruits are poisonous and used for fishing craft and as traditional medicine against hemorrhoids and toothaches (Gensel 1969). The trunk is used for beams in rural houses and is cultivated in numerous places as an ornamental (Diego–Pérez 2004). The poisonous properties of this plant have been described in several papers; it has been responsible for most of the cattle, pet and human deaths and intoxications due to plant poisoning in several countries, including Mexico (García and Luna 2003; González et al. 2003; Diego–Pérez 2004; Escobar et al. 2012; Sowjanya et al. 2013).

Notes: This species is frequently confused with *Cascabela gaumeri* (see above) and *C. thevetioides*. However, it can be easily distinguished by its inconspicuous secondary veins (exposed in *C. thevetioides*), glabrous leaves (abaxially tomentose in *C. thevetioides*) and the size of its lower corolla tube (20–35 mm in *C. thevetioides*, Fig. 1).

Cascabela thevetioides (Kunth) Lippold, Feddes Repert. 91: 53. 1980. ≡ *Cerbera thevetioides* Kunth, Nov. Gen. Sp. 3: 223. 1818 [1819]. ≡ *Thevetia humboldtii* (Kunth) Voigt, Hort. Suburb. Calcutt. 533. 1845. ≡ *Thevetia thevetioides* (Kunth) K.Schum., Nat. Pflanzenfam. 4(2): 159. 1895.—Type: MEXICO. Guerrero: Taxco, Apr 1803, *Humboldt* and *Bonpland s.n.* (holotype: P barcode P00670866 [web!], photo MEXU!) (Fig. 13).
= *Thevetia yccotli* A.DC., Prodr. 8: 343. 1844.—Type: MEXICO. Mexico and Morelos: In Mexico ad Gonacatepec, *Andrieux 253* (holotype: G-DC!; isotypes: P [n.v.]; K barcode K00587616 [web!]).

Description: Trees or shrubs 2.5–10 m tall, young branches sparsely pubescent. Leaves petiolate, petioles 1–5 mm long, pubescent; lamina 6–14 × 4–14 mm, elliptic-lanceolate to lanceolate, base and apex acute, membranaceous, glabrous adaxially and sparsely tomentulose abaxially, secondary venation conspicuous, 30–45 pairs of veins. Inflorescences (8–) 10–16 cm long, 8–18-flowered; peduncles (2–) 6–21 mm long, glabrous; bracts 4–11 mm long, ovate to ovate–lanceolate, foliaceous, glabrous on both surfaces, with colleters on the adaxial base; pedicels 8–25 mm long, glabrous. Sepals 6–13 × 2.5–4 mm, ovate–lanceolate, foliaceous, pubescent or glabrous on both surfaces, with 10–20 colleters in one or two rows. Corolla 80–100 mm long, yellow; lower tube 20–35 × 2.0–5.5 mm, glabrous outside, with retrorse hairs internally, upper tube 12–20 × 12–18 mm, glabrous, limb lobes 30–55 × 30–35 mm, obliquely oblong-obovate, spreading, margin sparsely ciliate or glabrous on both surfaces. Anthers 1.5–2.8 mm long, pollen grains 65–79 μm in polar view, 71–95 μm in equatorial view, oblate–spheroidal to prolate–spheroidal, foveolate to microreticulate. Pistil 25–40 mm long; ovary 2.3–4.5 mm long; style 18–20 mm long, style head 2.3–2.5 mm long; nectar disk (0.9–)2.0–3.0 mm, completely fused, lobed at apex. Drupe (25–) 30–45 × 30–65 mm, subglobose, glabrous, black, endocarp stony, irregularly deltoid, lenticellate; seeds oblongate, 15–18 × 15–20 mm, white to yellowish.

Phenology: The species flowers and bears fruits practically year-round.

Habitat and ecology: The species mainly grows in tropical dry forests (Fig. 4), scrublands, riparian forests, *Pinus–Quercus* and *Quercus* forests, as well as in disturbed vegetation, at elevations (750–) 1200–2300 m a. s. l.. The SDM suggests that the species grows in the tropical dry forests as well as in other kinds of vegetation, due to its ability to reach elevations above 2000 m.

Distribution area: Endemic to Mexico, distributed in Mexico City, Guanajuato, Guerrero, Jalisco, Mexico state, Michoacán, Morelos, Oaxaca, Puebla and Querétaro (Fig. 13). The SDM is supported by the locality data, and it predicts additional locations in the states of Chiapas, Colima, Jalisco, Tlaxcala and Veracruz, as well as in small areas in San Luis Potosí, Sonora and Zacatecas (Fig. 13).

Conservation status: Near threatened (NT). The species is distributed in the states located along the Trans-Mexican Volcanic Belt and southwestern Mexico. The SDM projected an area of occupancy of 250,383 km^2 (EOO 121,062 km^2 and AOO 504 km^2). It grows in different vegetation types, but mainly in the tropical dry forests of several natural protected areas, such as the Tehuacán–Cuicatlán Biosphere Reserve. Its tolerance to some anthropogenic disturbance easily allows its cultivation. Although these characteristics may suggest that does not have conservation problems, it shows a restricted distribution in states that suffer high rates of land use changes and landscape disturbances. For example, the natural habitats in the Trans-Mexican Volcanic have been drastically transformed (Mas et al. 2004; Sánchez-Cordero et al. 2005). In addition, the uses of its fruits by folk dancers and the uses of the seeds in traditional weight-loss programs, may affect the natural populations because management is not sustainable. We would suggest placing the species in the near threatened category.

Additional specimens examined: **Ciudad de Mexico**: Colonia Portales, Rumania, 6 Jul 1974, *Cayeros 226* (MEXU!). **Estado de México**: Mun Ixtapan de la Sal, Ixtapan de la Sal, Dec 1950, *Paray 541* (MEXU!); Mun Chiautla, Tepetitlán, 2400 m a. s. l., 23 Aug 1983, *Ventura 1239* (MEXU!), *1343* (ENCB!, MEXU!); Mun Temascaltepec, Temascaltepec, 14 Jul 1935, *Hinton 7961* (MO!, NY!); Mun Texcoco, 8 km al E de Texcoco, 2270 m a. s. l., 5 May 1980, *Pulido 464* (CHAPA!, MEXU!). **Guanajuato**: Mun Apaseo el Grande, Ixtla, 2000 m a. s. l., 26 Aug 1981, *Rzedowski 37549* (ENCB!!, IEB!, MEXU!, MO!); Mun Comonfort, Delgado, cerca de Neutla, 2000 m a. s. l., 15 Jun 1986, *Rzedowski 39849* (IEB!, MEXU!); Mun San Miguel de Allende, Hwy 51 between San Miguel de Allende-Comonfort, 3200 ft., 5 Jul 1971, *Genelle 899* (MO!, NY!); Mun Santa Cruz De Juventino Rosas, Las Fuentes, 3 Jun 2000, *M. Martínez* (IEB!). **Guerrero**: Mun Ahuacotzingo, Ajuatetla, reserva campesina, 6 Dec 1997, *Godínez 4* (FCME!, MEXU!); Mun Alcozauca, Amapilca, Barranca del Limón, 1650 m a. s. l., 3 Nov 1983, *Viveros 312* (MEXU!); Mun Atoyac de Álvarez, Ejido El Quemado, 900 m a. s. l., 3 Nov 1983, *Turrubiarte 46* (MEXU!); Mun Buenavista del Cuellar, Buenavista del Cuellar, 29 Jun 2000, *Diego 9296* (MEXU!); Mun Chilapa de Álvarez, 25 km al SE de Chilapa, brecha a Hueytenango (Hueycaltenango?), 23 Aug 1983, *Piña 107* (ENCB!, IEB!, MEXU!); Mun Chilpancingo de los Bravo, Barranca Pezoapa, 1250 m a. s. l., 14 Nov, *Lozada 4034* (FCME!); Mun Eduardo Neri, Xochipala, 1100 m a. s. l., 20 Jul 1983, *Diego 1539* (FCME!); Mun Heliodo Castillo, Campo Morado, 1360 m a. s. l., 29 Dec 1937, *Hinton 11153* (MO!, NY!); Mun Iguala de la Independencia, Iguala, 732 m a. s. l., 7 Apr 2012, *Lozada 1429* (FCME!); Mun Mártir de Cuilapan, La Esperanza (reserva campesina), 1650 m a. s. l., *Lozada 1565* (FCME!), *Diego 113* (FCME!, MEXU!); Mun Pilcaya, Cacahuamilpa 5 km al W de las Grutas, 1300 m a. s. l., 6 Dec 1997, *Calonico 6405* (MEXU!). Mun Taxco de Alarcón, Along roadsides N of the town of Taxco, 10 Jan 1943, *Gilly 1* (NY!); Mun Teloloapan, Teloloapan, 1650 m a. s. l., 30 Jun 2006, *Lozada 3386* (FCME!); Mun Tixtla de Guerrero, El puente del Ranchito, aprox. 5 km antes de Tixtla, sobre el río de la presa, 1550 m a. s. l., 7 Dec 1996, *Diego 75* (FCME!); Mun Tlapa de Comonfort, 3.2 km al WSW de Tototepec, 1550 m a. s. l., 18 Aug 1990, *Calzada 16149* (MEXU!); Mun Zitlala, Las Lomas Ayotzinapa, 1680 m, *Ortiz 7076* (FCME!). **Jalisco**: Mun San Cristóbal de la Barranca, San Cristóbal de la Barranca, 12 Jul 1987, *Cházaro* et al. (IEB!). **Michoacán**: Mun Quiroga, Cerca de San Andrés Tzíndaro, 2100 m a. s. l., 10 Feb 1992, *Diaz 6925* (MEXU!, IEB!); Mun Tuxpan, Al SE de Ciudad Hidalgo, cerca de Turundeo, 10 Oct 1983, *Ramamoorthy 4384* (MEXU!); Mun Tzintzuntzan, Ichupio, 2100 m a. s. l., 9 Apr 1992, *Díaz-Barriga 6932* (IEB!, MEXU!); Mun Tzitzio, Carretera Temazcal-Huetamo, 1350 m a. s. l., 24 Sep 1979, *Soto 1765* (MEXU!). **Morelos**: Mun Tepaltzingo, Tepaltzingo, 20 Mar 1941, *Miranda 1361* (MEXU!); Mun Cuernavaca, Cuernavaca, *Schmitz 748* (NY!); Mun Tepalcingo de Hidalgo, 1 km al N de El Limón, cañada camino a la presa, 1245 m a. s. l., 7 Apr 1991, *Bonilla 1469* (IEB!, MEXU!); Mun Tlayacapan, A 3 km al SW de Tlayacapan (sobre el camino Oaxtepec-Xochimilco), 1620 m a. s. l., 9 May 1978, *Lamy 141* (MEXU!); Mun Yautepec, 2 km al NW de Yautepec, carretera vieja Yautepec-Tepoztlan, 1211 m a. s. l., 5 Oct 1986, *Flores 121* (MEXU!). **Oaxaca**: Mun Oaxaca de Juárez, Barranca en terrenos de San Felipe, 1650 m a. s. l., 24 Mar 1937, *Conzatti 5278* (NY!); Mun San Andrés Dinicuiti, 3 km N de Tula, hacía Huajuapam, 2220 m a. s. l., 29 Jun 1992, *García-Mendoza 5655* (MEXU!); Mun San Pedro Tututepec, 3 km de la desviación A Santiago Jocatepec, 11 m a. s. l., 5 Oct 1984, *Lopez 416* (MEXU!); Mun Santiago Miltepec, 50 mi S of Tehuacán, 8 mi N of Santiago Miltepec on Mexican 125, 1860 m a. s. l., 9 Jun 1979, *Hess 4687* (MEXU!); Mun Santo Domingo Tonalá, Del Boquerón a Los Mangos, 1347 m a. s. l., 8 Jan 2009, *Torres 829* (MEXU!, SERO!); Mun Villa de Tamazulapam del Progreso, Río del Oro, 4 km E de Villa de Tamazulapam del Progreso, 1850 m a. s. l., 11 May 1981, *García-Mendoza 297* (MEXU!). **Puebla**: Mun San Sebastian Tenango, San Sebastian Tenango, 15 May 1966, *Boege 99* (MEXU!); Mun Acatlán de Osorio, En San Vicente Boquerón, 1000 m a. s. l., 27 May 1985, *Soto 8676* (MEXU!); Mun Caltepec, San Luis Tultitlanapa, 2500, Jun 1908, *Purpus 3235* (MEXU!, MO!, NY!); Mun Guadalupe Santana, Márgenes del Río Mixteco, 3 km al S de San Antonio Chiltepec, 1070 m a. s. l., 13 Jun 1998, *Guizar 3993* (CHAPA!, MEXU!); Mun Izúcar de Matamoros, 8 km al SE de Hacienda Raboso, 1500 m a. s. l., 2 Jul 1982, *Guizar 894* (CHAPA!, MEXU!); Mun Jolalpan, 2.5 km al NW de Zacacuautla, 1240 m a. s. l., 16 Jul 1984, *Guizar 1382* (CHAPA!, MEXU!); Mun Tepeji de Rodríguez, 5 km al E de Zacapala, brecha a Tepeji de Rodríguez, 1350 m a. s. l., 23 Oct 1986, *Tenorio 12235* (MEXU!). **Querétaro.** El Batán, 1950 m a. s. l., 3 Jun 1978, *Argüelles 1055* (MEXU!).

Common names and uses: "almendra quema grasa", "hueso de fraile", "narciso amarillo", "yoyote", "yecotle" (Mexico City, Estate of Mexico, Morelos), "anis", "ayoyote", "yoyote", "yoyotla" (Guerrero), "cabrito", "retama" (Jalisco), "chavaquín", "codo de fraile", "fraile" (Michoacán), "calaveritas", "rejalgar", "venenillo", "yoyote", "yucucaca "(Oaxaca), "chilca", "codo de fraile", "veneno de monte", "yoyote" (Puebla), "solimán", "tzinacanytlacuatl", "yoyotli". This species is cultivated in parks, houses backyards, as well as in living fences in all its range. The stone endocarp is widely used as a musical element in some ritual or folkloric dances, as well as in handcrafts (Fig. 7). In spite of the high toxicity of the seeds, they are still used as a remedy for weight-loss in some places in the country.

Notes: *Cascabela thevetioides* may be confused with *C. balsaensis*, since both of them share lanceolate to elliptic-lanceolate leaves with conspicuous secondary veins. However, *C. thevetioides* is easily distinguished by its numerous flowers, which are the largest in the genus; in addition, its leaves are abaxially tomentose (vs. pubescent on both sides in *C. balsaensis*).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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