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RESEARCH

Genome size variation and whole-genome duplications in the monocot order Poales

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Abstract

Nuclear genome sizes of 54 representative species from 44 genera of the monocot order Poales were investigated by flow cytometry. Small holoploid genomes with < 2 pg/2C are characteristic of the Poales; only some families have larger 2C values, although this is not consistently the case. The sizes of monoploid genomes as well as mean DNA content per chromosome (MC) show a similar pattern. A comparison of the genome size data with current molecular phylogenetic data suggests that small monoploid genomes (1Cx < 0.4 pg) and small chromosomes (MC ≤ 0.05 pg), as found in some families, are likely the ancestral features of the order Poales. Conspicuous increases in genome size occurred particularly in the Poaceae (grasses) and to a lesser extent in the xyrid clade and the Restionaceae. According to previous phylogenomic studies, the Poaceae are characterized by a whole-genome duplication (WGD) called ρ, which is absent in all other Poales families. However, it is clear from the 1Cx values that the ρ event is not, or no longer, associated with a significant increase in the minimum 1Cx genome sizes of grasses compared to other Poales families. Future studies need to clarify whether the smallest 1Cx values in the Poaceae are due to a secondary reduction of the nuclear genome after the ρ event and whether the relatively large minimal 1Cx values of the xyrid clade were caused by a further WGD within Poales.

Keywords Angiosperms · Commelinids · C-value · Evolution · Genome · Genome size

Abbreviations

2C value	DNA content of the non-replicated holoploid genome (chromosome complement) in the diplophase with the chromosome number $2n$
1Cx value	DNA content of one non-replicated monoploid genome (chromosome set) with chromosome base number x
bp	Base pairs
FCM	Flow cytometry, flow cytometric, flow cytometrically
Mbp	Mega base pairs = 10^6 bp
MC	Mean DNA content per chromosome
pg	Picogram = 10^{-9} g
PI	Propidium iodide

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Introduction

The size of genomes, here referred to as the total DNA content of the nucleus (2C value of the non-replicated holoploid genome, i.e., chromosome complement in the diplophase with the chromosome number $2n$), varies considerably among flowering plants as a whole, but also within smaller taxonomic groups such as families or even genera. The main reason for this variation is, of course, the number of chromosomes, which can be altered especially by the frequent polyploidy in plants, i.e., the multiplication of chromosome sets by whole-genome duplication (WGD) (e.g., Wendel 2000, 2015; Leitch and Leitch 2008; Soltis et al. 2015; van der Peer et al. 2017; Mandáková and Lysak 2018; Heslop-Harrison et al. 2023).

Another important factor of genome size variation is the increase or decrease in chromosome size, while the number of genes remains relatively unchanged. Such processes can be induced by structural changes in the chromosomes, which are known to trigger changes in the amounts of different types of transposable elements, especially LTR (long terminal repeat) retrotransposons. LTRs can amplify rapidly and reach extraordinarily high copy numbers in genomes

(Hawkins et al. 2006; Stritt et al. 2020). The proportions of all repetitive elements in genomes can vary considerably between closely related species of the same genus and even within species (Becher et al. 2021, 2022; Pellicer et al. 2021). On a family-wide scale, for example, all repetitive elements in diploid grasses account for 32% of total genome size in *Oryza sativa* (rice) to 83% in *Aegilops tauschii*, a wild relative of wheat (Novák et al. 2020). Genome shrinkage, a necessary process to counteract genome expansion through polyploidy or repeat amplification (Leitch and Bennett 2004; Wendel 2015), is a slow but steady process caused by DNA losses through spontaneous deletions, e.g., in the course of double-strand break repair, or genomic losses of repeat elements and duplicated regions after polyploidization (Petrov 1997; Devos et al. 2002; Chen 2007; Woodhouse et al. 2010; Freeling et al. 2012; Michael 2014; Pellicer et al. 2018; Schubert and Vu 2016; Wang et al. 2021; Levy and Feldman 2022; Feldman and Levy 2023).

Changes in genome size are associated with effects at the cellular level, such as cell cycle duration and cell size. They also have physiological effects, as they correlate with phenological or ecological traits such as climatic adaptations or nutrient requirements, and thus implications for macroecological and biogeographical patterns (Francis et al. 2008; Leitch and Leitch 2012; Greilhuber and Leitch 2013; Simonin and Roddy 2018; Doyle and Coate 2019; Roddy et al. 2020; Faizullah et al. 2021; Bartish et al. 2023; Bhadra et al. 2023; Bureš et al. 2024; Soto Gomez et al. 2024).

The Poales, an order of frequently grass-like looking plants, are one of the most species-rich and evolutionarily successful phylogenetic lineages of monocots, encompassing 14–17 families with estimated > 23,200 species (modified from Stevens 2001 onwards and Mabberley 2017). This large species diversity is mainly caused by three families, Poaceae (grasses) with > 11,300 species (Kellogg 2015; Mabberley 2017; Soreng et al. 2017), Cyperaceae (sedge family) with > 5600 (Larridon et al. 2021) and Bromeliaceae (bromeliads) with > 3700 species (Gouda et al. cont. updated).

Within our study group Poales, the genome size variation known to date ranges from 159 Mbp (≈ 0.16 pg) in the sedge *Carex nubigena* subsp. *albata* (Kük. ex Matsum.) T.Koyama to 21,132 Mbp (≈ 22.63 pg) in tall wheatgrass, *Thinopyrum ponticum* (Podp.) Barkworth & D.R.Dewey (Nishikawa et al. 1984; Vogel et al. 1999), implying a ca. 139-fold difference. Genome sizes differ more in Poales than in most other monocot lineages, indicating an increased rate of genome size evolution (Leitch et al. 2010).

The Poales are of outstanding economic significance, particularly because of the grass family, which provides roughly 60% of the food for human consumption and also offers grains and grasses converted to animal products, supplying ca. 20% of mankind's protein requirements (Jacobs and Wilson 2003). The principal cereals are, ordered by importance, maize, wheat, rice, barley, sorghum, oats, rye and various grasses, collectively called 'millets' (Lieberei and Reisdorff 2012; Röser et al. 2014; Statista 2023). About half the world's sugar is produced from sugar cane (*Saccharum officinarum* L.). Pineapple (*Ananas comosus* (L.) Merr., Bromeliaceae) is the only non-grass crop of significance, followed by some Cyperaceae with edible corms such as water chestnut (*Eleocharis dulcis* (Burm.f.) Trin. ex Hensch.) and tiger nut (*Cyperus esculentus* L.). Woody grasses (bamboos) are often used for construction purposes, and many species are important sources of fiber (Bromeliaceae, Cyperaceae, Juncaceae, Poaceae). Many species of Poales are horticulturally valuable (bromeliads, lawn and ornamental grasses, etc.), and others are among the world's most noxious weeds.

Poales species grow in almost all habitat, from the tropics to the polar regions, from sea level to the highest altitudes, from aquatic habitats to deserts. Some can form extensive stands and dominate entire ecosystems (savannas, steppes, prairies, wetlands), especially grasses, sedges, rushes (Juncaceae) and restios (Restionaceae). Bromeliads often grow as epiphytes in the Tropics and Subtropics of the New World.

The age of Poales was estimated at 130–125 Ma with diversification of its families around 125–120 Ma (Kessous et al. 2021), which is broadly consistent with the placement of the stem and crown nodes of Poales at 124 and 120 Ma (Givnish et al. 2018). Based on secondary dating, the Bromeliaceae arose at ca. 125 Ma (Kessous et al. 2021). Fossil evidence suggests an origin of grasses between the Lower Cretaceous at ca. 133 Ma and early Upper Cretaceous at ca. 100 Ma (Gallaher et al. 2019, 2022; Schubert et al. 2019). Based on single-copy gene data, Ma et al. (2021) estimated a crown age of the Poaceae of 98 Ma, which was confirmed by using nuclear genomic data and plastid DNA sequences (Gallaher et al. 2022; Huang et al. 2022; Hu et al. 2023). The history of the Cyperaceae is younger, dating back to the Upper Cretaceous at 96–85 Ma, when the divergence between Cyperaceae and Juncaceae took place (Spalink et al. 2016).

The evolutionary unfolding of the Poales, the circumscription and branching of their families and subfamilies, and their phylogenetic relationship were studied using a variety of morphological, ultrastructural, biochemical, DNA sequence, and ecological features (Kellogg and Linder 1995; Kite et al. 2000; Linder and Rudall 2005; Tillich 2007; Briggs et al. 2010, 2014; Bouchenak-Khelladi et al. 2014; Iles et al. 2015; Palma-Silva et al. 2016; Rocha et al. 2018; Oriani and Scatena 2019; Jo et al. 2021; Elliott et al. 2024). As a special feature of angiosperms, several complex structural rearrangements were discovered in the plastid DNA, from which, for example, close phylogenetic relationships between the families Joinvilleaceae, Ecdeiocoleaceae and Poaceae as well as between these families

and the Restionaceae can be inferred (Doyle et al. 1992; Michelangeli et al. 2003; Wysocki et al. 2016).

Recent DNA studies, including plastome-based analyses (Givnish et al. 2010, 2018; Li et al. 2021), nuclear multigene (Hochbach et al. 2018) and phylogenomic studies (McKain et al. 2016; Darshetkar et al. 2019; Baker et al. 2022; Timilsena et al. 2022), have resolved the branching order of most families in Poales. There is still uncertainty about the position of the Ecdeiocoleaceae and Typhaceae, the clade or grade of the xyrid families (Eriocaulaceae, Xyridaceae and possibly Mayacaceae), the structure of the restiid clade (Restionaceae and former Anarthriaceae and Centrolepidaceae) and the arrangement of the families within the graminid clade (Ecdeiocoleaceae, Flagellariaceae, Joinvilleaceae, Poaceae), including the question about the direct sister of Poaceae, whether Ecdeiocoleaceae, Joinvilleaceae or a clade of the latter two (Givnish et al. 2010, 2018; McKain et al. 2016; Hochbach et al. 2018; Darshetkar et al. 2019; Li et al. 2019, 2021; Baker et al. 2022; Timilsena et al. 2022).

The largest range of chromosome numbers within the Poales is found in the Poaceae, the grass family. The chromosome number ranges from $2n = 4$ in *Colpodium bieberstenianum* (Claus) Röser & Tkach (syn. *Zingeria bieberstenianiana* (Claus) P.A.Smirn.) and *C. versicolor* Woronow ex Grossh. (Tzvelev and Zhukova 1974; Sokolovskaya and Probatova 1977) to $2n =$ ca. 266 in *Poa litorosa* Cheeseman (Hair and Beuzenberg 1961; Hair 1968), which is also the highest number in Poales. Within the Poales, the chromosome number $2n = 4$ was found outside the grasses in the beak-sedge *Rhynchospora tenuis* Link, a member of the Cyperaceae (Vanzela et al. 1996; Guerra 2000).

The chromosome number of monoploid chromosome sets, i.e., the chromosome base number x, is easy to determine in lineages with orthoploidy (euploidy), i.e., the occurrence of exclusively diploids and polyploids. On the other hand, in groups with high somatic chromosome numbers, for example, $2n = 36$ or 38 as in the Joinvilleaceae or Flagellariaceae or $2n = 50$ in Bromeliaceae, the chromosome base numbers could be $x = 18$ or 19 or $x = 25$, respectively. For their part, they could indicate a polyploid origin beginning with lower numbers ($x = 5$–8, eventually 9) and would therefore represent 'secondary' chromosome base numbers (Goldblatt 1980; Grant 1982; Stebbins 1982; de Wet 1987; Hunziker and Stebbins 1987, etc.). Uncertainty about the 'original chromosome base number' is even greater in families with extensive dysploid variation such as Cyperaceae and Juncaceae, whereas the Bromeliaceae, once thought to have a fairly continuous range of chromosome numbers between $2n = 18$ and $2n = 200$, actually appear to be largely orthoploid, mostly based on $x = 25$ (Zanella et al. 2012; Gitaí et al. 2014; Cruz et al. 2020).

The variation in chromosome base number could be linked to a change in genome size. The general variation in genome size within the order Poales and within the main groups of the family Poaceae down to the subfamilies has already been summarized in a comprehensive review of the dynamics and evolution of genome size in monocotyledons (Leitch et al. 2010). Even within the Poales, the variation in genome size is by far the greatest in the Poaceae, although some of the families had not yet been studied at all or only rudimentarily. Since then, however, several studies have considerably expanded the state of knowledge in some of the larger families such as Bromeliaceae, Cyperaceae and Restionaceae (e.g., Gitaí et al. 2014; Šmarda et al. 2014; Linder et al. 2017; Müller et al. 2019; Paule et al. 2020; Elliott et al. 2022, 2023).

By using an exemplary sampling of families and major infrafamiliar phylogenetic lineages within the order Poales, some of which have been underrepresented in previous genome size studies, this study aims to both provide important baseline data for genomic studies and answer the following questions:

(1) How large is the frequently cited variation in genome sizes between and within families of the order Poales, and are there evolutionary trends associated with the striking change of chromosome base numbers (monoploid chromosome sets) in this large group of plants?
(2) Could the genome size data contribute to a better understanding of the evolution of Poales and in particular the early Poales?
(3) What is the significance of the genome size data firstly for the reconstruction of the ancestral chromosome complement and monoploid genome size in Poales and secondly for the impact of past whole-genome duplications (WGD), especially the ρ event of the grass family (McKain et al. 2016)?

This study is the first part of a series of publications on the genome sizes of the order Poales and some of its groups, namely the family Poaceae (grasses), one of its subfamilies, the subfamily Pooideae, and a larger complex of genera from this subfamily that can be summarized as supertribe Poodae.

Material and methods

Plant material

Our sample included 56 specimens from 54 species in 44 genera, representing 13 of altogether 14 families of Poales. One to two accessions per species were studied. We added a *Musa* accession (Musaceae, the banana family) from the closely related order Zingiberales, which belongs to the

'commelinoids', along with the Poales. *Musa* was one of the outgroups in our previous study on the molecular phylogeny of Poales (Hochbach et al. 2018). The purpose of including it was to compare its genome size with that of the Poales taxa. The fresh leaves for the genome size analyses were collected in the greenhouses or in the field facilities of the Botanical Garden of the University of Halle-Wittenberg. The leaf samples were either processed immediately or stored in plastic bags with moist tissue in the refrigerator at 4 °C for up to five days until processing. Voucher specimens of most accessions are deposited in the herbarium of the University of Halle-Wittenberg (HAL). Details on the collections of the analyzed taxa can be found in the Online Resource 1.

Measurement of genome sizes

Genome sizes were estimated by FCM following the protocols of Doležel et al. (2007), Sliwinska et al. (2022) and Loureiro et al. (2023) with minor modifications. This method is based on the detection of fluorescent signals from stained particles, in our case plant cell nuclei, in liquid suspension, a method originally developed for biomedical research in the 1960s and 1970s and later applied to plant cells (Heller 1973). To isolate cell nuclei by mechanical homogenization of plant tissues (Galbraith et al. 1983), fresh leaf tissue of the sample to be analyzed and an internal standard species was homogenized together with a razor blade in a plastic Petri dish. The cell nuclei were extracted in 2 mL staining buffer. Ten µL propidium iodide (PI) solution (10 mg × mL^{-1}) and 5 µL RNase A (5 mg × 1.5 mL^{-1}) were added using the ready-to-use CyStain PI OxProtect reagent kit (Sysmex Partec GmbH, Görlitz, Germany) according to the manufacturer's protocol. For FCM analyses, a CyFlow Ploidy Analyser (Sysmex Partec) equipped with a green laser of 532 nm for the DNA-intercalating fluorochrome PI was used.

Fluorescence intensity measurements for 5000 particles (nuclei) were performed with three replicates per specimen. Only histograms with coefficients of variation (CV) < 4% for the G0/G1 peak of the sample were considered. For CVs exceeding this threshold, the measurement was discarded, and the sample was re-analyzed.

The following internal standards, obtained as seed from the Institute of Experimental Botany, Academy of Sciences of the Czech Republic, and grown in our greenhouses, were used for the genome size estimates (Doležel et al. 2007, 2018; Temsch et al. 2022): *Glycine max* Merr. 'Polanka' (2.50 pg/2C), *Pisum sativum* L. 'Ctirad' (9.09 pg/2C), *Raphanus sativus* L. 'Saxa' (1.11 pg/2C), *Solanum lycopersicum* L. 'Stupické polní rané' (1.96 pg/2C), *Zea mays* L. 'CE-777' (5.43 pg/2C). The standard used for each measurement is listed in Online Resource 1 to allow for future recalculations and corrections if a more accurate genome size estimate becomes possible due to values that need to be corrected for an internal standard. For some of the standards used here, which were calibrated against human male leucocytes, other values have already been proposed based on a calibration against the sequenced genome size of rice (*Oryza sativa*), e.g., for *G. max* (2.077 pg/2C = 83%), *P. sativum* (8.018 pg/2C = 88%) and *S. lycopersicum* (1.735 pg/2C = 88%) (Šmarda et al. 2019). Calibration against *Agave americana* 'Aureomarginata', another long-used standard, which itself had been calibrated against human male leucocytes, resulted in values for *P. sativum* cv's (8.61 pg/2C = 95%), *R. sativus* (1.15 pg/2C = 104%), *S. lycopersicum* (2.03 pg/2C = 104%) and *Z. mays* (5.61 pg/2C = 103%) (Zonneveld 2021).

The 2C values of the samples, i.e., the amount of DNA in a somatic cell with non-replicated chromosomes, were calculated by multiplying the sample/standard ratios of the 2C peaks in the fluorescence histograms with the known genome size of each standard species used. Mean 2C values and standard deviations for each sample were calculated using FCS Express Version 5 software (De Novo Software, Pasadena, CA, USA).

The genome size data obtained in this study and standard species used in each measurement are listed in Online Resource 1. They are given in as physical mass in picograms [pg], which can be converted into DNA content in base pairs [bp] by multiplying it with the conversion factor 0.978×10^9 (Doležel et al. 2003).

Previously published DNA C-values were retrieved from the 'Plant DNA C-values Database' (Leitch et al. 2019; https://cvalues.science.kew.org/; release 7.1, April 2019) or were cited from the original publications if these have been published after 2019 (see Results and discussion, References). For comparison and to complement our data, only genome sizes estimated by FCM and using PI as fluorescent dye were used, as data from Feulgen microdensitometry, the most commonly used method in the past, often proved to be too unreliable for various reasons (see Greilhuber 2005; Greilhuber et al. 2007). The relevant literature data are listed in Online Resource 2.

Chromosome numbers and monoploid genome sizes (1Cx values)

Chromosome numbers were compiled from the 'Chromosome Counts Database' (CCDB 2023: see Rice et al. 2015; Rice and Mayrose 2023), the 'Index to plant chromosome numbers' (IPCN 1979 onwards) or were cited from original publications (see Results and discussion and References). The monoploid genome sizes (1Cx values) were calculated for species with known chromosome number or ploidy by dividing the 2C values by the respective ploidy level (Greilhuber et al. 2005). The mean DNA content per chromosome (MC), expressed as the average

physical mass of the chromosomes in the complement of a given plant, was calculated by dividing the 2C values by the diplophasic (sporophytic) chromosome number (2*n*) or by dividing the 1C values by the haplophasic (gametophytic) chromosome number (*n*), therefore 2C/2*n* or 1C/*n*.

Results and discussion

Genome and chromosome sizes of the Poales

2C values

The representatives from all 14 families of the order Poales, which were used for comparison, had 2C values (holoploid diplophasic, i.e., sporophytic genome sizes of the non-replicated nuclear DNA) between 0.52 and 45.26 pg (Tables 1, 2; Figs. 1a, 2; Online Resource 1; Vogel et al. 1999). However, most families had values < 2.8 pg/2C and thus fell into the category 'very small' (Leitch et al. 1998). This applies to all Bromeliaceae, Ecdeiocoleaceae, Joinvilleaceae, Mayacaceae, Thurniaceae and Typhaceae analyzed as well as to the majority of the Cyperaceae, Juncaceae and Restionaceae. The Eriocaulaceae, Flagellariaceae and Xyridaceae had 'very small' to 'medium-sized' 2C values. The greatest variation was found in the Poaceae, which ranged from 'very small' to 'very large', i.e., up to ≥ 35 pg/2C.

1Cx values

The size of the monoploid non-replicated chromosome sets was also small in most families, ranging between 0.2 and 0.9 pg/1Cx (Tables 1, 2; Fig. 1b, 2; Online Resource 1). The Eriocaulaceae and Restionaceae also had such small values, but in some cases up to ca. 2 pg/1Cx. The Poaceae again had the greatest variation, namely 0.26–9.45 pg/1Cx. The Xyridaceae consistently had comparatively high values of up to 3.51 pg/1Cx.

Mean chromosome DNA content (MC)

The chromosomes of most families had MCs < 0.2 pg, corresponding to the tiny size of most Poales chromosomes known from cytogenetic microscopical study. MCs > 0.1 pg occurred in the Eriocaulaceae and Xyridaceae. The greatest variation and the largest MCs of up to 1.84 pg were again found in the Poaceae (Tables 1, 2; Figs. 1c, 2; Online Resource 1).

Characteristics of the families

The data on genome size (2C and 1Cx values) and chromosomal DNA content (MC) for the Poales families are listed in Tables 1 and 2 and in Online Resource 1.

Bromeliaceae

The 22 bromeliad species analyzed had comparatively small 2C values of 0.52–2.45 pg, confirming the results

Table 1 Genome sizes (holoploid 2C and monoploid 1Cx values) and mean chromosome DNA content (MC) of the examined representatives of the Poales families

Families and chromosome base numbers	2C value [pg]	1Cx value [pg]	MC [pg]
Bromeliaceae (*x* = 17, 25)	0.52–2.45	0.26–0.89	0.01–0.04
Cyperaceae (*x* = ?)	0.54–11.63	N/A	0.005–0.04
Ecdeiocoleaceae (*x* = 9, 10 or 12?)	1.98	0.50	0.05
Eriocaulaceae (*x* = 8)	1.69–8.37	0.85?–2.09	0.11?–0.26
Flagellariaceae (*x* = originally? 9, 10)	1.80–3.48	0.87–0.90	0.09–0.10
Joinvilleaceae (= originally? 9)	2.37–2.72	0.68	0.08
Juncaceae (*x* = ?)	0.81–3.64	0.41–0.53	0.02–0.09
Mayacaceae (*x* = 8?)	0.94	0.47?	0.06?
Poaceae (*x* = 2, 5, 6, 7, 8, 9, 10, 11, 12)	0.67–45.26	0.26–9.45	0.02–1.84
Rapateaceae (*x* = ?)	11.54	N/A	N/A
Restionaceae (*x* = 7, 8, 9, 11, 12)	0.86–6.88	0.29–1.67	0.04–0.15
Thurniaceae (*x* = ?)	0.7	N/A	0.02
Typhaceae (*x* = 15)	0.55–1.40	0.28–0.70	0.02–0.05
Xyridaceae (*x* = 9, 13)	2.46–14.02	1.23–3.51	0.14–0.27
'Outgroup' Zingiberales: Musaceae (*x* = 11)	1.62	0.54	0.05

For details on our data, see Table 1 and Online Resource 1. For further data as specified in Material and methods, see the individual families in Results and discussion and Online Resource 2. Data for the Poaceae are from Tkach et al. (2024a, b) and Winterfeld et al. (2024). *N/A* not available

Table 2 Summary of the Poales taxa studied, providing their 2C values, chromosome numbers, ploidy levels, 1Cx values and mean chromosome DNA content (MC)

Taxon	2C value [pg]	2*n* chromosome number	Ploidy level	1Cx value [pg]	MC [pg]
Bromeliaceae					
Aechmea nudicaulis (L.) Griseb. var. *nudicaulis*	0.80	[50]	[2*x*]	0.40	0.02
Aechmea orlandiana L.B.Sm.	1.05	[50]	[2*x*]	0.53	0.02
Alcantarea edmundoi (Leme) J.R.Grant	1.11	[50]	[2*x*]	0.56	0.02
Billbergia chlorosticta Saunders	0.86	[50]	[2*x*]	0.43	0.02
Brocchinia reducta Baker	0.85	[50]	[2*x*]	0.43	0.02
Bromelia pinguin L.	0.86	[50]	[2*x*]	0.43	0.02
Catopsis sessiliflora (Ruiz & Pav.) Mez	1.04	50	2*x*	0.52	0.02
Dyckia velascana Mez	1.78	50	2*x*	0.89	0.04
Fascicularia bicolor (Ruiz & Pav.) Mez	1.13	50	2*x*	0.57	0.02
Glomeropitcairnia erectiflora Mez	1.47	N/A	N/A	N/A	N/A
Hechtia glauca Burt-Utley & Utley	0.94	[50]	[2*x*]	0.47	0.02
Neoglaziovia variegata (Arruda) Mez	2.45	100	4*x*	0.61	0.02
Neoregelia richteri W.Weber	0.95	[50]	[2*x*]	0.48	0.02
Orthophytum saxicola (Ule) L.B.Sm.	0.59	50	2*x*	0.30	0.01
Pitcairnia nigra (Carrière) André var. *nigra*	1.35	[50]	[2*x*]	0.68	0.03
Puya vasquezii Ibisch & E.Gross	0.88	[50]	[2*x*]	0.44	0.02
Quesnelia edmundoi L.B.Sm. var. *edmundoi*	0.52	50	2*x*	0.26	0.01
Racinaea schumanniana (Wittm.) J.R.Grant	1.88	N/A	N/A	N/A	N/A
Tillandsia secunda Kunth	2.06	N/A	N/A	N/A	N/A
Vriesea simplex (Vell.) Beer	1.10	[50]	[2*x*]	0.55	0.02
Werauhia vittata (Mez & Werckle) J.R.Grant	1.28	[50]	[2*x*]	0.64	0.03
Wittrockia superba Lindm.	1.13	[50]	[2*x*]	0.57	0.02
Cyperaceae					
Bolboschoenus laticarpus Marhold, Hroudová, Ducháček & Zákr.	0.54	110	N/A	N/A	0.005
Bolboschoenus maritimus (L.) Palla	0.58	110	N/A	N/A	0.01
Carex pilosa Scop.	1.12	44	N/A	N/A	0.03
Carex vesicaria L.	0.90	82	N/A	N/A	0.01
Cladium mariscus (L.) Pohl	0.57	36	N/A	N/A	0.02
Cyperus diffusus Vahl	1.35	38	N/A	N/A	0.04
Cyperus gracilis R.Br.	0.64	N/A	N/A	N/A	N/A
Cyperus macrocarpus (Kunth) Boeckeler	0.62	N/A	N/A	N/A	N/A
Eleocharis palustris (L.) Roem. & Schult.	11.63	N/A	N/A	N/A	N/A
Rhynchospora colorata (L.) H.Pfeiff.	0.62	120	N/A	N/A	0.01
Schoenoplectus tabernaemontani (C.C.Gmel.) Palla	1.31	42	N/A	N/A	0.03
Eriocaulaceae					
Eriocaulon compressum Lam.	6.00	40	[5*x*?]	1.20?	0.15
Flagellariaceae					
Flagellaria indica L.	3.48	38	N/A	N/A	0.09
Joinvilleaceae					
Joinvillea plicata (Hook.f.) Newell & B.C.Stone	2.72	36	N/A	N/A	0.08
Juncaceae					
Juncus articulatus L.	3.64	80	N/A	N/A	0.05
Juncus bufonius L.	1.78	108	N/A	N/A	0.02
Luzula campestris (L.) DC. *	0.81	12	2*x*	0.41	0.07
Luzula sylvatica (Huds.) Gaudin *	1.05	12	2*x*	0.53	0.09
Mayacaceae					
Mayaca fluviatilis Aubl.	0.94	N/A	N/A	N/A	N/A

Table 2 (continued)

Taxon	2C value [pg]	2*n* chromosome number	Ploidy level	1Cx value [pg]	MC [pg]
Rapateaceae					
Stegolepis guianensis Klotzsch ex Körn.	11.54	N/A	N/A	N/A	N/A
Restionaceae					
Baloskion tetraphyllum (Labill.) B.G.Briggs & L.A.S.Johnson	0.86	22	2*x*	0.43	0.04
Cannomois virgata (Rottb.) Steud.	3.19	N/A	N/A	N/A	N/A
Elegia capensis (Burm.f.) Schelpe	2.47	N/A	N/A	N/A	N/A
Restio subverticillatus (Steud.) Mast.	1.86	N/A	N/A	N/A	N/A
Rhodocoma foliosa (N.E.Br.) H.P.Linder & C.R.Hardy	1.66	N/A	N/A	N/A	N/A
Thurniaceae					
Prionium serratum (L.f.) Drège ex E.Mey.	0.70	46	N/A	N/A	0.02
Typhaceae					
Sparganium americanum Nutt.	1.40	[30]	[2*x*]	0.70	0.05
Sparganium erectum L.	1.05	30	2*x*	0.53	0.04
Typha laxmannii Lepech.	0.55	30	2*x*	0.28	0.02
Xyridaceae					
Xyris caroliniana Walter	2.68	18	2*x*	1.34	0.15
Xyris difformis Chapm.	4.46	18	2*x*	2.23	0.25
Xyris laxiflora F.Muell.	2.68	N/A	N/A	N/A	N/A
Zingiberales: Musaceae					
Musa×*paradisiaca* L.	1.62	33	3*x*	0.54	0.05

Mean values are given for multiple accessions of the same taxon and cytotype (asterisk). The chromosome numbers were sourced from CCBD and the original literature. Square brackets indicate inferred chromosome numbers and ploidy levels based on 2C values and available congeneric species data. Online Resource 1 provides complete details of the analyzed samples and measurements. *N/A* not available

of previous FCM studies in this large New World family with ca. 80 genera and 3,760 species (e.g., Gitaí et al. 2014; Moura et al. 2018; Hirsch et al. 2019; Müller et al. 2019; Cruz et al. 2020; Paule et al. 2020). There is increasing evidence that $x = 25$ represents the monoploid chromosome number of bromeliads, with a few exceptions resulting from reductional dysploidy, for example, $x = 17$ in the cryptanthoid complex (Ramírez-Morillo and Brown 2001; Gitaí et al. 2014; Cruz et al. 2020). Previously proposed lower numbers such as $x = 7$, 8 or 9 have not be proven to date, as there are no diploids in which correspondingly low chromosome numbers would occur. Most of the species we studied for their genome size must be considered diploid if $x = 25$ is taken as the chromosome base number, while *Neoglaziovia variegata* (Arruda) Mez is tetraploid. Accordingly, the 1Cx values varied between 0.26 and 0.89 pg and the chromosomes were small with a MC of 0.01–0.04 pg (Fig. 1). The chromosome numbers are not yet known for most taxa, so that the 1Cx values cannot be determined either. Judging by the 2C values, most of these taxa are probably diploid, which is also confirmed by the chromosome numbers analyzed for the genera *Aechmea* Ruiz & Pav., *Alcantarea* (É.Morren ex Mez) Harms, *Billbergia* Thunb., *Brocchinia* Schult.f., *Bromelia* L., *Hechtia* Klotzsch, *Neoregelia* L.B.Sm., *Pitcairnia* L'Hér., *Puya* Molina, *Vriesea* Lindl., *Werauhia* J.R.Grant and *Wittrockia* Lindm. (Gitaí et al. 2014), although not yet for the species used in this study. Their calculated 1Cx values and MCs would be 0.40–0.68 pg and 0.02–0.03 pg, respectively, as indicated by squared brackets in Table 2. These values are comparable to the data of the bromeliads with known chromosome number analyzed in this study (see Table 2). Our examined specimen *Quesnelia edmundoi* L.B.Sm. specimen was obviously diploid, which means that the previously studied *Quesnelia* Gaudich. species with twice as high 2C values (Paule et al. 2020) were in fact tetraploid and not diploid as assumed.

Cyperaceae

Ten of the eleven Cyperaceae species studied had low 2C values between 0.54 pg (*Bolboschoenus laticarpus* Marhold, Hroudová, Ducháček & Zákr.) and 1.35 pg (*Schoenoplectus tabernaemontani* (C.C.Gmel.) Palla). Such small genome sizes seem to be typical for this large family (5400 species in 106 genera) and have been found repeatedly in studies using FCM with PI as fluorescent dye (e.g., Bai et al. 2012; Kaur et al. 2012; Lipnerová et al. 2013; Šmarda et al. 2019; Zonneveld 2019; Burchardt et al. 2020; Elliott et al. 2022, 2024). According to the chromosome counts available for

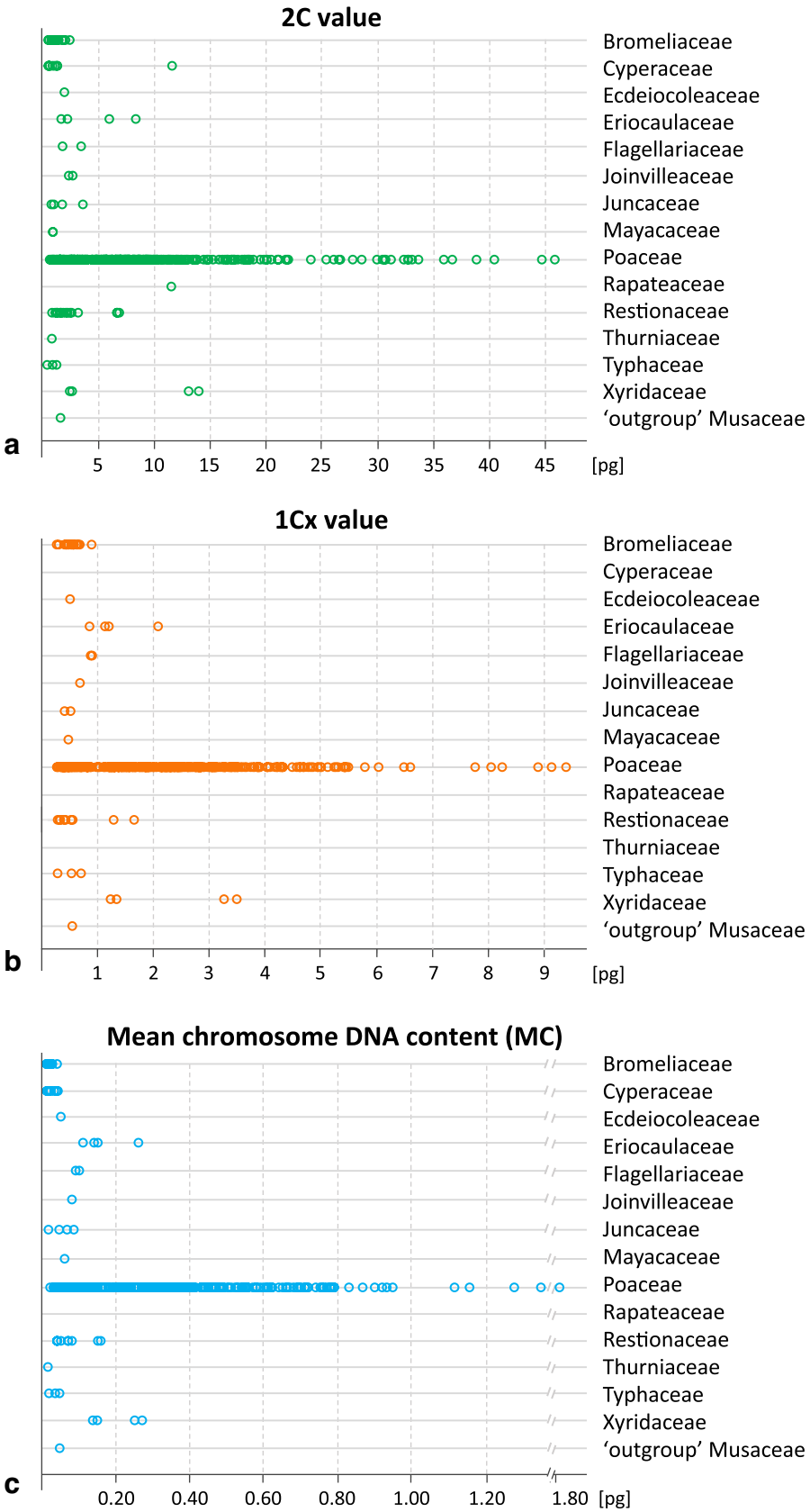


Fig. 1 Variation of genome sizes and chromosome DNA content in the families of Poales examined in this study. **a** Holoploid 2C genome sizes. **b** Monoploid 1Cx genome sizes. **c** Mean chromosome DNA contents (MC). For our data see Table 1 and Online Resource 1, and for further data as specified in Material and methods see the individual families in Results and discussion. Data for the Eriocaulaceae, Flagellariaceae and Xyridaceae include genome size estimates of Hanson et al. (2003) and Šmarda et al. (2014); for the Joinvilleaceae and Mayacaceae of Šmarda et al. (2014); for the Restionaceae of Šmarda et al. (2014) and Linder et al. (2017: Table 1, '2*n*' column); and for the Typhaceae of Šmarda et al. (2019) and Zonneveld (2019). These additional data are listed in Online Resource 2. Data for the Poaceae are from Tkach et al. (2024a, b) and Winterfeld et al. (2024)

our studied taxa (2*n* = ca. 36–120), their MCs would be rather small, from less than 0.01 to 0.04 pg (Tables 1, 2; Fig. 1).

The much larger genome size of 11.63 pg/2C in *Eleocharis palustris* (L.) Roem. & Schult. belongs to a probably highly polyploid cytotype of this species, for which genome sizes of 9.30 pg (presumably 10*x*) and 10.80 pg (ploidy unknown) have also been reported (Šmarda et al. 2019; Zonneveld 2019), but such large genome sizes are not characteristic of the entire genus (see Šmarda et al. 2019; Zonneveld 2019; Elliott et al. 2022). Polyploidy is not the only reason for the differences in genome size between different *Eleocharis* R.Br. species, with the smallest genome sizes of 0.86 pg/2C in *E. maculosa* (Vahl) R.Br. ex Roem. & Schult. (cytotype with 2*n* = 6) and 0.98–1.40 pg/2C recorded for *E. maculosa, E. ovata* (Roth) Roem. & Schult. and *E. parishii* Britton (all 2*n* = 10) (de Souza et al. 2018; Šmarda et al. 2019; Zonneveld 2019; Elliott et al. 2022). Indeed, a significant increase of Ty-*copia* LTR retrotransposons was recorded in the *Eleocharis* species with the largest genomes, accounting for up to 70% of total nuclear DNA (Zedek et al. 2010; Bureš et al. 2013; de Souza et al. 2018), which would also lead to considerable differences in their MCs.

The total range of variation in 2C values estimated with FCM for Cyperaceae appears to be 0.36 pg in *Scleria levis* Retz. to 23.61 pg (≈ 23.094 Mbp) in *Schoenus aureus* T.L.Elliott & Muasya (Elliott et al. 2022).

Monoploid genome sizes (1Cx values) are hard to determine in Cyperaceae. The excessive dysploid variation in chromosome numbers of 2*n* = 4–224 (Vanzela et al. 1996; Roalson 2008; Dias Silva et al. 2020), caused by holocentric chromosomes and agmatoploidy/symploidy, complicates the determination of chromosome base numbers in this family.

Ecdeiocoleaceae

This small west Australian family, which was not analyzed in this study, together with the families Flagellariaceae, Joinvilleaceae and Poaceae forms the graminid clade as delineated in most current classifications (e.g., Briggs et al. 2014). 2C genome sizes of 1.98 pg and 1,651 Mbp (≈ 1.69 pg) were estimated in *Ecdeiocolea monostachya* F.Muell. using FCM with PI as fluorescent dye (Hanson et al. 2005; Šmarda et al. 2014). A possible explanation for the genome size discrepancy could be the different chromosome numbers reported for *E. monostachya*. The chromosome number of this species has been reported as 2*n* = ca. 38 (Hanson et al. 2005) and 2*n* = ca. 48 (Linder et al. 1998, referring to an unpublished chromosome count of B.G. Briggs). The chromosome base number is thus probably either *x* = 9–10 or *x* = 12 if higher chromosome base numbers such as *x* = 18, 19 are not considered 'original' either in the Ecdeiocoleaceae or in the Joinvilleaceae and Flagellariaceae (see below). If we assume a fourfold ploidy in *E. monostachya*, the 1Cx value is 0.42–0.50 pg and the MC is 0.04–0.05 pg (Tables 1, 2; Fig. 1). If both chromosome numbers are correct, then *E. monostachya* comprises at least two distinct cryptic species, but this would require confirmation. If not, the discrepancy in genome size is an artifact that may be due to the use of different standards and their calibration.

Eriocaulaceae

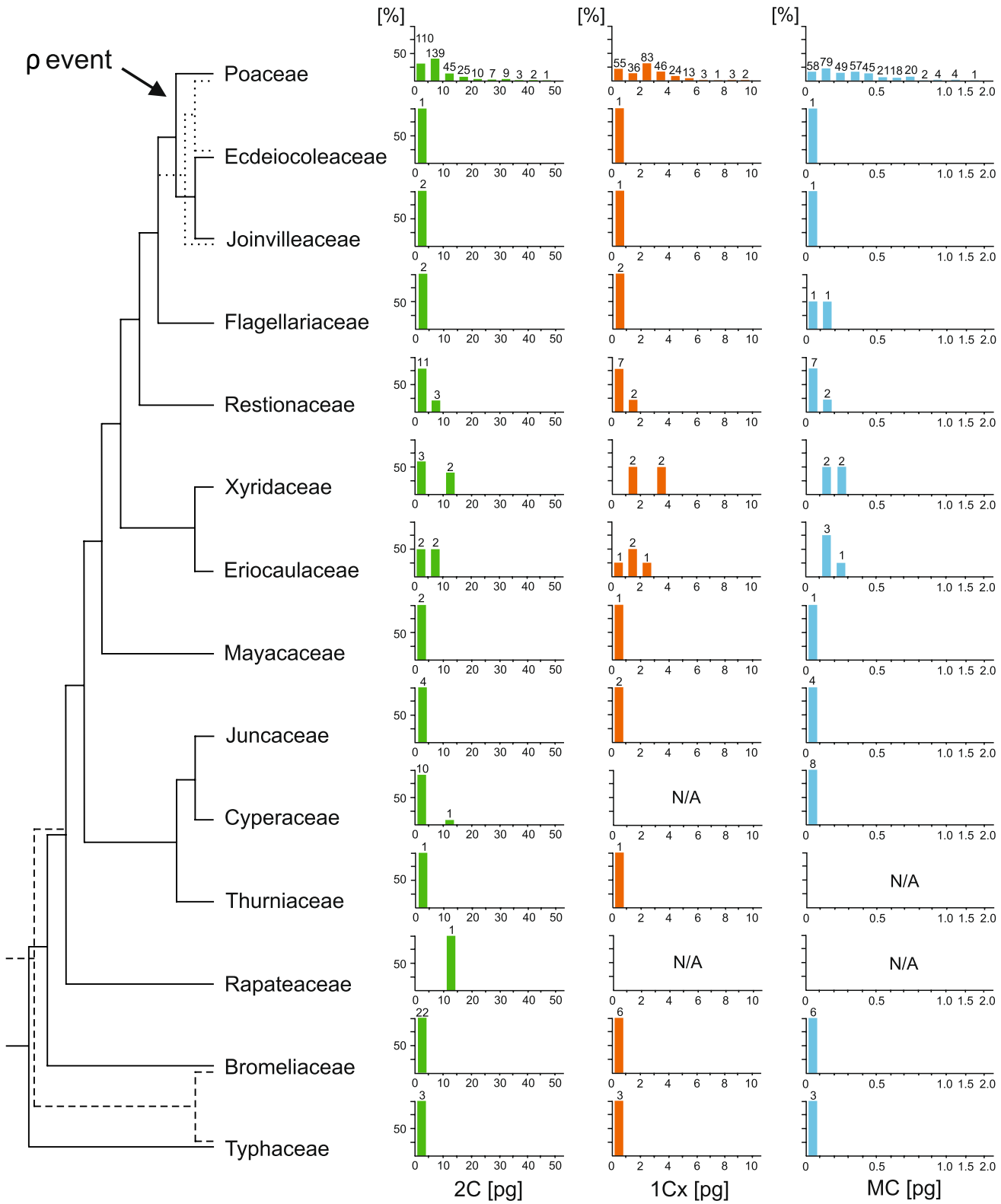
This family of seven genera and ca. 1200 species, which together with the Xyridaceae forms the 'xyrid clade', was represented in this study only by *Eriocaulon compressum* Lam. which had a 6.00 pg/2C. In this species, the chromosome number 2*n* = 40 has been recorded (Cave 1967), suggesting a MC of 0.15 pg (Tables 1, 2; Fig. 1). Chromosome numbers, involving polyploidy, are generally quite variable in *Eriocaulon* L. (CCDB 2023; Mane et al. 2021). There is increasing evidence for the chromosome base number *x* = 8 rather than *x* = 9 or 10 in this genus (see Mane et al. 2021), suggesting that *E. compressum* may be pentaploid and have a 1Cx value of 1.20 pg.

A 2C value of 8.37 pg, also estimated by FCM using PI as fluorescent dye, was recorded for *E. aquaticum* (Hill) Druce, which was a tetraploid with 2*n* = 32 (Hanson et al. 2003), giving a 1Cx value of 2.09 pg and a MC of 0.26 pg.

2C values of 2204 and 1655 Mbp (≈ 2.25 and 1.69 pg) were determined for *E. megapotamicum* Malme und *E.* sp., respectively (Šmarda et al. 2014). The chromosome numbers of the two accessions are unknown, but judging from the results in *E. aquaticum* and *E. compressum*, they are probably diploid rather than polyploid, implying 1Cx values of 1.13 pg and 0.85 pg, respectively.

Flagellariaceae

This small paleotropical family comprises only one genus with about five species. Our estimated 2C value of 3.48 pg in *Flagellaria indica* L. (Table 2) does not match the genome sizes of 1,352 Mbp (≈ 1.38 pg) and 2708 Mbp (≈ 2.76 pg) previously found in other accessions of this species (Šmarda et al. 2014). Another *Flagellaria* L. species, *F. guineensis* Schumach., was found to have a genome size of 1.80 pg (Hanson et al. 2003). These four genome size estimates, therefore, show a ratio 1:1.3:2:2.5, so that there may be doubled genome sizes (2 instead of 1 and 2.5 instead of 1.3), i.e., cases of polyploidy. However, this result is difficult to interpret because all available chromosome counts in both species are only 2*n* = 38 (CCDB 2023) and no chromosome counting was made in the accessions used for the genome size estimates. We suspect that there is more variation in chromosome number than is currently known. *Flagellaria* also shows a high degree of phenotypic variation



and sometimes unclear species boundaries when considering molecular phylogenetic characters, especially in relation to the widely distributed *F. indica* (Wepfer and Linder 2014). This could be a sign of hybridization and different ploidy levels, which would explain the observed variation in DNA C-values.

Our genome size estimate of 3.48 pg and the chromosome number $2n = 38$ could reflect fourfold ploidy, while

◂**Fig. 2** Holoploid (2C) and monoploid (1Cx) genome sizes and mean chromosome DNA content (MC) arranged according to a Poales phylogenetic tree. DNA content intervals are shown on the x-axis of the bar graphs, while the y-axis represents the corresponding percentage estimates, which sum to 100% for each family. The number of estimates falling within each interval is displayed above the corresponding bar. The simplified phylogenetic tree is taken from single-copy nuclear phylogenomic analyses (Timilsena et al. 2022). An alternative sister relationship of Typhaceae and Bromeliaceae based on Angiosperms353 bait capture analysis (Baker et al. 2022) is indicated by a dashed line. The dotted line indicates a different relationship within Poaceae/Ecdeiocoleaceae/Joinvilleaceae clade as depicted by plastome-based phylogenomics, which also showed Bromeliaceae, Typhaceae and the rest of Poales unresolved (Li et al. 2021; Wu et al. 2022). For our data see Table 1 and Online Resource 1, and for further data as specified in Material and methods see the individual families in Results and discussion. Data for the Eriocaulaceae, Flagellariaceae and Xyridaceae include genome size estimates of Hanson et al. (2003) and Šmarda et al. (2014); for the Joinvilleaceae and Mayacaceae of Šmarda et al. (2014); for the Restionaceae of Šmarda et al. (2014) and Linder et al. (2017: Table 1, '2*n*' column); and for the Typhaceae of Šmarda et al. (2019) and Zonneveld (2019). These additional data are listed in Online Resource 2. Data for the Poaceae are from Tkach et al. (2024a, b) and Winterfeld et al. (2024)

1.80 pg reflects twofold ploidy, implying the chromosome base number $x = 9–10$. This could also apply to the genome size estimates of Šmarda et al. (2014), who instead suggested $2n = 38$ and $2n = 76$ as possible chromosome numbers of their accessions. According to our considerations, the 1Cx value of our *F. indica* accession would be 0.87 pg and the MC 0.09 pg (Table 2; Fig. 1). It is clear that follow-up studies combining genome size measurements with chromosome counts of the respective accessions are needed to draw reliable conclusions.

Joinvilleaceae

The 2C value of 2.72 pg in *Joinvillea plicata* (Hook.f.) Newell & B.C.Stone is consistent with the previously estimated 2,414 Mbp (≈ 2.46 pg) in this species, a value very similar to that of the congener *J. borneensis* Becc., which had 2,324 Mpb (≈ 2.37 pg) (Šmarda et al. 2014). All four species recognized currently of *Joinvillea* Gaudich. ex Brongn. & Gris (Govaerts 2022) have the chromosome number $2n = 36$ (Newell 1969). Assuming that this number reflects a fourfold ploidy based on $x = 9$, the 1Cx value of *J. plicata* would be 0.68 pg and the MC would be 0.08 pg (Tables 1, 2; Fig. 1).

Juncaceae

Small holoploid genomes of 0.81–3.64 pg/2C were also characteristic of the examined species of the closely related family Juncaceae (rush family), which comprises a total of eight genera and ca. 460 species. The four accessions of two *Luzula* DC. species examined had smaller holoploid genome sizes (0.81–1.05 pg/2C) than the two *Juncus* L. species examined (1.78–3.64 pg/2C). The mean 1Cx values were 0.41–0.53 pg in the *Luzula* species studied, but are unknown in *Juncus*, due to the unknown ploidy level of the species sampled (Table 1, 2; Fig. 1). The MC was 0.07–0.09 and 0.02–0.05 pg in the studied *Luzula* and *Juncus* species, respectively. Both genera differ in their chromosome organization as the chromosomes of *Luzula* are holocentric, whereas *Juncus* has monocentric chromosomes as recently shown (Guerra et al. 2019).

The total range of variation in 2C values estimated for Juncaceae using FCM and PI appears to be from 0.33 pg in *J. maritimus* Lam. to 8.12 pg in *L. purpureosplendens* Seub. (Bożek et al. 2012; Zonneveld 2019).

In general, genome sizes tended to be small in the cyperid clade. MC did not seem to depend on whether the plant has holocentric (for example, *Carex* L., *Cyperus* L., *Eleocharis*, *Rhynchospora* Vahl, *Luzula*) or monocentric chromosomes such as *Juncus* and *Prionium* E.Mey. (Baez et al. 2020). Centromere information is apparently not available for *Bolboschoenus* (Asch.) Palla, *Schoenoplectus* (Rchb.) Palla and *Scirpus* Tourn. ex L.

Mayacaceae

The low 2C value of 0.94 pg estimated in *Mayaca fluviatilis* Aubl. is largely consistent with 845 Mbp (≈ 0.86 pg) previously recorded (Šmarda et al. 2014). In addition, 638 Mbp (≈ 0.65 pg) were recorded in a second accession of this species (Šmarda et al. 2014). The chromosome number of the Mayacaceae, of which *Mayaca* Aubl. is the sole genus with about ten species, was given as $n = 8$ (Goldberg 1989; Stevenson 1998) or $x = 8$ (Takhtajan 1997). Unfortunately, we were not able to research more precise information on the original chromosome count and the species identity. Therefore, if our *M. fluviatilis* had $2n = 2x = 16$, the 1Cx value would be 0.47 pg and the MC would be 0.06 pg (Table 1, 2; Fig. 1).

Poaceae

Grasses are by far the largest family of Poales, comprising about 11,800 species (Soreng et al. 2022). They have a cosmopolitan distribution, occurring on all continents. The species examined had a wide range of genome sizes, with 2C values of 0.67–45.26 pg, 1Cx values of 0.26–9.45 pg and MCs of 0.02–1.84 pg (Table 1; Figs. 1, 2; Vogel et al. 1999; Tkach et al. 2024a, 2024b; Winterfeld et al. 2024).

Rapateaceae

Stegolepis Klotzsch ex Körn., an endemic Guianan genus of the Rapateaceae, had a comparatively high 2C value of 11.54 pg in studied *S. guianensis* Klotzsch ex Körn. In the

same species, a 2C value of 5,343 Mbp (≈ 5.46 pg) was found (Šmarda et al. 2014), which is about half as high as our estimate and could indicate the occurrence of different ploidy levels. The chromosome number(s) and consequently the 1Cx values and the MC of *S. guianensis* are not yet known. The only known chromosome numbers for the Rapateaceae are $2n = 52$ in species of the South American *Spathanthus* Desv. and *Cephalostemon* R.H.Schomb., while $2n = 22$ occurs in the African *Maschalocephalus* Gilg & K.Schum. (Stevenson et al. 1998).

Restionaceae

Our sampled representatives of five genera had 2C values of 0.86–3.19 pg (Tables 1, 2; Fig. 1). *Baloskion tetraphyllum* (Labill.) B.G.Briggs & L.A.S.Johnson (0.86 pg/2C), which occurs in eastern Australia, is the only taxon of the **subfamily Leptocarpoideae** sampled in this study. It is diploid with $2n = 22$ (Briggs 1966), so its 1Cx value was 0.43 pg and the MC was 0.04 pg (Table 2). In the western Australian *Alexgeorgea nitens* (Nees) L.A.S.Johnson & B.G.Briggs, another member of this subfamily, a 2C genome size of 6,532 Mbp (≈ 6.68 pg) (Šmarda et al. 2014) and chromosome numbers of $2n =$ ca. 44 (Briggs 1963: Table 1) and also $2n = 22$ (Briggs 1963: p. 230) have been found. Assuming that the first chromosome number is the correct one, the 1Cx value would be 1.67 pg and the MC 0.15 pg, i.e., 2–threefold higher than in other restios except for the centrolepids (see below).

For the large African and Madagascan **subfamily Restionoideae**, we obtained 2C values of *Cannomois virgata* (Rottb.) Steud. (3.19 pg), *Elegia capensis* (Burm.f.) Schelpe (2.47 pg), *Restio subverticillatus* (Steud.) Mast. (1.86 pg) and *Rhodocoma foliosa* (N.E.Br.) H.P.Linder & C.R.Hardy (1.66 pg) but their chromosome numbers are not known. These values are consistent with previous genome size estimates available for many taxa in this subfamily (Šmarda et al. 2014 and, in particular, Linder et al. 2017). The latter study mostly counted $2n = 32$, which was considered diploid. In addition, accessions with larger genome sizes were found that were classified as tetra-, hexa- and octoploids, but also diploid species with $2n = 20$. The species with $2n = 32$ could therefore be actually tetraploids based on $x = 8$, which is also likely since the other subfamilies of the Restionaceae show a repeated occurrence of chromosome numbers based on $x = 7, 9, 11, 12$ (Briggs 1963, 1966, 2012). In this case, the recalculated 1Cx values of the African restios included in Fig. 1 are approximately 0.29–0.56 pg and the MC is 0.04–0.07 pg. Regarded for this graph were the nine taxa and accessions for which Linder et al. (2017: Table 1, '$2n$' column) provided chromosome counts.

These values are therefore comparable in magnitude to those of the Australian *Baloskion* Raf. In addition, accessions with larger genome sizes were found (Linder et al. 2017), presumably indicating tetra-, hexa- and octoploids.

Centrolepis aristata (R.Br.) Roem. & Schult., a member of the mainly Australasian **subfamily Centrolepidoideae**, is characterized by a large genome size of 6724 Mbp (≈ 6.88 pg) (Šmarda et al. 2104). In this species, $2n = 16$ has been recorded for two accessions (Briggs 2002) but also $2n =$ ca. 46–48 (Hamann 1960), indicating a diploid or tetra- to hexaploid level, respectively. The 1Cx value could therefore be either 3.44 or 1.15–1.72 pg and the MC 0.43 or 0.15 pg. In any case, the values are higher than those of most other restios. Compared to the typical Restionaceae, the centrolepids are also characterized by several remarkable morphological features (often diminutive annuals, well-developed leaf blades, absence of dioecy, etc.), which have been discussed as possible neoteny in vegetative morphology (Linder et al. 2000; Briggs et al. 2014; Sokoloff et al. 2015). The evolution of such morphological peculiarities could be related to the extremely rapid rates of nucleotide substitution detectable by molecular phylogenetic analyses of centrolepids (Briggs et al. 2014) and to their comparatively rapid generational turnover in the case of the annual life form, which is atypical in the Restionaceae. Furthermore, rapid genome evolution could also be responsible for the increase in genome size in *Centrolepis* Labill. Interestingly, similar correlations between genome size increase and simplification and reduction of morphological patterns have been found, for example, in the monocot family Araceae (including Lemnaceae, the duck-weed family). The series of genera *Pistia-Spirodela-Lemna-Wolffiella-Wolffia* shows a well-known progressive reduction in morphological complexity, size and generation time. Unexpectedly, *Wolffia* Horkel ex Schleid, the genus with the smallest angiosperms overall, and *Wolffiella* Hegelm. have significantly larger genomes than *Spirodela* Schleid. and *Pistia* L. (Greilhuber 1995; Wang et al. 2011; Kocjan et al. 2022). Larger genomes are associated with larger cell sizes and this relationship could be advantageous by allowing faster development and shortening of the minimum life cycle as addressed by the nucleotype theory (Bennett 1972). This may also be true for centrolepids and further research into this relationship would certainly be worthwhile.

Thurniaceae

This small family of four species belongs to the cyperid clade together with Cyperaceae and Juncaceae. It is disjunctively distributed in northeastern South America (*Thurnia* Hook.f.) and southern Africa (monospecific *Prionium*). *Prionium serratum* (L.f.) Drège had a 2C value of 0.70 pg (Tables 1, 2; Fig. 1), which is consistent with 670 Mbp (≈ 0.69 pg) previously recorded for this species, also

using FCM with PI as fluorescent dye (Baez et al. 2020). The ploidy level of *P. serratum* ($2n = 46$) and therefore the monoploid genome size (1Cx) are not known, but the chromosomes are comparatively small (MC 0.02 pg) and have a localized centromere (monocentric chromosomes).

Typhaceae

Species from both genera of this family, including the former Sparganiaceae, were examined. The 2C values were 0.55 pg in *Typha laxmannii* Lepech., which is broadly consistent with a previous estimate of 0.52 pg (Šmarda et al. 2019). Similar genome sizes of 0.46–0.57 pg/2C were recorded for other *Typha* species (*T. angustifolia* and *T. latifolia*), while recorded values of 0.85 pg/2C for *T. laxmannii* and 0.79 pg/2C for *T. minima* (Šmarda et al. 2019; Zonneveld 2019) could be due to higher ploidy.

The 2C values were 1.05 pg for *Sparganium erectum* L., broadly consistent with previous estimates of 0.85–0.90 pg and 1.03–1.11 pg, respectively (Šmarda et al. 2019; Zonneveld 2019), and 1.40 pg for *S. americanum* Nutt. Chromosome numbers available for many *Sparganium* L. and *Typha* L. species indicate that almost all are diploid with $2n = 2x = 30$ (CCDB 2023). Lower chromosome numbers have not yet been recorded for the family, suggesting $x = 15$ as the chromosome base number. Assuming that *S. americanum* is also diploid (no count available), this results in a low 1Cx value of 0.28–0.70 pg and a MC of 0.02–0.05 pg for the Typhaceae (Tables 1, 2; Fig. 1).

Xyridaceae

This family of five genera and about 400 species was represented in our study by three species of *Xyris* Gronov. ex L., which had almost identical 2C values of 2.46–2.68 pg. Together with chromosome numbers of $2n = 2x = 18$ (Lewis 1961; Lewis et al. 1962; Kral 1966), the North American species *X. difformis* Chapm. and *X. caroliniana* Walter had 1Cx values of 1.23–1.34 pg and a MC of 0.14–0.15 pg, respectively, (Tables 1, 2; Fig. 1). The reported 2C value of 2,385 Mbp (≈ 2.44 pg) for *X. caroliniana* (Šmarda et al. 2014) is consistent with our estimate. Taxonomically, *X. caroliniana* and *X. difformis* both belong to *X.* sect. *Xyris*.

Although a chromosome count is not yet available, the same somatic chromosome number $2n = 18$, also based on $x = 9$, is not unlikely for our third studied species, West Australian *X. laxiflora*, possibly suggested by its 2C value of 2.68 pg, which agrees remarkably well with that of the two American species examined. This would be particularly interesting from a cytogeographical point of view, as the Australian *Xyris* species studied cytogenetically so far had $x = 13$ throughout (Briggs 1966). *Xyris laxiflora* F.Muell. is a representative of the strictly Australian-New Caledonian sect. *Pomatoxyris* Endl. (Conn and Doust 1997). This suggests that $x = 9$, the 'primary' chromosome base number of *Xyris* (Benko-Iseppon and Wanderley 2002), may also occur in species of sect. *Pomatoxyris* and is not restricted to sect. *Xyris* as previously thought. However, a more detailed investigation would be necessary.

Two other genome size estimates in xyrids, both using FCM and PI, are available: The Bornean *X. complanata* R.Br. (sect. *Xyris*), which had a higher 2C value of 12,820 Mbp (≈ 13.11 pg) (Šmarda et al. 2014), is a tetraploid species with $2n = 50–52, 52$ (Briggs 1966). This holoploid chromosome number based on $x = 13$ is considered as a 'secondary' base number in *Xyris* (Benko-Iseppon and Wanderley 2002). Its 1Cx value would be 3.28 pg and the MC would be 0.25 pg. *Xyris gracilis* R.Br. subsp. *gracilis*, another Australian member of sect. *Pomatoxyris*, has a 2C value of 14.02 pg (Hanson et al. 2003). The chromosome number of this accession was not counted by these authors, but was considered to be diploid with $2n = 26$ according to an earlier chromosome count by Briggs (1966). However, comparison with the genome size estimate of tetraploid *X. complanata* (see above) suggests that this accession of *X. gracilis* subsp. *gracilis* was tetraploid ($2n = 4x = 52$) rather than diploid. Its 1Cx value would therefore be 3.51 pg and the MC 0.27 pg. All in all, there seems to be more variation in genome and chromosome sizes in *Xyris* than our preliminary results suggest.

'Outgroup'. For a representative of the **Musaceae**, the banana family from the distantly related order Zingiberales, a 2C value of 1.62 pg was estimated in *Musa* × *paradisiaca* L. (Table 2). This amount is broadly consistent with that reported for the triploid *M. acuminata* Colla (1,658 Mbp ≈ 1.70 pg) and for other cultivated triploid banana species or cultivars (Lysák et al. 1999; Šmarda et al. 2014; Li et al. 2024). Thus, the 1Cx genome size was 0.54 pg and the MC was 0.05 pg.

Genome sizes and phylogeny of the Poales

Recent phylogenetic studies on the Poales support the previously frequently questioned inclusion of the bromeliads in this order and show a broadly concordant branching order of the families (Fig. 2), regardless of whether plastid or nuclear DNA data are used (Li et al. 2021; Baker et al. 2022; Timilsena et al. 2022; Wu et al. 2022). However, the main differences concern, first, the relationship of the Bromeliaceae and Typhaceae, either in a clade or as monophyletic sister families, but they are consistently placed as the earliest divergent lineages in the Poales trees. Second, the relationships among the Ecdeiocoleaceae, Joinvilleaceae and Poaceae vary, but they are consistently placed in a graminid clade (see Fig. 2 and legend to Fig. 2).

2C values

Most lineages of the Poales have comparatively small holoploid DNA genome sizes of < 3 pg/2C. This is especially true for some of the phylogenetically 'early diverging' lineages, such as Bromeliaceae and Typhaceae, which have genomes usually < 2 pg/2C (Figs. 1A, 2). Only a few families of Poales have also larger holoploid genomes, including representatives of the Eriocaulaceae and Xyridaceae (xyrid clade), the Restionaceae, Cyperaceae and especially Poaceae (Figs. 1A, 2). The holoploid genome of Rapateaceae is rather large, with a 2C value of 11.54 pg (Fig. 2). However, it is uncertain whether this is representative of the entire family (see above). In summary, only a minority of Poales families has evolved large 2C values. Within the commelinoids, also most Zingiberales families, including presumably triploid *Musa*×*paradisiaca* with 1.62 pg/2C (Table 2; Online Resource 1) and other representatives of Musaceae and Rapateaceae (Šmarda et al. 2014; Čížková et al. 2015; Winterfeld et al. 2020), have comparably small 2C values, while most Commelinales and Arecales have larger genome sizes (Leitch et al. 2010).

1Cx values

While the fluctuations in the size of the holoploid genome (2C, 1C) are mainly caused by changes both in the amount of medium-repetitive DNA in the chromosomes and by the multiplication of chromosome sets, i.e., the polyploidy that often occurs in plants, the 1Cx value takes the latter factor into account by providing a measure of the genome size of a single (monoploid) chromosome set.

Although variations in 1Cx values are still primarily due to variations in repetitive DNA content, the 1Cx value nevertheless provides a genome size for a complete (monoploid) set of chromosomes with the full content of genes and genetic information of a given organism. It is thus more suitable for comparisons between organisms as it eliminates the random 'confounding factor' of polyploidy. The disadvantage is that knowledge of the ploidy level of an organism, i.e., its chromosome number $2n$ or n and the chromosome base number x, is required to calculate the 1Cx value. In the absence of this knowledge, in many cases therefore the 1Cx values of the taxa examined for 2C values in this study could not be calculated, namely for the Rapateaceae, Thurniaceae and all taxa with holocentric chromosomes such as the Cyperaceae and *Luzula* in the Juncaceae (Figs. 1B, 2).

The smallest monoploid genomes of Poales with a 1Cx of < 0.4 pg were found in the Bromeliaceae, Typhaceae, Poaceae and Restionaceae, although especially the Poaceae were often characterized by much larger genomes of > 2.0 pg/1Cx. The xyrid clade (Eriocaulaceae, Xyridaceae) was characterized by significantly larger 1Cx values of > 0.8 pg, which was also true for the sister families of the Poaceae in the graminid clade, namely Ecdeiocoleaceae and Joinvilleaceae, and to Flagellariaceae, although to a lesser extent.

Mean chromosome DNA content (MC)

The MC as a measure of chromosome size was also the lowest in the Bromeliaceae, Typhaceae, Cyperaceae, Thurniaceae and Ecdeiocoleaceae, whose chromosomes have ≤ 0.05 pg, mostly even ≤ 0.02 pg (Figs. 1C, 2). MCs of ≤ 0.05 pg also occurred in some Restionaceae and Poaceae, although most of them had larger chromosomes. The xyrid clade (Eriocaulaceae, Xyridaceae) was again characterized by comparatively large mean chromosome sizes of about 0.1–0.3 pg.

The impact of past whole-genome duplications (WGD)

The early diverging lineages of Poales, i.e., Bromeliaceae and Typhaceae, share consistently small monoploid genomes (1Cx values) and chromosome sizes (MC), which may represent the ancestral character states in this order. Small 1Cx values are also common in other Poales families, sometimes co-occurring together with larger 1Cx values and MCs, as seen in Restionaceae and especially Poaceae.

All Poales families share two ancient whole-genome duplications, the τ event, which occurred early in the history of monocots before the separation of Asparagales and commelinids, and the σ event after the divergence of Poales from other commelinids (Qiao et al. 2022). A further WGD, the ρ event, is restricted to the grasses and is also present in their earliest lineages, such as the subfamilies Anomochlooideae and Pharoideae (McKain et al. 2016; Ma et al. 2021; Seetharam et al. 2021). Such WGDs are expected to have affected the entire genome, i.e., not only genes, but also all other components of the genome, including repetitive DNA, which constitutes by far the largest fraction of the DNA in eukaryotes. Therefore, the minimum 1Cx values of Poaceae should be about twice as high as those of the other Poales families. This is not the case, however, because the minimum 1Cx values of Poaceae (0.26–0.29 pg) are similar to the minimum 1Cx values also found in other families, such as Bromeliaceae, Restionaceae and Typhaceae (Table 1; Figs. 1, 2). However, most 1Cx values of Poaceae nevertheless are significantly larger (Figs. 1, 2) and would fit the ancestral WGD of Poaceae. The minimum 1Cx values that occur within the Poaceae may be due to secondary nuclear genome reduction following the ρ-WGD event.

On the other hand, the relatively large minimum 1Cx values of the xyrid clade could be due to a further genome duplication within Poales that has not yet been discovered. Deep genomic sampling in Poales und further identification of duplicated genes would help to resolve this issue.

Information on Electronic Supplementary Material

Online Resource 1. Examined taxa with 2C values and standard deviation, 1C values, chromosome numbers, ploidy levels, 1Cx values, mean chromosome DNA content, FCM standard species and collection details.
Online Resource 2. Genome sizes (2C values) of taxa taken from the literature and used in this study.

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Author contribution All authors contributed to the study conception and design, M.R. and N.T. collected the samples and checked the identifications, G.W. administrated the FCM analyses, all authors performed the data analysis and interpretations, M.R. led the initial writing of the manuscript, and all authors participated in the writing, editing and the completion of the manuscript.

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Declarations

Conflict of interest The authors declare no competing interests.

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