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Chromosome studies in *Schoenocaulon* (Liliaceae: Melanthieae) a relict genus

DAWN FRAME*

Resumen. Se presentan los resultados de los recuentos cromosómicos de ocho taxa, representantes de siete especies de *Schoenocaulon* (Liliaceae: Melanthieae), un género principalmente mexicano. Una especie (*S. tenorioi*) presenta una cadena de tres cromosomas, cuyo posible origen se discute. Se describe brevemente la morfología cariotípica general y, junto con el número cromosómico, se considera en el contexto de otras Liliaceae cercanamente relacionadas. Además, se presentan hipótesis de tendencias evolutivas amplias, basadas en la evolución cromosómica de *Schoenocaulon*, con miras hacia estrategias futuras para la protección y conservación de estas plantas.

Palabras clave: cromosomas, *Schoenocaulon*, Liliaceae, evolución, conservación

Abstract. Results of chromosome counts of eight taxa representing seven species of *Schoenocaulon* (Liliaceae: Melanthieae), a primarily Mexican genus are presented. One species (*S. tenorioi*) shows a chain of three chromosomes, the possible origin of which is discussed. The general karyomorphology of *Schoenocaulon* chromosomes is briefly described and along with chromosome number considered in the context of closely related Liliaceae. Further, hypotheses of broad evolutionary trends based on *Schoenocaulon* chromosome evolution are developed, with an eye to future strategies for this plant's protection and conservation.

Key words: chromosomes, *Schoenocaulon*, Liliaceae, evolution, conservation.

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Introduction

The genus *Schoenocaulon* (Melanthieae) is a natural group of bulbo-rhizomatous perennial herbs distinguished from other members of its tribe by a spike-like racemose inflorescence and small flowers usually having exerted stamens. Restricted to the New World, it grows from southwestern United States to Andean South America; there is one disjunct species in Florida. The center of diversity for *Schoenocaulon* is Mexico. With the notable exceptions of *S. officinale* and *S. ghiesbreghtii*, the species are narrow endemics in undisturbed sites and slow growing, colonial plants. Several years of growth from seed are required before reaching sexual maturity. In fact, the length of time to sexual maturity from seed is unknown and may vary from species to species, but in any case is likely to be on the order of a minimum of five years growth. This fascinating plant is often overlooked by people in general and even by collectors because of its grass-like appearance, which allows it to blend anonymously into the landscape. For this reason, *Schoenocaulon* is often poorly represented in herbarium collections and few people have attempted its study. *Schoenocaulon* belongs to Melanthieae, a tribe considered by this and other authors (*e.g.* Krause, 1930; Takhtajan, 1969; Hutchinson, 1973) to be a basal, archaic lily group.

After field observation and collection, undertaken as part of revisionary studies of this genus, it has become clear that *Schoenocaulon* is a relict liliaceous genus that frequently occupies stable little-changing habitats. Presently in Mexico, plants are usually restricted to very steep canyons or rocky ledges where grazing animals cannot reach. Data from old herbarium specimens suggests that many species formerly had a wider range and plants were more numerous, but both range and number have been reduced because of human activities and widespread animal grazing. Some *Schoenocaulon* species are today represented by only a few populations (*e.g.* *S. pringlei*, *S. rzedowskii*) and despite new localities sometimes being discovered, it is evident that most species are very fragile and risk extinction related to habitat change.

There are published reports on the cytology of only two species of *Schoenocaulon* out of a total of 24 recognized species (Frame *et al.*, 1999); de Zerpa (1951) found that *S. officinale* had $2n=16$ and Cave (1967) reported $n=8$ for *S. dubium*. The remaining genera belonging to the Melanthieae (*Veratrum*, *Zigadenus*, *Stenanthium*) are better known cytologically. *Veratrum*, with approximately the same number of species as *Schoenocaulon* but these more widespread, has ploidy differences among and within species, *i.e.*, *V. nigrum* and *V. oxysepalum*, as well as one species (*V. stamineum*) that has $2n=32$ plus two chromosome fragments (Zimmerman, 1958; Federov, 1969; Moore, 1971). Preece's unpublished dissertation was a detailed cytological study of *Zigadenus* (1956), and revealed both karyotype and ploidy differences among the approximately 16 species. By far the smallest genus of the tribe with four species, *Stenanthium* is not without chromosome diversity; *S. occidentale* is reported to have eight pairs of relatively small chromosomes whereas *S. robustum* was found to have 10 pairs (Miller, 1930; Sato, 1942). Moreover, four satellite chromosomes were observed in the latter species (Sato, 1942). In Cave's perceptive study of lily chromosomes, she

comments (1970, p. 45): "Evolution within the tribe must have taken place by multiplication of the basic set of chromosomes as well as by increase in the basic number through fragmentation and recombination of the original 8".

Methods

Freshly collected young inflorescences were placed in either Carnoy's (1:3:1 chloroform: absolute ethanol: glacial acetic acid) or Farmer's (3:1 absolute ethanol: glacial acetic acid) solutions. After a minimum of 36 hrs, the fixed material was transferred to a storage solution of 70% ethanol. The preserved material was treated, examined and photographed at the Jodrell laboratory, Royal Botanic Gardens, Kew. For chromosome counts from pollen mother cells, anthers were dissected from the flowers and squashes were made in 1.8% aceto-orcein. For chromosome counts from root tips, germinating seeds with actively growing root tips were pretreated in μ -bromonaphthalene for 24 hrs at 4°C, then fixed in 1:3 ethanol: glacial acetic acid (v/v) at 4°C for at least 30 mins; thereafter, the material may be stored at 4°C until use. The fixed material was hydrolyzed in 1N HCl at 60°C for 10 mins (after this treatment the root tips usually became detached from the parent seed) followed by staining with Feulgen solution in the dark at room temperature for at least 30 minutes. The stained root tips were counterstained with 1.8% aceto-orcein, and squashes made. Coverslips were removed in liquid CO₂ and the slides dehydrated in absolute ethanol before mounting in Euparal. Photographs were taken using a Zeiss photomicroscope. A herbarium specimen of each collection used in this study is deposited at MEXU.

Results and discussion

Results of the chromosome counts are given in table 1 and figure 1 shows results for selected species. Eight taxa representing seven species of *Schoenocaulon* were examined; in all cases the number was found to be $2n = 16$ (Table 1; Fig. 1). This is in agreement with the findings of de Zerp (1951), Cave (1967) and Preece (1956, unpublished counts for *S. texanum* and *S. drummondii* = *S. ghiesbreghtii*). Chromosome size was on the order of 1.5 - 3 μ m (Fig. 1), and the chromosomes are considered small. For this reason, other methods of karyotype analysis such as Giemsa banding were not undertaken. Six of the species formed regular bivalents. However, a newly described species from near Rodeo, Puebla, *S. tenorioi* exhibited a chain of three chromosomes (Fig. 1e), the possible result of a heterozygous reciprocal translocation or adhesions between the chromosomes (see Price, 1956). This population is usually fertile. A similar chain of three chromosomes is also present in pollen mother cells of a population of the same species collected up the hill from the first at Cerro Verde (Fig. 1f). Conversely, pollen from this population is frequently aborted. The consequence of a simple case of heterozygous interchange, with pairing between two pairs of

Table 1. Chromosome counts in *Schoenocaulon*

Species and collection No.	Pollen mother cell	Root tip
<i>S. calcicola</i> , DF 275	2n = 16	2n = 16
<i>S. caricifolium</i> var. <i>caricifolium</i> , DF 288 & DF 283	2n = 16	2n = 16
<i>S. caricifolium</i> var. <i>oaxacense</i> , DF 289	2n = 16	
<i>S. comatum</i> , DF 347	2n = 16	
<i>S. ghiesbreghtii</i> , DF 254 & DF 386	2n = 16	
<i>S. intermedium</i> , DF 287	2n = 16	2n = 16
<i>S. jaliscense</i> var. <i>jaliscense</i> , DF 406	2n = 16	
<i>S. tenorioi</i> , DF 344 & 345	2n = 16	

homologous segments, would either be two pairs or a chain of three and a univalent (Darlington, 1937). It was not possible to discern whether a univalent was present in the material I studied because of the small size of the chromosomes. Interchange heterozygotes are semi-sterile due to the non-viability of those gametes that lack one of the chromosome segments present in the parental complement (Darlington, 1937). Notwithstanding this interesting correlation, it was beyond the scope of the present study to determine if the observed chain was the result of a genetic interchange or due to “sticky” adhesions.

All species of *Schoenocaulon* that I studied have heteropycnotic segments visible in the interphase nucleus (Fig. 1b) similar to those reported by Tanaka and Tanaka (1979) for *Chionographis* (Liliaceae: Helonieae), a genus belonging to a tribe closely related to Melanthieae. Albeit that *Schoenocaulon* chromosomes are morphologically similar with respect to size and general appearance to those of *Chionographis*, they differ in number and in having a distinct kinetochores (Fig. 1a-c, e-f) although depending upon the material and how it was treated, the kinetochores may not be apparent (Fig. 1d).

The most remarkable fact to emerge from this study is the homogeneity of *Schoenocaulon* chromosomes in terms of number, size and ploidy. This differs with what has been found in other members of the tribe. And, at least with respect to chromosome number, was anticipated by Zimmerman (1958) on the basis of the few counts available to him: “...that while the genus *Veratrum sensu lato* may be less diverse than *Zigadenus sensu lato*, it is less homogeneous than *Schoenocaulon*.”

Schoenocaulon may have been abundant locally in the recent past as evinced by the observation that in the 1980's *S. macrocarpum* was found growing in abundance on Cerro Viga, Coahuila, presumably because the site was protected from humans and grazing animals. Today, most species of *Schoenocaulon* are extremely rare, confined to the margins of what was likely their previous habitat. To the extent that karyotype diversity often provides indications of on-going speciation events, it would appear that the relative homogeneity of *Schoenocaulon*'s chromosome morphology and number mirror its relative evolutionary stasis. Present populations of *Schoenocaulon* are very isolated (partly as a result of habitat disturbance) and this may have further contributed

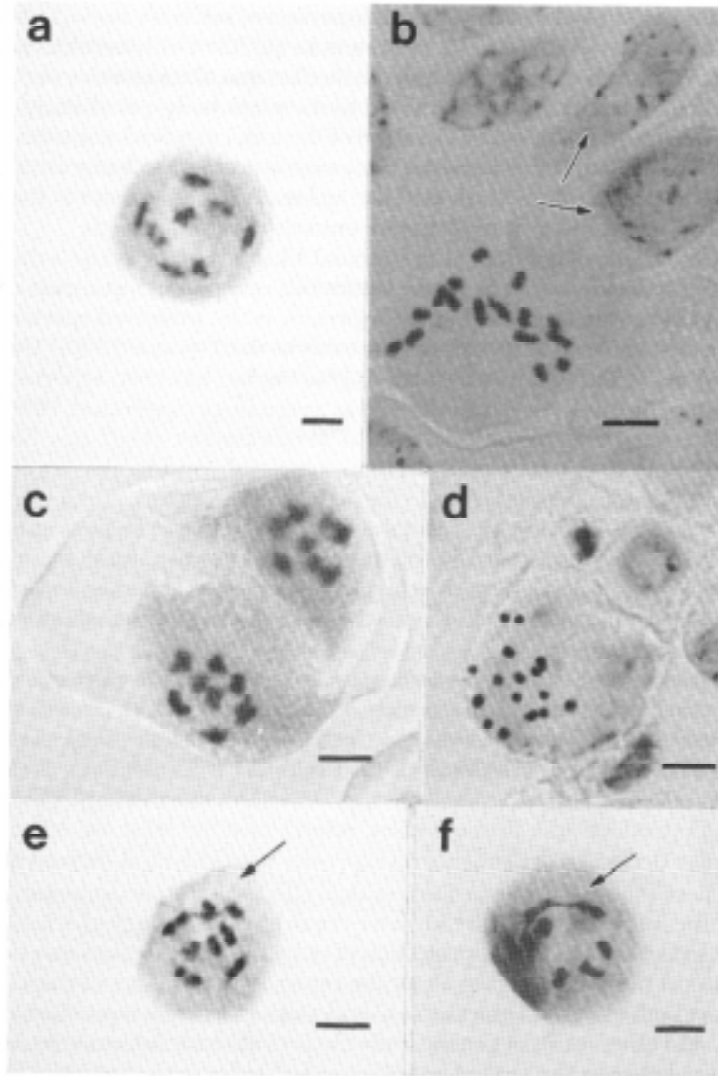


Fig. 1. Photographs of *Schoenocaulon* chromosomes. a) *S. intermedium* pollen mother cell, metaphase I, $n=8$. b) *S. intermedium* root tip cells $2n=16$, arrows denote heteropycnotic regions of interphase cells. c) *S. caricifolium* var. *caricifolium* pollen mother cells, late prophase II, $n=8$. d) *S. caricifolium* var. *caricifolium* root tip cells, $2n=16$. e) *S. tenorioi*, population from near Rodeo, pollen mother cell, metaphase I, $n=8$, arrow denotes chain of three chromosomes. f) *S. tenorioi*, population from Cerro Verde, pollen mother cell, metaphase I, $n=8$, arrow denotes chain of three chromosomes. Bar = 5 μm .

to its evolutionary slow-down. No special dispersers of seeds are known and indeed this is unlikely as the seeds are quite poisonous being filled with steroidal alkaloids, the chemical hallmark of the tribe. Indeed, the fact that *Schoenocaulon* accumulates steroidal alkaloids in its seeds as opposed to the plant body, particularly the bulb and bulb-rhizome as do the other members of the tribe, may have contributed to its general decline. With the introduction of free-ranging goats and other grazing animals in Mexico, the plants offered little defence against foraging, except at the time of fruit maturity; and sadly, grazed plants are unlikely to produce seeds.

The positive side of accumulating steroidal alkaloids in the seeds is their ready accessibility. *Schoenocaulon* seeds are the source of a very potent insecticide currently used in organic gardening. Although *S. officinale*, is the preferred species for this product, in fact, seeds of all species can probably be used (Frame 1990). Traditional use of *S. officinale* and to a lesser extent *S. ghiesbreghtii*, has been reported for the treatment of pediculosis, deep wounds and as a vermifuge (see Frame, 1990). Much information regarding traditional use of *Schoenocaulon* seeds has been lost. Notwithstanding, *S. officinale* seeds were an object of considerable trade among American indigenous peoples prior to the arrival of Europeans, and it is likely that they were aware of its strong insecticidal activity — and may even have applied it to crops. If so, it may represent one of the earliest known natural plant-derived insecticides. Such a remarkable and useful plant deserves greater attention and would be an excellent candidate for inclusion in schemes to develop sustainable agricultural practices in Latin America.

Dried, powered “sabadilla” seeds form the base of an effective insecticide useful against certain hard-to-control insects such as Diamond-back moth (*Plutella xylostella*), Mexican Bean beetle (*Epilacha varivestis*), Striped Cucumber beetle (*Acalymma vittatum*), Tarnished Plant bug (*Lygus oblineatus*), Leaf hoppers (Cicadellidae), Flea beetles (Alticinae) and Citrus thrips (*Scirtothrips* spp). Development and implementation of schemes to introduce and, in some cases, reintroduce the local use of “sabadilla” should lead to decreased dependence on expensive petrochemical-derived pesticides that often have long-term, hazardous residual effects on the environment.

Using the information we already have regarding the biology of *Schoenocaulon*, simple projects designed for the protection of remaining populations may be begun. And, as almost nothing is known about the reproductive biology of these plants it should prove both useful and practicable to undertake concurrent reproductive studies. Karyology and other forms of genetic study can provide basic information regarding relationships between and among populations and taxonomic categories, as well as vital evidence concerning evolutionary status. For these reasons, it is also recommended that the karyology survey of *Schoenocaulon* here begun be completed, and that an overall program of population genetic studies be undertaken.

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