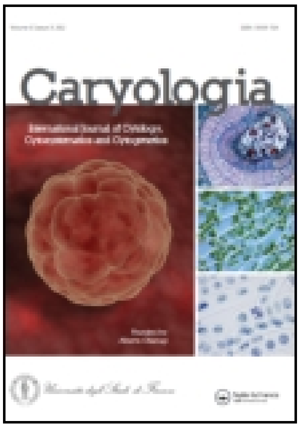

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Chromosome studies of some species of Vernonanthura and Vernonia (Asteraceae, Vernonieae)

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Chromosome studies of some species of *Vernonanthura* and *Vernonia* (Asteraceae, Vernonieae)

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The chromosome numbers of 18 populations belonging to 10 species of *Vernonanthura* H. Rob. and one species of *Vernonia* Schreb. (Vernonieae, Asteraceae) from South America were determined. First chromosome counts are presented for three taxa: *Vernonanthura lucida* (Less.) H. Rob. (n = 17, 2n = 34), *V. oligactoides* (Less.) H. Rob. (n = 17, 2n = 34) and *V. pseudolinearifolia* (Hieron.) Vega et Dematt. (2n = 34). In addition, a new cytotype is reported for *Vernonia echioides* Less. (2n = 34), a widely distributed species in which only tetraploid populations (n = 34, 2n = 68) were recorded to date. The chromosome numbers found in *Vernonanthura amplexicaulis* (R.E.Fr.) H. Rob. (2n = 34), *V. chamaedrys* (n = 17, 2n = 34), *V. ferruginea* (Less.) H. Rob. (2n = 34), *V. loretensis* (Hieron.) H. Rob. (2n = 34), *V. nudiflora* (Less.) H. Rob. (2n = 34), *V. squamulosa* (Hook. et Arn.) H. Rob. (n = 17, 2n = 34), *V. tweediana* (Baker) H. Rob. (2n = 34) and *Vernonia echioides* (n = 34) are in agreement with previous records for these species. All the species of *Vernonanthura* and *Vernonia* analyzed here showed basic number x_2 = 17 and almost all them were diploid with 2n = 34. The single exception was *Vernonia echioides* which showed diploid (2n = 34) and tetraploid (2n = 68) populations.

Keywords: base number; meiosis; plant chromosomes; polyploidy; Vernonieae

Introduction

Vernonieae Cass. (Asteraceae) comprises 124 genera and 1500 species concentrated around the tropical and subtropical regions of America, Asia and Africa. The members of the tribe are grouped into 21 different subtribes based on inflorescence pattern, persistence of phyllaries, anther appendages, style base, achene crystals, pollen morphology and chemical composition (Keeley and Robinson 2009).

The subtribe Vernoniinae Less. constitutes one of the largest groups within the Vernonieae, including nine genera and approximately 110 species. This group comprises many species previously placed into the huge genus *Vernonia* Schreb., whose status and delimitation are still widely discussed (Keeley and Turner 1990; Keeley and Jansen 1994; Keeley et al. 2007; Robinson 2007). According to the traditional infrageneric classification of *Vernonia*, most of de South American species belong to the section *Lepidaploa* (Cass.) DC. (Baker 1873; Bentham 1873). In a recent classification of the New World Vernonieae suggested by Robinson (1987, 1988, 1990, 1993, 1999), almost all the species of this section were segregated to 16 new genera, restricting the genus *Vernonia* almost exclusively to North America. However, according to Hind (1993), the elevation of the traditional sections and subsections to generic level is premature and does not resolve the taxonomic problems of *Vernonia.*

Almost all the taxonomic treatments on the tribe Vernonieae have been based on external morphological features such as inflorescence pattern, florets numbers and shape and number of phyllaries (Gleason 1906; 1923; Cabrera 1944; Jones 1979, 1981; Stutts 1988). Chromosome numbers have been not considered in the proposed classifications and less than 20% of the New World species have been analyzed (Dematteis 2002). However, the cytological data available show that chromosomes are widely variable in number and morphology, which suggest that they can be useful in taxonomic and evolutionary studies (Angulo and Dematteis 2009). According to Jones (1979), polyploids are very frequent in the New World and the most common basic chromosome number is x_2 = 17, while the Old World species present usually basic number x_1 = 9 and x_1 = 10 and polyploids are not frequently observed. Nevertheless, the more recent chromosome studies in New World species of the tribe have found other basic chromosome numbers such as x_1 = 9, x_1 = 10, x_1 = 12, x_1 = 14, x_2 = 15, x_2 = 16, x_2 = 17, x_2 = 18, x_2 = 19 and x_2 = 31 (Turner 1981; Ruas et al. 1991; Dematteis 1998; Mansanares et al. 2002; Angulo and Dematteis 2009, 2012; Salles de Melo et al. 2010). The ancestral basic chromosome number in the Vernonieae is considered to be x_1 = 9 or x_1 = 10, as reported for African and Asian species of the tribe (Jones 1979). Higher basic chromosome numbers would be

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derived through a combination of polyploidy and aneuploidy. Considering lower (primary) base numbers, it is interesting to note that most genera of Liabeae and Lactuceae include many taxa with x_1 = 9 and x_2 = 18, but few bearing x_1 = 10 and x_2 = 17 (Kadereit and Jeffrey 2007) suggesting that numbers based on x_1 = 9 may represent most ancestral taxa in a general sense within the family.

Vernonanthura H. Rob. was established to separate the taxa earlier arranged under *Vernonia* sect. *Lepidaploa* subsect. *Paniculatae* Benth. & Hook. This group consists of about 90 species distributed from southern Mexico to central Argentina, but mostly concentrated in southeastern Brazil (Robinson 1999; Vega and Dematteis 2011a). In southern South America, the species are mainly concentrated in the mountains of northwest Argentina and the fields and forests of Paraguay and eastern Argentina (Cristobal and Dematteis 2003). Members of *Vernonanthura* are shrubs or small trees having thyrsoid to pyramidal inflorescences, with individual branches cymose to corymbose (Robinson 1992). The pollen grains are spheroidal to prolate-spheroidal, sub-echinolophate, 3-colporate, with long colpi, pore lalongate, tectum continuous, comprising lophae surrounding irregular depressions. The tectum surface is densely microperforate with prominent spines on the ridges (Dematteis and Pire 2008; Vega and Dematteis 2011a).

Vernonanthura is a well-defined group based on pollen morphology and external morphological features (Robinson 1999; Vega and Dematteis 2011b). However, there are still some species included in *Vernonia sensu lato* whose status and taxonomic position remains unclear (Robinson 1999; Dematteis 2006). Among them could be cited two South American species, *Vernonia incana* Less. and *V. echioides* Less. (Robinson 1999; Dematteis 2010).

Despite the tribe being widely variable in chromosome numbers, *Vernonanthura* and *Vernonia* are relatively homogeneous with basic chromosome number x_2 = 17. Previous reports show that almost all the species are diploid with 2*n* = 34, while polyploids are not frequent, and only two tetraploid taxa have been reported, one per genus (Hunter 1964; Jones 1979, 1982; Galiano and Hunziker 1987; Stutts 1988; Ruas et al. 1991; Dematteis 1996, 1997, 2002; Dematteis and Fernandez 1998, 2000; Oliveira et al. 2007; Salles de Mello et al. 2010).

Due to wide variability in chromosome numbers found in tribe Vernonieae, the lack of cytological data and its relevance in taxonomic treatments, our main purpose was to determine the chromosome numbers of some South American species of *Vernonanthura* and *Vernonia*.

Material and methods

The specimens were obtained from natural populations in Argentina, Bolivia and Uruguay. The source of examined species is presented in Table 1. Voucher specimens are deposited at the herbarium of Instituto de Botánica del Nordeste (CTES).

The meiotic analysis was realized on flower buds previously fixed in ethanol and lactic acid in proportion 5:1 v:v and then stored in ethanol 70% at 4°C. Squashes of pollen mother cells were made using acetic carmine 3%. For mitotic studies, meristematic tissues were pretreated with 8-hydroxiquinoline 0.002 M for 4 hours, fixed in ethanol and acetic acid in proportion 3:1 v:v and stained following Feulgen's technique. Permanent microscope slides were prepared by mounting in Euparal. In all samples at least 20 counts of 7–10 individuals were made to verify the observations.

Results

The chromosome numbers of 18 populations belonging to 10 taxa of *Vernonanthura* and one species of *Vernonia* from South America were determined. The analyzed taxa and their chromosome numbers are given in Table 1. First chromosome counts are presented for three taxa: *Vernonanthura lucida* (*n* = 17, 2*n* = 34), *V. oligactoides* (*n* = 17, 2*n* = 34) and *V. pseudolinearifolia* (2*n* = 34). In addition, a new cytotype is reported for *Vernonia echioides* (2*n* = 34), a widely distributed species in which only tetraploid populations (2*n* = 68) have been recorded at the present (Figure 1).

Somatic chromosome numbers were determined for *Vernonanthura amplexicaulis* (2n = 34), *V. chamaedrys* (2n = 34), *V. ferruginea* (2n = 34), *V. loretensis* (2n = 34), *V. lucida* (2n = 34), *V. nudiflora* (2n = 34), *V. oligactoides* (2n = 34), *V. squamulosa* (2n = 34), *V. tweediana* (2n = 34), *V. pseudolinearifolia* (2n = 34) and *Vernonia echioides* (2n = 34, 2n = 68). Despite all the species showing the same chromosome number, some differences in chromosome size and morphology were observed (Fig. 1A–K). In general, the species presented a greater proportion of metacentric chromosomes, accompanied by a lesser number of submetacentric pairs. Chromosome numbers in meiosis were determined for *Vernonanthura chamaedrys* (n = 17), *V. lucida* (n = 17), *V. oligactoides* (n = 17), *V. squamulosa* (n = 17) and *Vernonia echioides* (n = 34). The meiotic behavior was almost regular in all stages of meiosis with exclusive formation of bivalents at diakinesis (Fig. 1L–O). A low percentage of chromosomes outside plate and some laggard chromosomes were observed. In *Vernonanthura chamaedrys*, *V. squamulosa* and *Vernonia echioides*, less than 1.00% of cells analyzed showed chromosomes outside plate and some laggard chromosomes. *Vernonanthura lucida* presented 3.40% of cells with chromosomes outside plate, 1.00% of laggard chromosomes and also showed 0.50% of bridges at telophase I.

Discussion

All the species of *Vernonanthura* and *Vernonia* analyzed here showed basic chromosome number x_2 = 17 and almost all them were diploid with 2*n* = 34, excluding *Vernonia echioides* which showed also a tetraploid

Table 1. Meiotic (*n*) and somatic (2*n*) chromosome numbers observed in specimens of *Vernonanthura* and *Vernonia* analyzed.

Species	n	2*n*	Location and voucher specimens
Vernonanthura H. Rob.			
V. amplexicaulis (R.E.Fr.) H. Rob.		34	Bolivia. Department Santa Cruz. Province Ñuflo de Chavez. 11.6 km N of San Javier, on the road to the curtiembre. *Dematteis et al. 3846* (CTES, SI).
V. chamaedrys (Less.) H. Rob.	17	34	Argentina. Corrientes. Department San Roque, Santa Lucia river, low moist soils near the river. *Dematteis el al. 2754* (CTES).
V. chamaedrys (Less.) H. Rob.		34	Argentina. Corrientes. Department Ituzaingó. Provincial route 34, to 4 km S of National route 12. *Vega et al. 7* (ASU, CTES).
V. ferruginea (Less.) H. Rob.		34	Bolivia. Department Santa Cruz. Province Ñuflo de Chavez. 12 km W of San Javier. *Dematteis et al. 3818* (CTES, SI).
V. loretensis (Hieron.) H. Rob.		34	Argentina. Misiones. Department San Ignacio. San Ignacio, house of Horacio Quiroga. *Dematteis et al. 3046* (CTES).
[*]*V. lucida* (Less.) H. Rob.	17	34	Argentina. Misiones. Department San Pedro. National Park Moconá, Embarcadero, coast of the Uruguay river. *Dematteis et al. 3095* (CTES, G, MBM).
V. nudiflora (Less.) H. Rob.		34	Uruguay. Department Rivera. Tranqueras, high lands near Arroyo Sauzal, on the route 30. *Dematteis et al. 3721* (CTES).
[*]*V. oligactoides* (Less.) H. Rob.	17	34	Argentina. Misiones. Department General Manuel Belgrano. Campina de Americo. *Dematteis et al. 3077* (CTES).
[*]*V. pseudolinearifolia* (Hieron.) A. J. Vega & Dematt.		34	Uruguay. Department Rivera. 13 km E of Tranqueras, on the road to Paso de Ataques. *Dematteis et al. 3710* (CTES).
[*]*V. pseudolinearifolia* (Hieron.) A. J. Vega & Dematt.		34	Uruguay. Department Tacuarembó. Gruta de los Cuervos, ca. 20 km NW of Tacuarembó. *Dematteis et al. 3784* (CTES).
V. squamulosa (Hook. & Arn.) H. Rob.		34	Argentina. Jujuy. Department Santa Barbara. 31 km N of Santa Clara, on the road to El Fuerte. *Dematteis et al. 2967* (CTES, ASU).
V. squamulosa (Hook. & Arn.) H. Rob.		34	Argentina. Jujuy. Department El Carmen. Dique La Cienaga, on the forest border. *Dematteis et al. 2998* (CTES).
V. squamulosa (Hook. & Arn.) H. Rob.		34	Argentina. Jujuy. Department El Carmen. Pozo Verde. *Sato et al. 25* (CTES).
V. squamulosa (Hook. & Arn.) H. Rob.	17		Argentina. Salta. Department Santa Victoria. On the access road to Los Toldos. *Vega et al. 12* (CTES).
V. tweediana (Baker) H. Rob.		34	Paraguay. Department Canindeyú. Ñandurokai, disturbed cerrado, sandy soils. *Dematteis et al. 2854* (CTES, FCQ, G).
Vernonia Schreb.			
[+]*V. echioides* (Less.) H. Rob.		34	Argentina. Corrientes. Department Alvear. 5.5 km N of Alvear, on the road to Santo Tomé. *Dematteis et al. 4135* (CTES).
V. echioides (Less.) H. Rob.	34		Argentina. Misiones. Department Capital. Low moist soils near Arroyo Zaimán. *Dematteis et al. 3030* (CTES).
V. echioides (Less.) H. Rob.		68	Uruguay. Department Rivera. 1.6 km S de Masoller, on the road to Tranqueras, route 30. *Dematteis et al. 3736* (CTES).

[*]First chromosome count for the taxon.
[+]New cytotype for the taxon.

cytotype (2*n* = 68). These results are in agreement with the cytological data available for both genera, which shows mostly diploid taxa with base chromosome number x_2 = 17 (Hunter 1964; Jones 1974, 1979, 1982; Galiano and Hunziker 1987; Stutts 1988; Ruas et al. 1991; Dematteis 1996, 1997, 2002; Dematteis and Fernandez 1998; Oliveira et al. 2007; Salles de Mello et al. 2010). Within the Vernonieae, the basic chromosome number x_2 = 17 is most frequent in subtribe Vernoniinae. However, the remaining South American subtribes of Vernonieae show other basic numbers such as x_1 = 10, x_1 = 14, x_2 = 15 and x_2 = 16 (Angulo and Dematteis 2012). One of the more frequent numbers in New World species is x_2 = 16, which is present in all the species of the large genus *Lessingianthus* H. Rob. Among the New World genera, this group presents the greatest proportion of polyploids known, with over 82.5% out of a total of 39 taxa (Ruas et al. 1991; Oliveira et al. 2007; Angulo and Dematteis 2012).

In Neotropical floras, several species have not been analyzed from the cytological viewpoint because of their restricted distribution. Among the species analyzed for the first time, *Vernonanthura oligactoides* is widely distributed in the south of Brazil (Mato Grosso do Sul, Paraná, Santa Catarina, São Paulo), the east of Paraguay (Alto Paraná, Amambay, Canindeyú) and the eastern extreme of Argentina (Vega and Dematteis 2008). However, *V. lucida* is a rare species that usually grows on stony fields from southern Brazil, Paraguay and northeastern Argentina, while *V. pseudolinearifolia* is an endemic taxon of a restricted area in northern Uruguay (Vega and Dematteis 2011b).

The chromosome counts determined in *Vernonanthura amplexicaulis*, *V. ferruginea*, *V. loretensis* and *V. squamulosa* (2*n* = 34) agree with the studies of Dematteis (1998, 2002). The chromosome number found in *V. tweediana* is in concordance with those reported by Galiano and Hunziker (1987) and Oliveira et al. (2007)

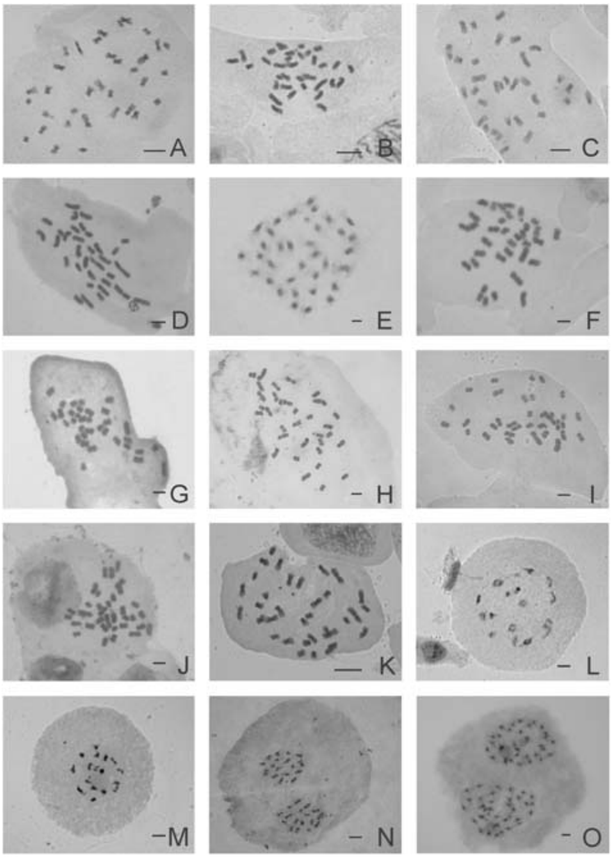

Figure 1. Somatic and meiotic chromosomes of *Vernonanthura* and *Vernonia*, showing differences in chromosome size among the species. (A) *Vernonanthura amplexicaulis*, 2*n* = 34; (B) *V. lucida*, 2*n* = 34; (C) *V. nudiflora*, 2*n* = 34; (D) *V. squamulosa*, 2*n* = 34; (E) *V. ferruginea*, 2*n* = 34; (F) *V. pseudolinearifolia*, 2*n* = 34; (G) *V. oligactoides*, 2*n* = 34; (H) *V. loretensis*, 2*n* = 34; (I) *V. tweediana*, 2*n* = 34; (J) *V. chamaedrys*, 2*n* = 34; (K) *Vernonia echioides*, 2*n* = 34; (L) *Vernonanthura squamulosa*, diakinesis with 17 II; (M) *V. lucida*, diakinesis with 17 II; (N) *V. chamaedrys*, diakinesis with 17 II; (O) *Vernonia echioides*, PII with 34–34 chromosomes.

for specimens from Argentina and Brazil respectively. *Vernonanthura chamaedrys* has been analyzed previously by several authors and all they showed *n* = 17 or 2*n* = 34 (Stutts 1988; Dematteis and Fernandez 1998; Dematteis 2002), which agree with the results obtained here.

Vernonanthura nudiflora has been one of the most studied species of the genus and almost all the reports indicate 2*n* = 34 (Jones 1974; Bernardello 1986; Stutts 1988; Ruas et al. 1991; Dematteis 1997; Dematteis and Fernandez 1998; Angulo and Dematteis 2009). However these results disagree with a prior analysis carried out by Covas and Hunziker (1954) on a population from western Argentina that recorded *n* = 16 (2*n* = 32) for this species. Although this chromosome number report could be attributed to incorrect species identification, it is most likely due to the small size of plant chromosomes, which in some cases contributes to the disparity of reported chromosome numbers (Guerra 1988).

The single species of the genus *Vernonia* analyzed here was *V. echioides*, which is tetraploid with *n* = 34 (Dematteis 2002). In this study we analyzed three populations of *V. echioides*, two of them were tetraploid (*n* = 34, 2*n* = 68), while the other one was diploid with 2*n* = 34. Although this constitutes the first record of the diploid cytotype (2*n* = 34) for *V. echioides*, several species of Vernonieae from South America have populations with different ploidy levels or cytotypes. For the genus *Chrysolaena* H. Rob., have been reported three species with different cytotypes. *Chrysolaena cognata* (Less.) Dematt. and *C. flexuosa* (Sims) H. Rob. has diploid (2*n* = 20), tetraploid (2*n* = 40) and hexaploid (2*n* = 60) populations, while *C. platensis* (Spreng.) H. Rob. shows from diploid to octoploid cytotypes (Dematteis 2009). Within the genus *Lessingianthus*, which presents a basic number of x_2 = 16, diploid and tetraploid cytotypes have been found in *L. rubricaulis* (Humb. et Bonpl.) H. Rob. and *L. saltensis* (Hieron.) H. Rob. (Dematteis 2002; Angulo and Dematteis 2009). However, in *Vernonia sensu stricto* there are not previous records of species with different cytotypes and consequently this constitutes the first chromosome analysis that reports diploid (2*n* = 34) and tetraploid (2*n* = 68) populations for the genus.

Some genera of Vernonieae show a positive correlation between the size of the pollen grains and the chromosome number. In *Lessingianthus* H. Rob., the species with high ploidy levels always has large pollen grains (Dematteis and Pire 2008; Angulo and Dematteis 2010). In *Vernonia* this relationship has not been examined, however in *Vernonanthura* the pollen size of the diploid taxa seems to be similar to the tetraploid species. Almost all the species of *Vernonanthura* are diploid with 2*n* = 34, excluding *V. pinguis* (Griseb.) H. Rob., which constitutes the single tetraploid species of the genus with 2*n* = 68 (Dematteis 1998, 2002). However, according a recent analysis of the pollen morphology of *Vernonanthura* (Vega and Dematteis 2011a), the pollen size of *V. pinguis* is similar to or smaller than that the diploid species and consequently a certain correlation between these two features cannot be established for the genus.

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