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CHROMOSOME NUMBERS IN *VERBESINA* (ASTERACEAE, HELIANTHEAE, VERBESININAE)

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Abstract: We report chromosome counts for 107 samples of *Verbesina* collected in Ecuador, Mexico, and Venezuela. These counts represent 77 species with 47 of these belonging to species never counted before. Most samples have the hypothesized diploid number for the genus of $2n = 34$; a few taxa have $2n = 36$; 19 collections are polyploid. Polyploidy was found in a majority of the South American samples counted (13/23); polyploidy was not broadly distributed in samples counted for Mexican species (6/84). We report the first octoploid for a collection of *Verbesina*, *V. pedunculosa* from northcentral Mexico at $n(4x) = 68$. Previously published counts for *Verbesina* amount to 175 records representing 90 species. Together with the counts we report here, chromosome numbers are now known for 137 species of *Verbesina*.

INTRODUCTION

Polyploidy or whole genome duplication is broadly distributed in plants (Leebens-Mack et al., 2019) and is a source of genomic variation that can contribute to species diversification (Levin 1983; Otto, 2007; Barker et al., 2016a; Soltis et al. 2016). Most Asteraceae are paleohexaploid and share with their sister family Calyceraceae a paleotetraploid ancestor (Barker et al., 2016b). However, diploidization and subsequent polyploidization events have occurred multiple times in the evolution of the Asteraceae (Panero & Crozier, 2016). For example, all taxa of the Heliantheae alliance except Helenieae share a whole genome duplication (Leebens-Mack et al., 2019) but all members of the alliance have a hypothesized base chromosome number of $x = 19$ (Smith, 1975; Robinson et al., 1981a). Here, we explore the distribution of polyploidy in *Verbesina* using chromosome numbers.

With more than 325 species, *Verbesina* is the largest genus of tribe Heliantheae (Panero, 2007). Most species occur in Mexico, the tropical Andes, and eastern Brazil with a few taxa in the temperate regions of North America, South America,

and the Caribbean. The genus is very diverse in habit. Some species are trees in montane moist or cloud forests but a majority of the species are shrubs in various montane tropical vegetation assemblages. Perennial herbs and a few annuals are common in the Caribbean and the hardwood forests of the eastern USA but the greatest diversity of these herbaceous species is found in the xerophytic shrublands and grasslands of northern Mexico and the southwestern USA. The capitula in *Verbesina* can be discoid or radiate and the corolla colors are mostly golden yellow or white; few species have red, orange, green, cream-colored, or light yellow, rarely pink, corollas. *Verbesina* can be easily separated from other Verbesininae and Heliantheae by its biconvex fruits with mostly symmetrical wings and a pappus of two awns without intervening squamellae.

Verbesina does not have a comprehensive revision. Robinson and Greenman (1899) divided the genus into 12 sections based mostly on capitulum size, habit, and corolla color. Since then, revisions of various sections have been published: *Lipactinia* (Blake, 1925), *Pterophyton*, *Sonoricola*, and *Ximenesia* (Coleman, 1964, 1966a, 1966b), *Pseudomontanoa* (Turner, 1985), and *Ochractinia*, *Platypteria*, and *Verbesina* (Olsen, 1985, 1986, 1988).

Results from molecular studies show that most of these sections are not monophyletic (Panero and Jansen, 1997) and echo commentary by Robinson and Greenman (1899), who considered some of their sections in their synopsis of *Verbesina* not natural. The same molecular results show that for the most part, leaf phyllotaxy is a good indicator of evolutionary history with opposite-leaved species more closely related to each other than to species with alternate leaves (Panero and Jansen, 1997).

Molecular phylogenetic studies of the chloroplast DNA show *Verbesina* is closely related to *Podachaenium* and *Squamopappus* in a clade sister to *Tetrachyron* (Panero and Jansen, 1997). This result was used by Panero (2007) to remove *Podachaenium*, *Squamopappus*, and *Verbesina* from subtribe Ecliptinae (sensu Robinson, 1981a) and amend the concept of subtribe Verbesiniinae to include only these three genera and *Tetrachyron*, the latter of which was previously classified in subtribe Neurolaeniinae. Molecular studies using transcriptomic data of the nuclear DNA indicate that *Verbesina* is sister to the Engelmanniinae but this relationship is not strongly supported (Zhang et al., 2021). All chromosome numbers for *Verbesina* to date show that the genus has a base number of $x = 17$ or 18 with some tetraploid species (Robinson et al., 1981b; Jansen et al., 1984; Carr et al., 1999) and two records for taxa with higher ploidy levels (Jansen et al., 1984; Strother, 1976). *Podachaenium* and *Squamopappus* have a base chromosome number of $x = 19$ (Panero, 2007), whereas *Tetrachyron* has species with $2n = 30, 32,$ and 34 (Strother & Panero, 2001).

Herein, we review all chromosome numbers available in the literature for *Verbesina* and report chromosome numbers for 107 collections of *Verbesina* gathered by the first author between 1992-1996 in Ecuador, Mexico, and Venezuela.

MATERIALS AND METHODS

Capitula were fixed in the field in a 3:1 solution of ethanol and acetic acid. Large

capitula were split in half to allow the fixative to reach inner parts of the inflorescence. All preserved capitula were collected shortly after the capitulescence started to develop. Anthers were excised from flowers and pollen parent cells were squeezed out of anther thecae. Hoyer's solution and acetocarmine stain were used to preserve cells and stain chromosomes.

Previously published chromosome counts for *Verbesina* were obtained from the index to chromosome numbers of Asteraceae webpage (http://www.lib.kobe-u.ac.jp/infolib/meta_pub/G0000003asteraceae_e) and downloaded on April 9, 2021.

RESULTS AND DISCUSSION

We counted chromosome numbers for 107 collections of *Verbesina* with 47 of these counts corresponding to species that have not been counted before. Chromosome counts reported in the literature amounted to 175 records representing 90 species. Including the first counts we report here, 137 of the approximately 325 species of the genus now have chromosome number counts.

Most of the species counted were diploid at $2n = 34$; two species, *V. potosina* and *V. sericea*, were $2n = 36$. Tetraploids, although found in some species growing in Mexico, Ecuador, and Venezuela, were more commonly represented in South American species. Only six of the 84 Mexican collections that we counted were polyploid versus 13 of the 23 South American collections. Our three collections of the Mexican species *V. longipes* represented polyploid individuals of which one was hexaploid. Hexaploids are rare in the genus and have been reported only twice previously (Jansen et al., 1984; Strother, 1976). Here we report the first octoploid count for any species of *Verbesina* (observed in an individual of *V. pedunculosa* from Zacatecas, Mexico). Three North American species, *V. crocata*, *V. sericea* and *V. tetraptera* have individuals with either $n = 17$ or $n = 18$ corresponding to the two base chromosome numbers for the genus. *Verbesina callilepis*, *V. laevis* and *V. potosina* have

only counts of $n = 18$. An interesting result is that *Verbesina barclayae* from central Ecuador has counts of $2n = 66$ (one count with fragments), a count not recorded in any other species of the genus.

Below we provide a list of all the species counted for chromosome numbers in the genus with citations where the counts were previously published. For the most part counts are reported as in the original publications.

Chromosome counts in bold are new counts reported in this study. An exclamation mark (!) before a species name indicates a first count for the species. We include the state and country for our collections and country for vouchers used in previous studies.

Verbesina abscondita Klatt. **$2n = 17$ II**, *Panero 2506* (TEX) from a plant collected in Oaxaca, Mexico. Turner and King (1964), Mexico.

Verbesina alternifolia (L.) Britton. $n = 34$, Coleman, 1968; Heiser & Smith, 1955; Parfitt, 1981; Solbrig et al., 1972. All vouchers were collected in the U.S.A.

Verbesina apleura S. F. Blake. $n = 17$, Robinson et al. (1981), Guatemala.

! *Verbesina arborea* Kunth. **$2n = 34$ II**, *Panero 2999* (TEX), Pichincha, Ecuador; **$2n = 34$ II + 0-2 fragments**, *Panero 3025* (QCA), Imbabura, Ecuador.

Verbesina aristata (Ell.) A. A. Heller. $n = 17$, Coleman (1968, 1971, 1974), U.S.A.

Verbesina ayabacensis Sagast. **$2n = ca. 32$ II**, *Panero 2965* (TEX), from a specimen collected in Loja, Ecuador. Robinson & Panero (2006), reported $n = 34$.

Verbesina badilloi Panero. **$2n = 17$ II + 0-7 fragments**, *Panero 2685* (TEX) from a specimen collected in Mérida, Venezuela. $n = 17$, Panero et al. (1993).

! *Verbesina barclayae* H. Rob. **$2n = 33$ II + 0-2 fragments**, *Panero 2954* (QCA); **$2n = 33$ II**, *Panero 2943* (TEX). Both collections were gathered in Azuay, Ecuador.

Verbesina barragana Cuatr. $n = 34$, Jansen et al. (1984), Colombia.

Verbesina bipinnatifida Baker in Martius. $n = 17$, Lopes Moreira and Barbosa Cavalcanti (2020), Brazil.

Verbesina boliviana Klatt. $n = 17$, Robinson et al. (1981), Bolivia.

! *Verbesina brachypoda* S. F. Blake. **$2n = 34$ II**, *Panero 2920* (TEX), Chimborazo, Ecuador; *Panero 2925* (QCA), Cañar, Ecuador.

Verbesina callilepis S. F. Blake. $n = 18$, De Jong & Longpre (1963), Mexico.

! *Verbesina caracasana* B. L. Rob. & Greenm. **$2n = 34$ II**, *Panero 2623* (TEX), Carabobo, Venezuela; *Panero 2636* (TEX), Portuguesa, Venezuela.

Verbesina chapmanii J. R. Coleman. $2n = 34$, Coleman 1974; Strother (2016), Mexico.

! *Verbesina chilapana* B. L. Turner. **$2n = 17$ II + 1 f**, *Panero 2037* (TEX). This specimen was collected in southern Mexico in the state of Guerrero.

Verbesina clausenii L. $n = 17$, Watanabe et al. (2007), Brazil.

! *Verbesina corral-diazii* B. L. Turner. **$2n = 17$ II**, *Panero 2241* (TEX). This specimen was collected in northwestern Durango state, Mexico.

Verbesina costata Fay. $2n = 17$ II, Sundberg et al. (1986), Mexico.

Verbesina crassicaulis S. F. Blake. $n = 17$, Jansen et al. (1984), Colombia.

! *Verbesina crassipes* B. L. Rob. & Greenm. **$2n = 17$ II**, *Panero 2473* (TEX), Oaxaca, Mexico.

Verbesina crocata (Cav.) Less. **$2n = 17$ II**, *Panero 2445* (TEX); **$2n = 17$ II + 0-1 f**, *Panero 2446* (TEX). $2n = 34$, Keil & Stuessy, (1977); $2n = 36$, Turner et al. (1961), Turner et al. (1962). Collections for our counts were gathered in Guerrero, Mexico; published counts based on collections gathered in Mexico.

Verbesina cronquistii B. L. Turner. $2n = 34$, Turner (1985), Mexico.

! *Verbesina curatella* McVaugh. **$2n = 17$ II**, *Panero 2857* (TEX), Jalisco, Mexico.

! *Verbesina cymbipalea* S. F. Blake. **$2n = 17$ II + 1 fragment**, *Panero 2210* (TEX), Durango, Mexico.

! *Verbesina dissita* A. Gray. **$2n = 17$ II**, *Panero 2802* (TEX), Baja California, Mexico.

Verbesina eggersii Hieron. **$2n = 17$ II**, *Panero 2985* (TEX), El Oro, Ecuador; $2n = 34$, Robinson et al. (1981b).

- Verbesina elegans* Kunth. $n = 51 + 11$ f, Jansen et al. (1984), Colombia.
- Verbesina encelioides* (Cav.) Benth. & Hook. f. ex A. Gray. $2n = 17$ II, *Panero* 2171 (TEX), Coahuila, Mexico. $2n = 34$, Badr et al. (1997); Carlquist (1954); Carr et al. (1999); Coleman (1968); Covas & Schnack (1946); DeJong & Longpre (1963); Dematteis et al. (2007); Gupta & Hill (1983); Gupta and Hill (1989); Jose & Mathew (1995); Hunziker et al. (1990); Keil & Stuessy (1977); Keil et al. (1988); Morton (1981); Oberprieler & Vogt (1993); Pinkava & Keil (1977); Powell & Powell (1977a, 1977b); Robinson et al. (1981b); Solbrig et al. (1972); Strother & Panero (2001); Turner & Ellison (1960); Turner et al. (1979); Ward (1983); Weedon & Powell (1980). The most counted species in the genus and invariably $2n = 34$. The species has been introduced to many tropical and subtropical regions of the world. Previously published chromosome counts from collections gathered in Argentina, Bolivia, Dominican Republic, Egypt, India, Mexico, Morocco, and U.S.A.
- Verbesina fastigiata* B. L. Rob. & Greenm. $2n = 17 + 0-1$ f, *Panero* 2423 (TEX), Michoacán, Mexico. $2n = 34$, Solbrig et al. (1972); Strother (1983); Sundberg et al. (1986); Turner & King (1964, as *V. greenmanii*); Turner (1985). Previously published chromosome counts from collections gathered in Mexico.
- ! *Verbesina fayi* B. L. Turner. $2n = 17$ II, *Panero* 2483 (TEX), Oaxaca, Mexico.
- Verbesina gigantea* Jacq. $2n = 34$, Powell & King (1969), Dominican Republic; Robinson et al. (1981b), Guatemala.
- ! *Verbesina glaucophylla* S. F. Blake. $2n = 17$ II, *Panero* 2865 (TEX), Jalisco, Mexico.
- Verbesina glabrata* Hook. & Arn. $2n = 34$, Coleman (1968), Brazil; $2n = 68$, Robinson et al. (1981b), Bolivia.
- ! *Verbesina gracilipes* B. L. Rob. $2n = 17$ II + 2 f, *Panero* 2592 (TEX), Puebla, Mexico.
- ! *Verbesina grayi* (Sch.-Bip.) Benth. & Hook. f. ex Hemsl. $2n = 17$ II, *Panero* 2779 (TEX), Durango, Mexico; *Panero* 2889 (TEX), Jalisco, Mexico.
- ! *Verbesina guatemalensis* B. L. Rob. & Greenm. $2n = 17$ II, *Panero* s. n. (TEX), Chiapas, Mexico.
- Verbesina helianthoides* Michx. $2n = 34$, Heiser & Smith (1955); Coleman (1971); Keil & Stuessy (1977). All collections were gathered in the U.S.A.
- Verbesina heterophylla* (Chapman (A. Gray). $2n = 34$, Coleman (1971, 1974), U.S.A.
- ! *Verbesina hidalgoana* B. L. Turner. $2n = 17$ II, *Panero* 2552 (TEX), Hidalgo, Mexico.
- Verbesina humboldtii* Spreng. $n = 17$, Jansen et al. (1984), Colombia.
- Verbesina hygrophila* Panero & Villaseñor. $2n = 17$ II + 2-3 f, *Panero* 2253 (TEX), Durango, Mexico; Panero et al. (1993).
- Verbesina hypargyrea* B. L. Rob. & Greenm. $2n = 17$ II, *Panero* 2521 (TEX), Chiapas, Mexico. $2n = 34$, Turner et al. (1962).
- Verbesina hypoglauca* Sch. Bip. $2n = 17$ II, *Panero* 2478, $2n = 17$ II + 0-1 f, *Panero* 2550 (TEX), Oaxaca, Mexico. $2n = 17$ II, Powell et al. (1977); Sundberg et al. (1986). $n = 17$ II + 1 f, Strother (1983). Previously published chromosome counts based on collections gathered in Mexico.
- Verbesina hypomalaca* B. L. Rob. & Greenm. $n = 16$, Turner et al., (1961). $n = 17$ II, Strother (1976). *Verbesina hypomalaca* var. *saltillensis*, $n = 17$, Turner (1982). All counts based on collections gathered in Mexico.
- ! *Verbesina jacksonii* B. L. Turner. $2n = 17$ II, *Panero* 2197 (TEX), Durango, Mexico.
- ! *Verbesina juxtlahuacensis* Panero & Villaseñor. $2n = 17$ II, *Panero* 3531 (TEX), Oaxaca, Mexico.
- Verbesina laevis* S. F. Blake. $2n = 36$ II, Carr et al. (1999), Peru.
- Verbesina lanata* B. L. Rob. & Greenm. $2n = 17$ II, Strother (1983), Mexico, Olsen (1980), Colombia.
- Verbesina latisquamata* S. F. Blake. ca. $n = 34$, Robinson et al. (1981b), Ecuador; $2n = 34$ II, Carr et al. (1999), Ecuador.
- ! *Verbesina liebmännii* Sch. Bip. ex Klatt. $2n = 17$ II, *Panero* 2479 (TEX), *Panero* 2488

- (TEX), *Panero* 2489 (TEX). All collections from Oaxaca, Mexico.
- Verbesina lilloi* S. F. Blake. $n = 34$, Rozenblum et al., (1985), Argentina.
- Verbesina lindenii* (Sch. Bip.) S. F. Blake. $n = 17$, Coleman (1968), Robinson et al. (1981b), Turner et al. (1961), Urbatsch (1964). All collections from Mexico and Guatemala.
- Verbesina lindheimeri* B. L. Rob. & Greenm. $n = 17$, Urbatsch (1975), U.S.A.
- ! *Verbesina lloensis* Hieron. ex Sodiro. $2n = 34$ II, *Panero* 3010 (TEX), Pichincha, Ecuador.
- Verbesina longifolia* (A. Gray) A. Gray. $2n = 34$ II + 1-2 f, (some cells with 1 VI + 4 IV + 23 II + 1-2 f), *Panero* 2199 (TEX), Durango, Mexico. $n = 17$, Coleman (1968); $2n = 17$ II, Pinkava & Keil (1977), U.S.A.
- ! *Verbesina longipes* Hemsl. $2n = 34$ II + 1-4 f, *Panero* 2181; $2n = 34 + 0-2$ f, *Panero* 2182; $2n = 51$ II, *Panero* 2361 (TEX). Both counts from specimens gathered in Coahuila, Mexico.
- ! *Verbesina lottiana* B. L. Turner & Olsen. $2n = 17$ II, *Panero* 2868 (TEX), Jalisco, Mexico.
- Verbesina luetzelburgii* Mattf. $2n = 34$, Lopes Moreira et al. (2020), Brazil.
- ! *Verbesina maldonadoensis* H. Rob. & Panero. $2n = \text{ca. } 34$ II, *Panero* 3035 (TEX), Carchi, Ecuador.
- Verbesina mexicana* Cerv. ex DC. $2n = 34$, Zhao (1996), Mexico.
- Verbesina microptera* DC. $2n = 17$ II + 0-1 f, *Panero* 2343 (TEX), Nuevo León, Mexico. $2n = 34$, Turner (1966); Weedon & Powell (1977), Olsen (1979), Zhao & Turner (1993). Previously published chromosome counts based on collections gathered in Mexico and U.S.A.
- Verbesina minuticeps* S. F. Blake. $n = 17 + 1$ f, Robinson et al. (1981b), Ecuador.
- Verbesina montanoifolia* B. L. Rob. & Greenm. $2n = 17$ II + 2 f, *Panero* 2425 (TEX), Michoacán, Mexico; $2n = 17$ II + 1 f, *Panero* 2415, (TEX), Michoacán, Mexico. $n = 17$, Fay (1974), Turner (1985), Mexico.
- ! *Verbesina myriocephala* Sch. Bip. ex Klatt. $2n = 17$ II + 0-1 f, *Panero* 2656 (TEX), Trujillo, Venezuela.
- Verbesina nana* (A. Gray) B. L. Rob. & Greenm. $2n = \text{ca. } 34$, Watson (1973), U.S.A.
- ! *Verbesina negrensis* Steyererm. $2n = 17$ II + 2 f, *Panero* 2703 (TEX), Táchira, Venezuela.
- Verbesina nelidae* Cabrera. $n = 34$, Rozenblum et al. (1985), Argentina.
- ! *Verbesina nelsonii* B. L. Rob. & Greenm. $2n = 17$ II, *Panero* 2463 (TEX); $2n = 17$ II + 2 f, *Panero* 2459 (TEX). The two collections gathered along the Chilapa-Tlapa highway in central Guerrero, Mexico.
- ! *Verbesina neotenoriensis* B. L. Turner. $2n = 17$ II + 1 f, *Panero* 2310 (TEX), Puebla, Mexico.
- Verbesina neriifolia* Hemsl. $2n = 17$ II, *Panero* 2517 (TEX), Chiapas, Mexico. $n = \text{ca. } 17$, Solbrig et al. (1972), Mexico.
- Verbesina occidentalis* (L.) Walter. $n = 17$, Heiser & Smith (1955), Coleman (1968), U.S.A.
- Verbesina oerstediana* Benth. $n = \text{ca. } 17$; $n = 15-17$, Robinson et al. (1981b), Costa Rica.
- Verbesina oligactis* S. F. Blake. $n = 17$, Olsen (1980), Colombia.
- Verbesina oligocephala* I. M. Johnst. $n = 17 + 1-2$ B, Coleman (1966), $n = 17$, Coleman (1968), Mexico.
- Verbesina olsenii* B. L. Turner. $2n = 17$ II, *Panero* 2156 (TEX), Nuevo León, Mexico. $2n = 34$, Turner (1985), Mexico.
- Verbesina oncophora* B. L. Rob. & Greenm. $n = \text{ca. } 17$, Solbrig et al (1972), Mexico.
- Verbesina oreopola* B. L. Rob. & Greenm. $n = 17 + 5$ f, Jansen & Stuessy (1980), Mexico.
- Verbesina ovatifolia* A. Gray. $2n = 17$ II, *Panero* 3096 (TEX), Chiapas, Mexico. $2n = 17$ II + 1 B, Sundberg et al. (1986), Mexico, $2n + 17$ II, Carr et al. (1999), Costa Rica.
- Verbesina pallens* Benth. $n = 17$, Solbrig et al. (1972), Nicaragua.
- ! *Verbesina pantoptera* S. F. Blake. $n = 17$ each pole in dyads, *Panero* 2194 (TEX), Zacatecas, Mexico.

- Verbesina papasquiara* Panero & Villaseñor. **2n** = 17 II, Panero 2264 (TEX), Durango, Mexico. *n* = 17, Panero et al. (1993).
- Verbesina parviflora* (Kunth) S. F. Blake. **2n** = 17 II, Panero 2180 (TEX), Nuevo León, Mexico; **2n** = 17 II, Panero 2204 (TEX), Durango, Mexico.
- ! *Verbesina pauciflora* Small. **2n** = 17 II, Panero 2571 (TEX), Sinaloa, Mexico.
- ! *Verbesina pedunculosa* B. L. Rob. **n** = 17 each pole in dyads, Panero 2195 (TEX); **2n** = 68 II (some cells with 66 II + 1 IV), Panero 2224 (TEX). Panero 2224 is an octoploid individual collected in Zacatecas, Mexico, and represents the highest ploidy level recorded for *Verbesina*.
- Verbesina pellucida* Panero & Villaseñor. **2n** = 17 II, Panero 2746 (TEX), Oaxaca, Mexico. *n* = 17, Villaseñor & Panero (1993).
- Verbesina peninsularis* S. F. Blake. *n* = 17, Coleman (1966), Mexico.
- Verbesina pennellii* S. F. Blake. *n* = 34, Jansen et al. (1984), Colombia.
- Verbesina pentantha* S. F. Blake. **2n** = ca. 32 II, Panero 2960 (QCA), Loja, Ecuador. *n* = 34, Robinson et al. (1981b), Ecuador.
- ! *Verbesina peraffinis* S. F. Blake. **2n** = 17 II, Panero 2624 (MY), Cojedes, Venezuela.
- Verbesina persicifolia* DC. **2n** = 17 II + 3-6 f, Panero 2235 (TEX), San Luis Potosí, Mexico; **2n** = 17 II + 0-1 f, Panero 2351 (TEX), Nuevo León, Mexico. *n* = 17 II, Strother (1983), Mexico.
- Verbesina perymenioides* Sch. Bip. ex Klatt. **2n** = 17 II, Panero 2527 (TEX) Chiapas, Mexico. *n* = 17, Solbrig et al., (1972), Mexico, *n* = 17 II, Strother (1983), Mexico.
- ! *Verbesina petrophila* Brandegees. **2n** = 17 II, Panero 2597 (TEX), Puebla, Mexico.
- ! *Verbesina pietatis* McVaugh. **2n** = 17 II, Panero 2426 (TEX), Michoacán, Mexico.
- ! *Verbesina platyptera* Sch. Bip. ex Klatt. **2n** = 17 II, Panero 3637 (TEX), Colima, Mexico.
- Verbesina pleistocephala* (J. D. Smith) B. L. Rob. *n* = 17 II, Strother (1983), Mexico.
- ! *Verbesina potosina* B. L. Rob. **2n** = 18 II + 0-1 f, Panero 2375 (TEX), San Luis Potosí, Mexico.
- ! *Verbesina pterocarpha* S. F. Blake. **2n** = 17 II, Panero 2556 (TEX), Michoacán, Mexico.
- ! *Verbesina pterocaula* (Moc. & Sessé) DC. **2n** = 17 II, Panero 2291 (TEX), Guerrero, Mexico.
- ! *Verbesina punctata* B. L. Rob. & Greenm. **2n** = 17 II, Panero 2124 (TEX), Chiapas, Mexico.
- Verbesina purpusii* Brandegees. *n* = 17, *n* = 17 II + 2 B, Sundberg et al. (1986), Mexico.
- ! *Verbesina resinosa* Klatt. **2n** = 17 II, Panero 2455 (TEX), Guerrero, Mexico.
- Verbesina rivettii* Hieron. *n* = 34 II, Carr et al. (1999), Ecuador.
- Verbesina robinsonii* (Klatt) Fernald ex B. L. Rob. & Greenm. **2n** = 17 II + 3 f, Panero 2302 (TEX), Hidalgo, Mexico; **2n** = 17 II, Panero 2342 (TEX) San Luis Potosí, Mexico. *n* = 34, Zhao & Turner (1993), Mexico.
- Verbesina rothrockii* B. L. Rob. & Greenm. *n* = 17, Coleman (1968); *n* = ca. 88, Strother (1976). Strother (1976) states that his count based on a collection made in Mexico (Strother 1113, UC) has low pollen stainability (18%) and represents a pentaploid individual.
- Verbesina saubinetioides* S. F. Blake. *n* = 17, Diers (1961), Peru.
- Verbesina seatonii* S. Blake. *n* = 17, Turner et al. (1962), Mexico.
- Verbesina seemannii* Sch. Bip. *n* = 17, Turner & Flyr (1966), Mexico.
- Verbesina semidecurrens* Kuntze. *n* = 17, Robinson et al. (1981b), Bolivia, *n* = 17 II, Carr et al. (1999), Bolivia.
- ! *Verbesina sericea* Kunth & Buché. **2n** = 18 II, Panero 2328 (TEX), Puebla, Mexico; **2n** = 17 II, Panero 2499 (TEX), Oaxaca, Mexico.
- Verbesina serrata* Cav. *n* = 17, Turner et al. (1961), Coleman (1968). *Verbesina serrata* var. *amphichlora* B. L. Rob. & Greenm. *n* = 17, Pinkava & Keil (1977). All collections were gathered in Mexico

- ! *Verbesina simulans* S. F. Blake. **2n = 17 II**, *Panero* 2676 (TEX), Mérida, Venezuela.
- Verbesina sodiroi* Hieron. **2n = 34 II**, *Panero* 2916 (TEX); Cañar, Ecuador; **2n = 34 II**, *Panero* 3013 (QCA), Pichincha, Ecuador. *n* = 34, Robinson et al. (1981b); *2n* = 34 II, Carr et al (1999), Ecuador.
- Verbesina sororia* A. Gray. **2n = 34 II + 1 f**, *Panero* 2341 (TEX), San Luis Potosí, Mexico. *n* = 34, Turner & Flyr (1966), Mexico.
- ! *Verbesina sousae* J. J. Fay. **2n = 17 II + 2-3 f**, *Panero* 6227 (TEX), Chiapas, Mexico.
- ! *Verbesina sphaerocephala* A. Gray. **2n = 17 II**, *Panero* 2420 (TEX), Michoacán, Mexico.
- Verbesina stenophylla* Greenm. *n* = ca. 17, Turner & Flyr (1966), Mexico.
- Verbesina stricta* A. Gray. *n* = 17, Turner et al. (1961), Mexico.
- Verbesina strotheri* Panero & Villaseñor. **2n = 17 II**, *Panero* 2526 (TEX), Chiapas, Mexico. *n* = 17, Panero et al. (1993).
- Verbesina subcordata* DC. *2n* = 34, Schnack & Covas (1947), Argentina, DeMatteis et al. (2007), Paraguay.
- Verbesina sublobata* Benth. *2n* = 34, Solbrig et al. (1972), Costa Rica, Jansen & Stuessy (1980), Nicaragua, Carr et al. (1999), Costa Rica.
- ! *Verbesina synotis* S. F. Blake. **2n = 17 II**, *Panero* 2371 (TEX), Chihuahua, Mexico.
- Verbesina tequilana* J. R. Coleman. **2n = 17 II + 10 f**, *Panero* 2227 (TEX), Jalisco, Mexico. *n* = 17, Keil & Stuessy (1977), Mexico.
- Verbesina tetraptera* L. *n* = 17, Turner et al. (1961), Mexico. *n* = ca. 18, De Jong & Longpre (1963), Mexico.
- Verbesina trilobata* B. L. Rob. & Greenm. **2n = 17 II + 1-2 f**, *Panero* 2334 (TEX); **2n = 17 II**, *Panero* 2325 (TEX), both collections from Puebla, Mexico. *2n* = 34, Turner (1985), Mexico.
- ! *Verbesina trujillensis* Aristeg. **2n = 17 II**, *Panero* 2661 (MY); **2n + 17 II**, *Panero* 2662 (MY). The two collections were gathered in the state of Trujillo, Venezuela.
- Verbesina turbacensis* Kunth. **2n = 17 II**, *Panero* 2462 (TEX), Guerrero, Mexico; **2n = 17 + 2-5 f**, *Panero* 2494 (TEX), Oaxaca, Mexico; **2n = 17 II**, *Panero* 2536 (TEX), Chiapas, Mexico; **2n = 17 II**, *Panero* 2634 (TEX), Portuguesa, Venezuela. *n* = 17, Turner & King (1964), Solbrig et al. (1972), Robinson et al. (1981b). *n* = ca. 17, Robinson et al. (1981b). *2n* = 17 II, Strother (1983). Published counts belong to specimens gathered across the range of the species in Costa Rica, Mexico, and Venezuela.
- ! *Verbesina vallartana* B. L. Turner. **2n = 17 II**, *Panero* 2570 (TEX), Nayarit, Mexico.
- Verbesina virgata* Cav. **2n = 17 II + 3 f**, *Panero* 2757 (TEX), Oaxaca, Mexico; **2n = 17 II**, *Panero* 2250 (TEX), Durango, Mexico; *2n* = 17 II, *Panero* 2448 (TEX), Jalisco, Mexico; **2n = 17 II**, *Panero* 2567 (TEX), Jalisco, Mexico; **2n = 17 II + 1 f**, *Panero* 2303 (TEX), Hidalgo, Mexico; **2n = 17 II**, *Panero* 2392 (TEX), Ciudad de México, Mexico. *n* = 17, Turner et al. (1961), Mexico, Soto-Trejo et al. (2011), Mexico.
- Verbesina virginica* L. *n* = 17, Coleman (1968), Jones (1970), Solbrig et al., (1972). All collections were gathered in the U.S.A.
- Verbesina walteri* L. *n* = 17, Coleman (1971), U.S.A.
- Verbesina warei* L. *n* = 17, Coleman (1968), U.S.A. *n* = ca. 17, Turner & Flyr (1966), U.S.A.
- Verbesina zaragosana* B. L. Turner. *2n* = 34, Zhao (1996), Mexico.

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LITERATURE CITED

- Badr, A., Kamel, E.A., Garcia Jacas, N.,** 1997. Chromosomal studies in the Egyptian flora VI. Karyotype features of some species in subfamily Asteroideae (Asteraceae). *Compositae Newslett.* 30, 15–28.
- Barker, M.S., Arrigo, N., Baniaga, A.E., Li, Z., Levin, D.A.,** 2016a. On the relative abundance of autopolyploids and allopolyploids. *New Phytol.* 210, 391–398. <https://doi.org/10.1111/nph.13698>
- Barker, M.S., Li, Z., Kidder, T.I., Reardon, C.R., Zhao, L., Oliveira, L.O., Scascitelli, M., Rieseberg, L.H.,** 2016b. Most Compositae (Asteraceae) are descendants of a paleohexaploid and all share a paleotetraploid ancestor with the Calyceraceae. *Am. J. Bot.* 103, 1203–1211. <https://doi.org/10.3732/ajb.1600113>
- Carlquist, S.,** 1954. Documented chromosome numbers of plants. *Madroño* 12, 210. <https://www.jstor.org/stable/41422820>
- Carr, G.D., King, R.M., Powell, A.M., Robinson, H.,** 1999. Chromosome numbers in Compositae. XVIII. *Am. J. Bot.* 86, 1003–1013. <https://doi.org/10.2307/2656618>
- Coleman, J.R.,** 1964. A taxonomic revision of sections *Pterophyton*, *Sonoricola* and *Ximenesia* of the genus *Verbesina* (Compositae). Ph.D. thesis, Indiana University, Bloomington.
- Coleman, J.R.,** 1966. A taxonomic revision of section *Sonoricola* of the genus *Verbesina* L. (Compositae). *Madroño* 18, 129–137. <https://www.jstor.org/stable/41423212>
- Coleman, J.R.,** 1966. A taxonomic revision of section *Ximenesia* of the genus *Verbesina* (Compositae). *Amer. Midl. Nat.* 76, 475–481.
- Coleman, J.R.,** 1968. A cytotoxic study in *Verbesina* (Compositae). *Rhodora* 70, 95–102. <https://www.jstor.org/stable/23311412>
- Coleman, J.R.,** 1971. The status of the genus *Actinomeris* Nutt. (= *Verbesina* L.) revealed by experimental hybridization. *J. Torrey Bot. Soc.* 98, 327–331.
- Coleman, J.R.,** 1974. Experimental hybridization of *Verbesina helianthoides*, *V. heterophylla*, *V. aristata*, and *V. chapmanii* (Compositae). *Bot. Gaz.* 135, 5–12.
- Covas, G., Schnack, B.,** 1946. Número de cromosomas en antofitas del Cuyo (República Argentina). *Revista Argent. Agron.* 13, 153–166.
- De Jong, D.C.D., Longpre, E.K.,** 1963. Chromosome studies in Mexican Compositae. *Rhodora* 65, 225–240. <https://www.jstor.org/stable/23306598>
- Dematteis, M., Molero, J., Angulo, M.B., Rovira, A.M.,** 2007. Chromosome studies on some Asteraceae from South America. *Bot. J. Linn. Soc.* 153, 221–230.
- Diers, L.,** 1961. Der Anteil an Polyploidien in den Vegetationsgürteln der Westkordillere Perus. *Zeitsch. Bot.* 49, 437–488.
- Fay, J.J.,** 1974. In: Löve, A., IOPB chromosome number reports XLV. *Taxon* 23, 619–624. <https://www.jstor.org/stable/1218789>
- Guerra, M.,** 1986. Citogenética de angiospermas coletadas em Pernambuco-I. *Genet. Mol. Biol.* 9, 21–40
- Gupta, R.C., Gill, B.S.,** 1983. Cytology of family Compositae of the Punjab plains. *Proc. Indian Nat. Sci. Acad.* B49, 359–370.
- Gupta, R.C., Gill, B.S.,** 1989. Cytology of north and central Indian Compositae. *J. Cytol. Genet.* 24, 95–105.
- Heiser, C.B., Smith, D.N.,** 1965. New chromosome numbers in *Helianthus* and related genera (Compositae). *Proc. Indiana Acad.* 64, 250–253.
- Hunziker, J.H., Escobar, A., Xifred, C.C., Gamarro, J.C.,** 1990. Estudios cariológicos en Compositae. VI. *Darwiniana* 30, 115–121. <https://www.jstor.org/stable/23222521>
- Jansen, R.K., Stuessy, T.F.,** 1980. Chromosome counts of Compositae from Latin America. *Am. J. Bot.* 67, 585–594. <https://doi.org/10.1002/j.1537-2197.1980.tb07688.x>
- Jansen, R.K., Stuessy, T.F., Piedrahita, D., Funk, V.A.,** 1984. Recuentos cromosómicos en Compositae de Colombia. *Caldasia* 14, 7–20. <https://www.jstor.org/stable/23641462>
- Jones, S.B.,** 1970. Chromosome numbers in Compositae. *Bull. Torrey Bot. Club* 97, 168–174. <https://www.jstor.org/stable/2483355>
- Jose, J.C., Mathew, P.M.,** 1995. Chromosome numbers in the south Indian Heliantheae (Compositae). *Compositae Newslett.* 27, 7–10.
- Keil, D.J., Stuessy, T.F.,** 1977. Chromosome counts of Compositae from Mexico and the United States. *Am. J. Bot.* 64, 791–798. <https://doi.org/10.1002/j.1537-2197.1977.tb11921.x>
- Keil, D.J., Luckow, M.A., Pinkava, D.J.,** 1988. Chromosome studies in Asteraceae from the United States, Mexico, the West Indies, and South America. *Am. J. Bot.* 75, 652–668. <https://doi.org/10.1002/j.1537-2197.1988.tb13488.x>
- Leebens-Mack, J.H., Barker, M.S., Carpenter, E.J., Deyholos, M.K., Gitzendanner, M.A., Graham, S.W., et al.,** 2019. One thousand plant transcriptomes and the phylogenetics of green plants. *Nature* 574, 679–685. <https://doi.org/10.1038/s41586-019-1693-2>
- Levin, D.A.,** 1983. Polyploidy and novelty in flowering plants. *Am. Nat.* 122, 1–25. <https://www.jstor.org/stable/2461002>
- Lopes Moreira, G., Barbosa Cavalcanti, T.,** 2020. *Verbesina* (Asteraceae: Heliantheae) do Brasil. *Rodriguesia* 71, e01092018.2020, 1–20. <https://doi.org/10.1590/2175-7860202071108>
- Morton, J.K.,** 1981. Chromosome numbers in Compositae from Canada and the U.S.A. *Bot. J. Linn.*

- Soc. 82, 357–368. <https://www.doi.org/10.1111/j.1095-8339.1981.tb00967.x>
- Oberprieler, C., Vogt, R.** 1993. Chromosome numbers of north African phanerogams. II. Willdenowia 23, 211–238. <https://www.jstor.org/stable/3996806>
- Olsen, J.** 1979. Taxonomy of the *Verbesina virginica* complex (Asteraceae). Sida 8, 128–134. <https://www.jstor.org/stable/23909675>
- Olsen, J.** 1980. In: Löve, A., In: Chromosome number reports LXVII. Taxon 29, 347–367. <https://www.jstor.org/stable/1220313>
- Otto, S.P.** 2007. The evolutionary consequences of polyploidy. Cell 131, 452–462. <https://doi.org/10.1016/j.cell.2007.10.022>
- Panero, J.L., Jansen, R.K.** 1997. Chloroplast DNA restriction site study of *Verbesina* (Asteraceae: Heliantheae). Am. J. Bot. 84, 382–392. <https://doi.org/10.2307/2446011>
- Panero, J.L., Villaseñor, J.L., Medina, R.** 1993. New species of Asteraceae-Heliantheae from Latin America. Contr. Univ. Michigan Herb. 19, 171–193.
- Panero, J.L.** 2007. Compositae: Tribe Heliantheae. In: Kaderit, J. W., Jeffrey, C. (Eds.), Families and Genera of Vascular Plants, vol. VIII, Flowering Plants, Eudicots, Asterales. Springer-Verlag, Berlin, pp. 440–477.
- Panero, J.L., Crozier, B.S.** 2016. Macroevolutionary dynamics in the early diversification of Asteraceae. Mol. Phylogenet. Evol. 99, 116–132. <http://dx.doi.org/10.1016/j.ympev.2016.03.007>
- Parfitt, B.D., Harriman, N.A.** 1981. In: Löve, A., Chromosome number reports LXXI. Taxon 30, 506–517. <https://www-jstor-org.ezproxy.lib.utexas.edu/stable/1220167>
- Pinkava, D.J., Keil, D.J.** 1977. Chromosome counts of Compositae from the United States and Mexico. Am. J. Bot. 86, 1003–1013. <https://doi.org/10.1002/j.1537-2197.1977.tb11909.x>
- Powell, A.M., King, R.M.** 1969. Chromosome numbers in the Compositae: West Indian species. Sida 3, 319–320. <https://www.jstor.org/stable/41966358>
- Powell, A.M., Powell, S.A.** 1977. Chromosome numbers of gypsophilic plant species of the Chihuahuan desert. Sida 7, 80–92. <https://www.jstor.org/stable/41966517>
- Powell, A.M., Powell, S.A.** 1978. Chromosome numbers in Asteraceae. Madroño 25, 160–169. <https://www.jstor.org/stable/41424162>
- Robinson, B.L., Greenman, J.M.** 1899. A synopsis of the genus *Verbesina*, with and analytical key to the species. Proc. Am. Acad. Arts 34, 534–564. <https://doi.org/10.2307/20020930>
- Robinson, H.** 1981a. A revision of the tribal and subtribal limits of the Heliantheae (Asteraceae). Smithsonian Contrib. Bot. 51, 1–102. <https://doi.org/10.5479/si.0081024X.51>
- Robinson, H., Powell, A.M., King, R.M., Weedon, J.F.** 1981b. Chromosome numbers in Compositae XII: Heliantheae. Smithsonian Contrib. Bot. 52, 1–28. <https://doi.org/10.5479/si.0081024X.52>
- Robinson, H., Panero, J.L.** 2006. 61 *Verbesina* L. In: Flora of Ecuador, Compositae-Heliantheae Part II: genera M-Z, Harling, G., Andersson, L. (editors), 77(2), 168–195.
- Rozenblum, E., Waisman, C.E., Hunziker, J.H.** 1985. Estudios cariológicos en Compositae. II. Darwiniana 26, 15–25. <https://www.jstor.org/stable/23218121>
- Schnack, B., Covas, G.** 1947. Estudios cariológicos en antófitas. Haumania 1, 32–41.
- Smith, E.B.** 1975. The chromosome numbers of North American *Coreopsis* with phyletic interpretations. Bot. Gaz. 136, 78–86. <https://www.jstor.org/stable/2473795>
- Solbrig, O.T., Kyhos, D.W., Powell, M., Raven, P.H.** 1972. Chromosome numbers in Compositae VIII: Heliantheae. Am. J. Bot. 59, 869–878. <https://doi.org/10.1002/j.1537-2197.1972.tb10162.x>
- Soltis, D.E., Visger, C.J., Marchant, D.B., Soltis, P.S.** 2016. Polyploidy: Pitfalls and paths to a paradigm. Am. J. Bot. 103, 1146–1166. <https://doi.org/10.3732/ajb.1500501>
- Soto-Trejo, F., Palomino, J., Villaseñor, J.L.** 2011. Chromosome numbers in Asteraceae of the ecological reserve of the Pedregal de San Angel (REPSA), Mexico City, Mexico. Rev. Mex. Biodivers. 82, 383–393. <http://dx.doi.org/10.22201/ib.20078706e.2011.2.486>
- Strother, J.L.** 1976. Chromosome studies in Compositae. Am. J. Bot. 63, 247–250. <https://doi.org/10.1002/j.1537-2197.1976.tb11808.x>
- Strother, J.L.** 1983. More chromosome numbers in the Compositae. Am. J. Bot. 70, 1217–1224. <https://doi.org/10.1002/j.1537-2197.1983.tb12470.x>
- Strother, J.L., Panero, J.L.** 2001. Chromosome studies: Mexican Compositae. Am. J. Bot. 88, 499–502. <https://doi.org/10.2307/2657115>
- Strother, J.L.** 2006. *Verbesina*. In: Flora North America editorial committee, eds. 1993+, Flora North America north of Mexico 22+ vols. New York and Oxford, vol 21, pp. 106.
- Sundberg, S., Cowan, C.P., Turner, B.L.** 1986. Chromosome counts of Latin American Compositae. Am. J. Bot. 73, 33–38. <https://doi.org/10.1002/j.1537-2197.1986.tb09677.x>
- Turner, B.L., Ellison, W.L.** 1960. Chromosome numbers in the Compositae I. Meiotic chromosome counts for 25 species of Texas Compositae including 6 new generic reports. Texas J. Sci. 12, 146–151.
- Turner, B.L., Beaman, J.H., Rock, H.F.L.** 1961. Chromosome numbers in the Compositae. V. Mexican and Guatemalan species. Rhodora 63, 121–129. <https://www.jstor.org/stable/23306348>
- Turner, B.L., Ellison, W.L., King, R.M.** 1961. Chromosome numbers in the Compositae. IV. North American species, with phyletic interpretations. Am. J. Bot. 48, 216–223. <https://doi.org/10.1002/j.1537-2197.1961.tb11628.x>
- Turner, B.L., Powell, A.M., King, R.M.** 1962. Chromosome numbers in the Compositae. IV. Additional Mexican and Guatemalan species.

- Rhodora 64, 251–271. <https://www.jstor.org/stable/23306502>
- Turner, B.L., King, R.M.**, 1964. Chromosome numbers in the Compositae. VIII. Mexican and Central American species. *Southw. Naturalist* 9, 27–39. <https://doi.org/10.2307/3669100>
- Turner, B.L., Flyr, D.**, 1966. Chromosome numbers in the Compositae. X. North American species. *Amer. J. Bot.* 53, 24–33. <https://doi.org/10.1002/j.1537-2197.1966.tb07294.x>
- Turner, B.L., Bacon, J., Urbatsch, L., Simpson, B.**, 1979. Chromosome numbers in South American Compositae. *Am. J. Bot.* 66, 173–178. <https://doi.org/10.1002/j.1537-2197.1979.tb06211.x>
- Turner, B.L.**, 1982. New taxa in *Verbesina* (sect. *Verbesinaria*) from north-central Mexico. *Southw. Naturalist* 27, 345–346. <https://www.jstor.org/stable/3670885>
- Turner, B.L.**, 1985. Revision of *Verbesina* sect. *Pseudomontanoa*. *Plant Syst. Evol.* 150, 237–262. <https://www.jstor.org/stable/23673686>
- Urbatsch, L.E.**, 1974. In: Löve, A., IOPB chromosome number reports XLV. *Taxon* 23, 619–624. <https://www.jstor.org/stable/1218789>
- Urbatsch, L.E.**, 1975. First chromosome number reports for some Compositae. *Southw. Naturalist* 20, 283–285. <https://doi-org.ezproxy.lib.utexas.edu/10.2307/3670451>
- Villaseñor, J.L., Panero, J.L.**, 1993. *Verbesina pellucida* (Asteraceae-Heliantheae), a new species from the Isthmus of Tehuantepec, Oaxaca, Mexico. *Contr. Univ. Michigan Herb.* 19, 93–95.
- Ward, D.E.**, 1983. Chromosome counts from New Mexico and southern Colorado. *Phytologia* 54, 302–309.
- Watanabe, K., Yahara, T., Hashimoto, G., Nagatani, Y., Soejima, A., Kawahara, T., Nakazawa, M.**, 2007. Chromosome numbers and karyotypes in Asteraceae. *Ann. Missouri. Bot. Gard.* 94, 643–655. <https://www.jstor.org/stable/40035659>
- Watson, T.J.**, 1973. Chromosome numbers in Compositae from the southwestern United States. *Southw. Naturalist* 18, 117–124. <https://www.jstor.org/stable/3670413>
- Weedin, J.F., Powell, A.M.**, 1980. In: Löve, A., Chromosome number reports LXIX. *Taxon* 29, 703–730. <https://www.jstor.org/stable/1220359>
- Zhang, C., Huang, C.-H., Liu, M., Hu, Y., Panero, J.L., Luebert, F., Gao, T., Ma, H.**, 2021. Phylo-transcriptomic insights into Asteraceae diversity, polyploidy, and morphological innovation. *J. Integr. Plant Biol.* <https://doi.org/10.1111/ijpb.13078>
- Zhao, Z., Turner, B.L.**, 1993. Documented chromosome numbers: 3 Miscellaneous U.S.A. and Mexican species, mostly Asteraceae. *Sida* 15, 649–653. <https://www.jstor.org/stable/41967065>
- Zhao, Z.**, 1996. Documented chromosome numbers 1996: 2. Miscellaneous U.S.A. and Mexican species, mostly Asteraceae. *Sida* 17, 259–263. <https://www.jstor.org/stable/41960975>