



CHROMOSOMES OF TWO *OLYRA* L. SPECIES FROM MISIONES, ARGENTINA (POACEAE, BAMBUSOIDEAE, OLYREAE)



CROMOSOMAS DE DOS ESPECIES DE *OLYRA* L. DE MISIONES, ARGENTINA (POACEAE, BAMBUSOIDEAE, OLYREAE)

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ABSTRACT

The subfamily Bambusoideae comprises three monophyletic tribes, Arundinarieae, Bambuseae and Olyreae. Here we report the gametic number and the chromosomal meiotic behavior of two species belonging to the herbaceous tribe Olyreae, *Olyra latifolia* and *Olyra humilis*. Accessions were collected in Misiones, at Northeastern Argentina. We report a new gametic number for *O. humilis*, $n=18$, and we confirmed $n=11$ for *O. latifolia*. Chromosomal features, like the basic and gametic chromosome number, are important in understanding the evolution of the Poaceae family, especially in delimiting clades and elucidate inter and intra-clades relationships, and therefore it is necessary to continue producing this type of data.

Key words: bamboos, cytogenetics, meiosis, ploidy, Poaceae

RESUMEN

La subfamilia Bambusoideae comprende tres tribus monofiléticas, Arundinarieae, Bambuseae y Olyreae. Aquí reportamos el número gamético y el comportamiento meiótico de los cromosomas de dos especies pertenecientes a la tribu Olyreae de bambúes herbáceos, *Olyra latifolia* y *Olyra humilis*. Las introducciones se recolectaron en la provincia de Misiones, en el noreste argentino. Reportamos un nuevo número gamético para *O. humilis*, $n=18$, y confirmamos $n=11$ para *O. latifolia*. Los números cromosómicos básicos y gaméticos son importantes para comprender la evolución de la familia Poaceae, especialmente para delimitar sus clados y las relaciones existentes entre ellos, por lo que es necesario continuar produciendo este tipo de datos.

Palabras clave: bambúes, citogenética, meiosis, ploidía, Poaceae

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INTRODUCTION

The subfamily of bamboo grasses (subfamily Bambusoideae) comprises 1,700 species belonging to 128 genera which are distributed worldwide (Clark *et al.*, 2015; Zhang *et al.*, 2020). Bambusoideae comprises three monophyletic tribes, Arundinarieae, Bambuseae and Olyreae; the first two are represented by woody bamboos, whereas Olyreae species are herbaceous without woody characteristic (Ruiz-Sanchez *et al.*, 2021). Herbaceous bamboos have a wide distribution, inhabiting from sea level towards 2,200 m.a.s.l. (Clark *et al.*, 2015). Olyreae species are native to the New World with one exception, *i.e.* *Buergersiochloa* that is a monotypic endemic genus of New Guinea (Oliveira *et al.*, 2014; Clark *et al.*, 2018).

The tribe Olyreae comprises 22 genera and 124 species, and occurs widely in the Neotropical region, from Mexico and the Caribbean to North Argentina, and Paraguay (Oliveira *et al.*, 2014). Most genera in this tribe have species defined by vegetative characters. Generally, the spikelets exhibit little interspecific variation, with the exception of *Olyra* L., the most widespread and heterogeneous genus in the tribe (Judziewicz and Zuloaga, 1992). In addition, *Olyra* was defined as paraphyletic and polyphyletic, in order to explain diverse incongruences in phylogenetic trees based on plastid molecular markers (Judziewicz *et al.*, 1999; Ruiz-Sanchez *et al.*, 2019).

Olyra is the largest genus within the subtribe Olyrinae, with *ca.* 24 species. Probably this estimate will soon change since phylogenetic studies evidenced its non-monophyletic nature (Oliveira *et al.*, 2014, 2020). Currently, four species of *Olyra* habit in Argentina, *O. ciliatifolia* Raddi, *O. fasciculata* Trin., *O. humilis* Nees and *O. latifolia* L. and the only two chromosome counts

known for Argentinian specimens are from *O. latifolia*. Chromosomal and ploidy data are useful for clarifying phylogenetic relationships and tracing evolutionary trajectories (Honfi *et al.*, 2021; Deanna *et al.*, 2022). For this reason, this work aims to contribute with meiotic studies of *O. latifolia* and *O. humilis*, two significant herbaceous species of the tropical forest in Misiones.

MATERIAL AND METHODS

Table 1 shows a complete list of the studied accessions, including their geographic origin, voucher specimens, and herbaria. Herbarium acronyms follow Thiers (2017 onward). Voucher herbarium specimens were deposited at Universidad Nacional de Misiones Herbarium (MNES) and duplicates at the following herbaria: Instituto de Botánica del Nordeste (CTES), Instituto de Botánica Darwinion (SI) and Conservatoire et Jardin Botaniques de la Ville de Genève (G).

The analyses of chromosome meiotic behavior were made according to Honfi *et al.* (2021) and Reutemann *et al.* (2021). Briefly, young inflorescences were fixed in 3:1 ethanol: acetic acid solution for at least 24 h at room temperature. Then, spikelets were transferred to 70% ethanol at 4°C. Pollen mother cells (PMCs) were obtained from immature anthers and were stained with acetocarmine 2%. Permanent slides were made with Venetian Turpentine solution. At least 50 PMCs at diakinesis and/or metaphase I were analyzed for each accession of both species. Anaphase (I and II) and telophase (I and II) were analyzed to observe abnormal segregation. Microphotographs were taken with a Leica camera added to a Leica optical microscope.

Table 1. Chromosome gametic number (*n*) of *Olyra* species and studied accessions.

Species	<i>n</i>	Provenance
<i>O. humilis</i> Nees	18	Arg. Misiones, San Pedro, Parque Provincial Moconá. Honfi 500, 25/11/1993 (MNES, CTES, G).
		Arg. Misiones, San Pedro, Parque Provincial Moconá. Honfi 511, 25/11/1993 (MNES, CTES, G).
		Arg. Misiones, Caingúas, Campo Grande. Honfi 582, 19/2/1994 (MNES)
		Arg. Misiones, Parque Provincial Moconá. Seijo 856, 29/11/1993 (MNES).
		Arg. Misiones, Parque Provincial Moconá. Daviña 125, 18/12/1992 (MNES, CTES, SI)
<i>O. latifolia</i> L.	11	Arg. Misiones, Parque Provincial Moconá. Seijo 863, 29/11/1993 (MNES, CTES, G)

RESULTS AND DISCUSSION

Chromosome meiotic behavior of six *Olyra* South American accessions was studied (Table 1). The two *Olyra* species studied in this work exhibited a persistent nucleolus, which was clearly distinguishable up to (and including) diakinesis in agreement with Nicora and Rugolo de Agrasar (1987) karyosystematic definition of Bambusoideae family.

Chromosome gametic number, ploidy levels and meiotic behavior for *O. humilis* are reported for the first time. Persistent nucleoli, sometimes four small ones, were present in PMCs at diakinesis (Figure 1A). The studied accessions showed a regular meiotic behavior with 18 bivalents at diakinesis and metaphase I (Figure 1B). Few PMCs exhibited 17 bivalents and 2 univalents. Chromosome segregation was normal without laggards. The gametic chromosome number of $n=18$ is a new haploid chromosome number for the genus. Alternatively, there is a new derived basic chromosome number $x=18$, or a polyploid based on $x=9$, which is an uncommon basic chromosome number for *Olyra*. Previous reports of a tetraploid cytotype with $x=9$ were originally described as *Olyra* (Davidse and Pohl, 1978). Currently, these accessions belong to *Parodiolyra lateralis* (Presl. ex Nees von Essenbeck) Soderstrom & Zuloaga (Soderstrom and Zuloaga, 1989). Therefore, there is no basic number in *Olyra* to explain the gametic number $n=18$ found here.

In Olyreae, chromosome data suggest that *Olyra* species have a descending aneuploid series in basic numbers that started from an ancestral and original $x=12$, and nowadays is composed by $x=11$, 10 and 7 (Table 2). However, several authors considered $x=12$ as a secondary ancestral basic number (Hunziker *et al.*, 1982). At least two hypotheses can explain the chromosome number found in *O. humilis*. The first

hypothesis is an allotetraploid origin based on $x=9$, with regular chromosome pairing in bivalents. In the second one, a new derived basic chromosome number of $x=18$ for *Olyra* results from an ascending aneuploid series. For example, a polyploid origin for $n=18$ found in *Anomochloa marantoideae* Brongn. (Anomochloaceae) was previously proposed, considering a primitive base number $x=6$ for bamboos and Poaceae in general (Hunziker *et al.*, 1989).

Judziewicz and Zuloaga (1992) suggested four morphological natural groups of species within *Olyra*, mainly based on the presence and distribution of trichomes on the female floret. The Glaberrima group of *Olyra* consists in species closely related to *O. glaberrima* Raddi, such as *O. humilis*, *O. maranonensis* Swallen and *O. davidseana* Judz. & Zuloaga (Judziewicz and Zuloaga, 1992). In addition, a close relationship between *O. glaberrima* and *O. humilis* is highly supported by recent phylogenetic analyses (Oliveira *et al.*, 2014; 2020). Furthermore, Oliveira *et al.* (2014) corroborated the monophyly of *Arberella* with species of *O. glaberrima* group. Cytological studies in all members of *Arberella* and Glaberrima group can shed light in the new chromosome number found in *O. humilis*, especially if they are multiple of $n=18$ or $x=9$ or 18.

In *O. latifolia*, a gametic chromosome number of $n=11$ was found. Meiotic behavior was regular with the presence of a persistent nucleolus and 11 bivalents or 10 bivalents and two univalent in PMCs at diakinesis and metaphase I (Figure 2 A, B, C). Chromosomes segregated normally at anaphase I and microsporogenesis resulted in an isobilateral tetrad of microspores (Figure 2 D, E). Our data agree with previous chromosome counts reported in several works (Tateoka, 1962; Pohl and Davidse, 1971; Davidse and Pohl, 1972a, b; 1974; Olorode, 1975; Dujardin, 1978; Hunziker *et al.*, 1989; Guo *et al.*, 2019). Besides, a tetraploid cytotype was registered in Bahia, Brazil (Hunziker *et al.*, 1982), Aragua and Bolivar, Venezuela (Davidse and Pohl, 1974; 1978) and Trinidad (Davidse and Pohl, 1972b). The basic chromosome number for this species is $x=11$ and the meiotic behavior indicates that the studied materials from Misiones are diploid accessions. *O. latifolia* is a robust herbaceous species widespread in the Neotropics, and the studied accessions are from the southernmost localities in South America. Diploids are the most frequent cytotype in Neotropics (America), and the only ploidy level found in Africa. Tetraploids are commonly detected in tropical areas (Table 2, Davidse and Pohl, 1974, 1978). Clearly, *O. latifolia* is a polymorphic complex with diploid and polyploid phenotypes. According to Davidse and Pohl (1972b), plants with very broad leaf blades, named *O. cordifolia* Kunth with $2n=ca. 30$ (Gould and Soderstrom, 1967) are similar to tetraploid plants ($n=22$) of *O. latifolia*. Furthermore, in highly fertile diploid Mexican accessions of this species, meiotic unpaired chromosomes behaving as univalents or heterozygous translocation were also

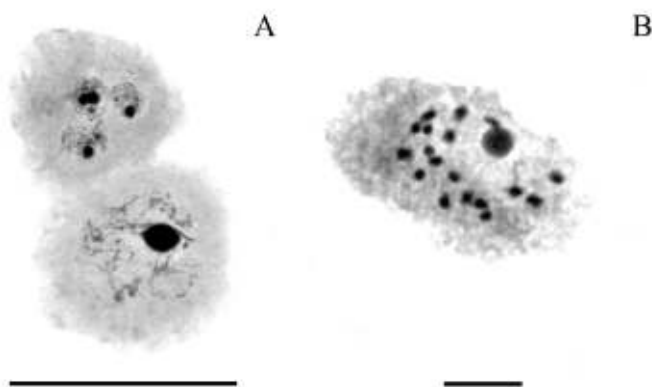


Figure 1. Pollen mother cells (PMCs) of *Olyra humilis* (Honfi 582) at meiosis. **A.** Prophase I; upper PMC with four small nucleoli, lower PMC with one unique and big nucleolus. **B.** Diakinesis with a persistent nucleolus and 18 bivalents. Scale [A]= 50 μ m, [B]= 10 μ m.

Table 2. Records of chromosome numbers and ploidy level (x) of *Olyra* species.

Species	Chromosome data	x	Location	References
<i>O. ciliatifolia</i> Raddi	n=11	2x	Brazil: Rio de Janeiro	Hunziker <i>et al.</i> , 1982
<i>O. fasciculata</i> Trin.	2n=14, n=7	2x	Brazil: Rio de Janeiro, Guanabara, Estrada da Gávea. Brazil. Rio de Janeiro	Calderon and Soderstrom, 1973 Hunziker <i>et al.</i> , 1982
<i>O. humilis</i> Nees	n=18	4x		This work
<i>O. latifolia</i> L.	2n=22; n=11	2x	Costa Rica: San José, La Cisica between Alto de San Juan and La Alfombra, highway 223, 11 mi. SW of San Isidro de General Costa Rica: Cartago IICA, Turrialba; Guanacaste: 6 km S of La Cruz; 1km W of Cafias Dulces; Puntarenas; 5 km SW of Rincón de Osa; 4km NE of Escuela Santa Constanza Mexico: Veracruz, near San Jose de Mata Clara; El Salvador: Chalatenango, near Chalatenango; Nicaragua: Zelaya, Lecus. Costa Rica: Guanacaste: 30 km N of Caiias; El Salvador: Santa Ana: 2 km SE of Metapin; Trinidad: 1 mi W of Arirna Venezuela.: bolivar, 17 km W of the Rio Caura Cote-d'Ivoire Nigeria: University Campus, Ile-Ife; forest floor Zaire: Kinshasa, Mont Ngafula, Lukaya Valley, 25 km S of Kinshasa; Bas-Zaire, Kasangulu, Kindongo, 15 krn N of Kasangulu Brazil. Bahia Argentina: Misiones, Depto Iguazu, Cataratas del Iguazu. Argentina: Misiones, Depto Gral. M. Belgrano, 5 km SW of Deseado. Germplasm Bank of Wild Species in Kunming	Reeder, 1969 Pohl and Davidse, 1971 Davidse and Pohl, 1972a Davidse and Pohl, 1972b Davidse and Pohl, 1978 Kamacher <i>et al.</i> , 1973 Olorode, 1975 Dujardin, 1978 Hunziker <i>et al.</i> , 1982 Hunziker <i>et al.</i> , 1985 Hunziker <i>et al.</i> , 1989 Guo <i>et al.</i> , 2019 This work
	2n=ca. 30		Brazil: Distrito Federal	Gould and Soderstrom, 1967
	n=22	4x	Venezuela. Aragua: Rancho Grande	Davidse and Pohl, 1974
	2n=48	4x	Colombia: Caqueta	Gould and Soderstrom, 1970
<i>O. lorentensis</i> Mez	2n=22	2x	Colombia. Amazonas	Gould and Soderstrom, 1970
<i>O. obliquifolia</i> Steud.	2n=23, 44	2x, 4x	Brazil: Para. Suriname: Zuid Rivier	Gould and Soderstrom, 1967
<i>O. taquara</i> Swallen	2n=20	2x	Brazil: Distrito Federal	Gould and Soderstrom, 1967

No data available for the following species: *Olyra amapana* Soderstrom & Zuloaga; *O. bahiensis* R. P. Oliveira & Longhi-Wagner; *O. buchtienii* Hackel; *O. caudata* Trin.; *O. davidseana* Judz. & Zuloaga; *O. ecaudata* Doell.; *O. filiformis* Trin.; *O. glaberrima* Raddi; *O. holttumiana* Soderstrom & Zuloaga; *O. juruana* Mez; *O. latispicula* Soderstrom & Zuloaga; *O. longifolia* Kunth; *O. maranonensis* Swallen; *O. retrorsa* Soderstrom & Zuloaga; *O. standleyi* Hitchc.; *O. tamanquareana* Soderstr. & Zuloaga; *O. wurdackii* Swallen.

reported (Davidse and Pohl, 1972a). Extensive genetic system studies might be very helpful to understand the polymorphisms of *O. latifolia* complex across its range.

Olyra latifolia and *O. humilis* have distinct positions in the phylogenetical topology in highly supported trees (Oliveira *et al.*, 2014; 2020), and the basic and gametic chromosome numbers found here for both species agree with this result. Olyreae chromosome numbers are highly variable, and the tribe has the greatest variation in basic chromosome numbers and ploidy levels. In addition, polyploid complexes with $2x$ and $4x$ were described in *O. latifolia*. Intensive cytogenetical studies on Southamerican herbaceous bamboos are necessary to understand evolutionary trends in bambusoid subfamily, considering that all bamboos probably derived from herbaceous ancestors (Soderstrom and Calderon, 1974).

Recently, the ploidy levels of bamboo grasses were reviewed by Zhou *et al.* (2017). As a rule, the chromosome number in temperate woody bamboo species remains constant with $2n=4,8$, instead the chromosome number of paleotropical woody bamboos, was variable with

$2n=70 \pm 2$, and a few species having $2n=64, 80, 96, 98,$ and 104 (Zhou *et al.*, 2017 and references therein). The neotropical woody bamboos were also diverse but in a minor degree with $2n=40, 44$ or 48 chromosomes (Zhou *et al.* 2017). A revision of chromosome data of herbaceous bamboo is not available yet. *Olyra* is the largest genus in Olyreae and has been poorly studied regarding its cytogenetics. Further cytological studies are needed to clarify the chromosome number evolution in this genus as a supporting contribution to understand phylogenetical and reproductive ongoing analyses.

Species of Olyreae are endangered due to the continuing loss of forests (Oliveira and Clark, 2009). Under the climatic change impact, is necessary to claim for conservation efforts of bamboo species because several species are endemic and poorly studied. Besides, we ignore if they are an important resource for other species as food, forage or grains in forest ecosystems. The conservation of natural populations in subtropical South America should be considered as the focus of future studies in this tribe.

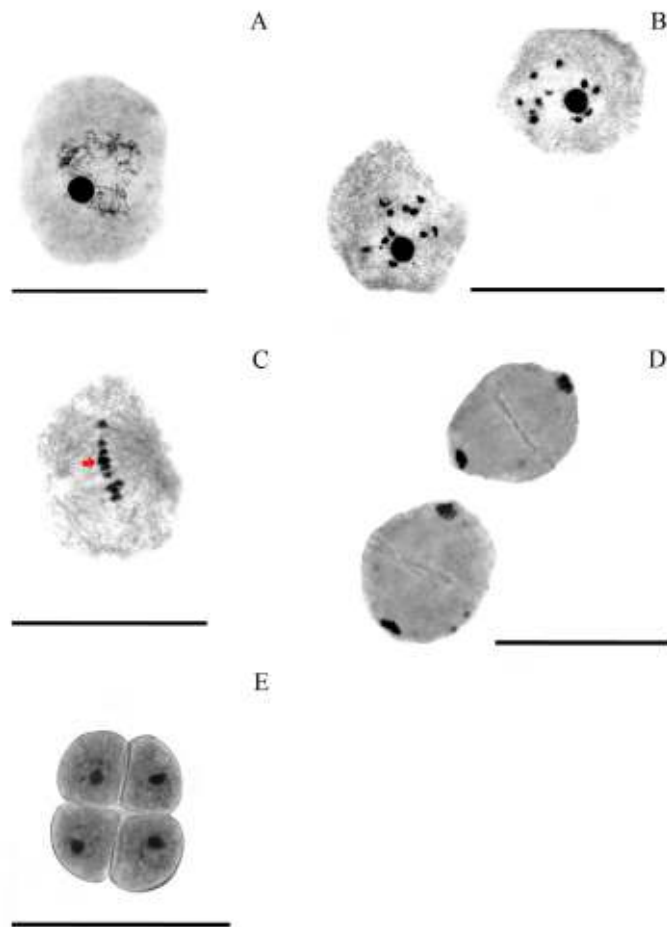


Figure 2. Pollen mother cells (PMCs) of *Olyra latifolia* (Seijo 872) at meiosis. **A.** Early prophase I with a unique prominent nucleolus. **B.** Two PMCs at diakinesis with II bivalents and a persistent nucleolus. **C.** Metaphase I with II II in the equatorial plate. Two overlapping bivalents are indicated with an arrow. **D.** Two PMCs in telophase I with regular behavior. **E.** Isobilateral tetrad of microspores. Scale = 50 μ m.

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