

EVOLUTIONARY PATTERNS OF GENOME SIZE AND CHROMOSOME NUMBER VARIATION IN BEGONIACEAE

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Cytological data resources are crucial to the study and understanding of the evolution of complex taxa. Recent research on the genus *Begonia* L. has provided a robust phylogenetic background for the analysis of evolutionary patterns across the group and has established that *Begonia* is variable in genome size and chromosome number. This paper provides an overview of the genome structural variation present in *Begonia* and an updated chromosome number and genome size dataset for the genus. Chromosome numbers of more than 400 species are presented and discussed within their current taxonomic and phylogenetic context. A more complete chromosome number dataset is available for Neotropical and Asian *Begonia* sections than for those from Africa. The distribution of chromosome numbers across phylogenetic trees supports the idea of *Begonia* sections as natural groups, because most variation is found between sections rather than within them. Some larger *Begonia* clades were found to have larger chromosome number variation. Moreover, groups with the most variable chromosome numbers belong to some of the taxonomically complex or unresolved *Begonia* sections. Genome size variation was found not to correlate with changes in chromosome number. It suggests that *Begonia* genome dynamics are caused not only by large-scale duplications, rearrangements, and changes in ploidy levels but also by changes in the repetitive fraction of the genome, which probably cause changes in chromosome size. This could potentially play an important role in species radiations.

Keywords. *Begonia*, chromosomes, evolution, c-values

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Introduction

Cytological data are essential for the understanding of evolution. Changes in chromosome number and structure can trigger speciation events by establishing nuclear incompatibilities that lead to crossing barriers (Lowry & Willis, 2010; Winterfeld *et al.*, 2014; Baack *et al.*,

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2015). Events such as chromosomal rearrangements, polyploidy and dysploidy (gain or loss of single chromosomes through fusion or fission) are frequent in plant evolution (Wood *et al.*, 2009; Winterfeld *et al.*, 2020). Angiosperms have one of the widest known ranges of chromosome numbers: from $n = 2$, described in approximately six species (Vanzela *et al.*, 1996; Cremonini, 2005; Vimala *et al.*, 2021) to $n > 320$ (Uhl, 1978). Cytogenetic and evolutionary studies have detected an ancient polyploidisation event in the early divergence of seed plants, as well as ancestral polyploidy events in the crown nodes of many angiosperm clades (Jiao *et al.*, 2011; Li *et al.*, 2015). A more recent study identified more than 100 whole-genome duplication events in angiosperms (Landis *et al.*, 2018), illustrating the important role of chromosome change in many plant lineages.

Although changes in ploidy levels generate high levels of evolutionary novelty (Doyle & Coate, 2019) and have a widely established evolutionary role in the diversification of major angiosperm families (Stebbins, 1971; Husband & Sabara, 2004; Knight *et al.*, 2005; Han *et al.*, 2020), dysploidy events are reported to be more frequent than polyploidy in flowering plants (Grant, 1981). Recent studies have shown that these events have strong evolutionary effects in some plant lineages, and that these types of chromosomal changes can persist longer than those arising from polyploidy (Escudero *et al.*, 2014).

Studies of cytological variation across a taxonomic group provide broad information about its evolutionary history and can contribute new insights regarding species diversification events. The large and fast-growing genus *Begonia* has previously been reported to have highly variable chromosome numbers (Dewitte *et al.*, 2009). The results of studies of genome structure within the Begoniaceae family may suggest how genome dynamics affect evolutionary patterns of diversification and speciation.

In lineages with stable chromosome counts, genome size changes due to repetitive DNA dynamics are responsible for genome size variation and evolution in most cases (Bennetzen *et al.*, 2005). In angiosperms, genome size (traditionally also referred to as the C-value and defined as the amount of DNA in an unreplicated, gametophytic nucleus [the 1C value]) has been shown to have the widest range for any comparable group of eukaryotes: from 61 to 148,852 Mbp (Schubert & Vu, 2016), a 2440-fold difference (Pellicer *et al.*, 2018).

The evolutionary forces behind this variation have been widely studied (for reviews, see Schubert & Vu, 2016; Blommaert, 2020; Carta *et al.*, 2020). Many studies have focused on C-value dynamics within a specific phylogenetic framework or taxonomic group. For example, C-value variation has been studied at the genus level in many genera, including *Sorghum* Moench. (Price *et al.*, 2005), *Cuscuta* L. (Neumann *et al.*, 2021) and *Genlisea* A.St.-Hil. (Boutanaev & Nemchinov, 2020); at the family level in, for example, Liliaceae (Leitch *et al.*, 2007), Brassicaceae (Lysak *et al.*, 2009), Orchidaceae (Leitch *et al.*, 2009) and Melanthiaceae (Pellicer *et al.*, 2014); and even at the order level, such as in Nymphaeales (Pellicer *et al.*, 2013).

Kraaijeveld (2010) studied the link between speciation rates and genome size and was able to link some genome reductions and expansions to the base of a number of species

radiations. However, the general pattern found was that higher diversification rates are observed in small-genome taxa. By contrast, Puttick *et al.* (2015) have suggested that the rate of genome size evolution, not genome size, is linked to speciation rates in angiosperms. This means that taxonomic groups with larger genome size variation, but not necessarily with larger genomes, have higher speciation rates (Puttick *et al.*, 2015).

Dewitte *et al.* (2009) were the first to report *Begonia* C-values and highlighted the large variation found between even closely related species. Research into variation in genome sizes in *Begonia*, as well as the phylogenetic distribution of genome size data, will provide insights into genome dynamics not explained by changes in chromosome number or ploidy but probably driven by the presence, and the proliferation and elimination, of repetitive DNA.

Besides being one of the largest angiosperm genera in terms of number of species, the genus *Begonia* is taxonomically very complex, and some species and group relationships are still poorly resolved (Moonlight *et al.*, 2018). Nevertheless, Moonlight *et al.* (2018) presented the most taxonomically complete genus-wide *Begonia* phylogeny to date and provided a sectional division of *Begonia* species as a “natural classification” for subgeneric divisions.

The results of studies of karyotype variation across this phylogeny can be used to reveal patterns of chromosome dynamics in this genus. Chromosome number variation in *Begonia* has been studied previously (Legro & Haegeman, 1971; Forrest, 2000; Hong-Zhe *et al.*, 2005a; Dewitte *et al.*, 2009; Hughes *et al.*, 2011; Peng *et al.*, 2014a, 2014b). However, most of this research focused on exploring karyotype compatibility of commercial hybrids and on species descriptions. Although useful, these studies do not provide a broad overview of chromosome number variation across *Begonia* or the stability of these numbers across different *Begonia* clades. Other studies that have been carried out to investigate *Begonia* karyotype variation have focused mostly on specific sections or clades of the genus (Legro & Doorenbos, 1969; Oginuma & Peng, 2002; Kono *et al.*, 2020, 2021a, 2021b), and hence fail to provide a holistic view across *Begonia* as a whole.

Dewitte (2010) compiled a small list of genus-wide chromosome data grouped by continent of origin and concluded that the karyotypic variation found made it impossible to assign a basic chromosome number within the genus. Dewitte’s work not only describes genome size variation, polyploidy, aneuploidy, and the presence of B chromosomes in this genus but also indicates that *Begonia* ‘subgroups’ could be characterised by particular chromosome numbers. Dewitte concluded, however, that a larger chromosome number dataset is needed to enable a deeper understanding of chromosome evolution in *Begonia*.

Over the past few years, several newly published descriptions of *Begonia* species have included karyotype information, and the number of species karyotyped has increased (Peng *et al.*, 2017; Tseng *et al.*, 2017; Liu *et al.*, 2020). However, there are issues that make karyotype descriptions for this group difficult. For example, *Begonia* species have very small chromosomes (from 8.73 to 110 Mbp [a 12-fold variation]), with a mean chromosome size of

32.8 Mbp; Dewitte *et al.*, 2009), and counts can produce variable results due to the presence of satellite chromosomes and high levels of dysploidy, meaning that published values vary within species (see the Chromosome Counts Database: Rice *et al.*, 2015).

Genome size variation in *Begonia* species has also been studied previously. Dewitte *et al.* (2009) used flow cytometry to estimate the genome sizes of 37 species and 23 *Begonia* hybrids. Their data showed a 7-fold range in C-values (from 0.23 to 1.46 pg/1C) and up to 12-fold differences in chromosome size. Dewitte and coauthors highlighted for the first time the large variation in genome size in this genus, and suggested that this had arisen, in part, as a result of chromosome and genome size evolution following polyploidisation events involving chromosome number decreases and genome stabilisation (as previously suggested by Oginuma & Peng, 2002).

Although Dewitte *et al.* (2009) identified chromosome size trends when grouping species by continent, their species sampling was not large enough to provide a good overview of the evolution of this trait across *Begonia*. Certainly, additional genome size data to confirm these patterns, and further investigations to determine which genomic factors are triggering the distinctive genome dynamics within the different *Begonia* groups, would provide stronger insights regarding the impact of these genomic processes on the evolution of *Begonia* species.

In the present study, we aimed to address data knowledge gaps by collecting and curating all available *Begonia* chromosome number and genome size data available and to place this information within the most recent phylogenetic framework (Hughes *et al.*, 2015–; Moonlight *et al.*, 2018) to gain insights into genome size and chromosome number variation in the genus. By studying these changes across *Begonia*, we aimed to better understand the potential role of chromosome dynamics in the evolution of this megadiverse genus.

Materials and methods

Data collection, phylogenetic sorting and curation

Chromosome number and most genome size data were collected from literature. First, all available *Begonia* chromosome number and genome size data and sources were downloaded from the Chromosome Counts Database (Rice *et al.*, 2015) and the plant C-value database (Pellicer & Leitch, 2020). Then, original data and those from additional sources were added to the datasets. All data were phylogenetically sorted by clade and section following Moonlight *et al.*, (2018). Nomenclature and classifications follow the Royal Botanic Garden Edinburgh (RBGE) *Begonia* Resource Centre (Hughes *et al.*, 2015–). Both datasets (chromosome numbers and C-values) are available as Supplementary tables 1 and 2.

For some *Begonia* species, different chromosome numbers have been reported by different sources. In such cases, only one value is represented in Figure 1 and Supplementary tables 1 and 2. These values are marked with an asterisk (*). In these cases, the following principles were used to select the value presented.

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- The chromosome number with the highest number of references.
 - The chromosome number most common in the section of *Begonia* in which the species is placed (when the same number of references was found for different chromosome numbers).
 - The lower value was selected when two chromosome numbers were reported an equal number of times and there was no consensus regarding chromosome number within the relevant section. Such cases are indicated by the presence of a plus sign (+) in the *Dysploidy or B chromosome reported* column of [Supplementary table 1](#).
 - When a difference involved a chromosome number reported by Heitz (1927), the Heitz number was discarded following Legro & Doorenbos (1969), who cited a “high incidence of incorrect results”.

Seven species in the chromosome number dataset have not been yet classified into a section (*Begonia* sect. *ignota* in Moonlight *et al.*, 2018) and are therefore not included in Figures 1 and 2. Unnamed species (listed as *Begonia* sp.), horticultural hybrids, and taxa with several widely differing chromosome numbers and no consensus regarding them were not included in the dataset.

To avoid the frequent variation caused by polyploid species, basic chromosome numbers were assigned by reducing their ‘n’ to the greatest common divisor within each section. Polyploid species within sections are indicated in [Supplementary table 1](#), and sections containing polyploid species are indicated in [Figure 1](#).

For species with a range of reported C-values of the same ploidy level, a mean value was used. Data for Figures 1 and 2 were plotted using the R (v3.6.3) package ggplot2 (Wickham, 2016).

Genome size estimation

At least three fresh leaves were collected from each Begoniaceae species growing at RBGE and selected for genome size analysis. The leaves were stored with damp tissue inside Ziploc resealable bags, and their nuclear DNA content (C-values) was measured the next day in the Jodrell Laboratory at the Royal Botanic Gardens, Kew. The measurement of nuclear DNA content followed the two-step protocol described by Pellicer & Leitch (2014).

Solanum lycopersicum ‘Stupiké polní rané’ was used as a reference standard for all samples except *Begonia bipinnatifida* J.J.Sm., for which *Petroselinum crispum* ‘Champion Moss Curled’ was used. For all samples, a sharp razor blade was used to chop intact leaf tissues in a Petri dish containing 500 µL of ice-cold Nuclei Extraction Buffer (CyStain PI Absolute P, Sysmex, Kobe, Japan). The crude suspension was filtered through a nylon mesh filter (30 µm pore size, CellTrics Disposable Filters, Sysmex). After a 5 min incubation period at room temperature, 2 mL of Staining Buffer (CyStain PI absolute P, Sysmex) was added.

Samples were then analysed using a CyFlow SL3 Partec flow cytometer (Sysmex-Partec, Munster, Germany) fitted with a 100 mW green lamp (532 nm solid-state Cobalt Samba laser; Cobolt AB, Solna, Sweden). The resulting flow histograms were analysed using the Partec software for flow cytometry FloMax 2.9 (Sysmex-Partec). At least 5000 nuclei were analysed per sample.

Three tissue samples of each species were analysed, and the nuclear DNA content of each sample was measured three times. The reference standards used in this study have the following 2C-values: *Solanum lycopersicum*, 2.0 pg (Praça-Fontes *et al.*, 2011); and *Petroselinum crispum*, 4.5 pg DNA (Obermayer *et al.*, 2002).

Nuclear DNA content was estimated using the formula

$$2CS = \frac{G1S * 2CST}{G1ST},$$

in which 2CS = sample 2C nuclear DNA content (pg); G1S = sample G1 fluorescence peak mean; 2CST = standard 2C nuclear DNA content (pg); and G1ST = standard G1 fluorescence peak mean.

DNA amounts in picograms were converted to the number of base pairs, using the conversion factor 1 pg DNA = 978 Mbp (Doležel *et al.*, 2003).

Results and discussion

Cytological data compilation and geographical and taxonomic distribution

For this work, 419 chromosome number reports were obtained for 402 *Begonia* species and *Hillebrandia sandwicensis* Oliv., which is sister to *Begonia* (Moonlight *et al.*, 2018; [Supplementary table 1](#)). The chromosome number data obtained represent 21% (37) of the currently described African species, 23% (157) of all current Neotropical species, and 18% (209) of all Asian *Begonia*. According to the *Begonia* Resource Centre (Hughes *et al.*, 2015–, accessed 5 August 2021), there are currently 2032 species of *Begonia*. This means that chromosome numbers are known for only c.20% of the genus.

In the *Begonia* species classification of Moonlight *et al.* (2018), six African clades, two main Neotropical clades, and three main Asian clades are recognised. For each of these clades, the number of *Begonia* sections and species, as well as a cytological data summary, are presented in [Table 1](#). A section-level data summary is presented in [Supplementary table 3](#). Of the 70 *Begonia* sections, no chromosome number data were available for 23. In the Neotropical sections of *Begonia*, cytological data are lacking for 11 of the 33 sections; for Africa, 5 of 18 sections; and for Asia, 8 of 19 sections. For the remaining sections, the numbers of chromosome counts reported were highly variable (see [Supplementary table 3](#) and the bar chart in [Figure 1](#)).

Although the amount of available cytological data for each *Begonia* clade is variable, there is chromosome information on more than 10% of the species in the Neotropical and

Table 1. Chromosome number data arranged by the clades of *Begonia* recognised by Moonlight *et al.* (2018), including the number of sections and species in each clade, and the number of species whose chromosome counts and C-values were included in our datasets

| <i>Begonia</i> clade | No. of sections | No. of species | No. of species whose chromosome counts were included (%) | No. of species whose C-values were included (%) |
|---|-----------------|----------------|--|---|
| Yellow-flowered African <i>Begonia</i> | 6 | 58 | 9 (15.5) | 0 (0) |
| Fleshy-fruited African <i>Begonia</i> | 5 | 56 | 3 (7.1) | 0 (0) |
| Malagasy <i>Begonia</i> | 3 | 36 | 15 (41.6) | 0 (0) |
| Socotran <i>Begonia</i> | 1 | 2 | 1 (50) | 1 (50) |
| Seasonally dry African <i>Begonia</i> 1 | 2 | 10 | 5 (50) | 1 (10) |
| Seasonally dry African <i>Begonia</i> 2 | 1 | 12 | 4 (33.3) | 2 (16) |
| Early diverging Asian <i>Begonia</i> | 3 | 31 | 5 (16.1) | 0 (0) |
| Asian clade C | 8 | 373 | 76 (20.3) | 25 (6.7) |
| Asian clade D | 8 | 740 | 121 (16.4) | 9 (1.2) |
| Neotropical clade 1 | 8 | 201 | 55 (27.3) | 15 (7.4) |
| Neotropical clade 2 (NC2) | 24 | 463 | 101 (21.8) | 25 (5.3) |
| NC2-i | 4 | 135 | 50 (37) | 15 (11) |
| NC2-ii | 15 | 225 | 32 (14) | 7 (3) |
| NC2-iii | 5 | 103 | 19 (18) | 3 (2) |

Asian *Begonia* clades. For the African clades, however, we found that even though our data represent a good sample of African *Begonia* sections, there are few available chromosome counts per section in this group (between zero and 11 species per section with data). This could be due to the difficulty of keeping these species in cultivation. This group is well understood thanks to a systematic study on African *Begonia* (de Wilde, 1985); however, there have been no new studies contributing novel cytological data since that by Legro & Doorenbos (1969). New cytological studies on African *Begonia* would help elucidate the origins of the chromosome number variation found in Asian and Neotropical *Begonia*.

Across the Neotropical and Asian clades, Asian *Begonia* clades were found to have a lower proportion of karyotyped species. This could be due to Asian *Begonia* groups having the highest number of species, with some sections currently increasing in species numbers due to recent species discoveries (e.g. Mazo & Rubite, 2022; Randi *et al.*, 2022). Nonetheless, some clades, such as Neotropical clade 2-i and Asian clade C, contain relatively high numbers of chromosome data (Figure 1). This is probably due to the presence in these clades of *Begonia* sections *Gireoudia* and *Platycentrum*, which are two of the largest and most widely studied *Begonia* sections (Burt-Utley, 1985; Tebbitt & Dickson, 2000; Nguyen, 2004; Tebbitt *et al.*, 2006; Dewitte *et al.*, 2011; Ali, 2013; Twyford *et al.*, 2013). For *Begonia* sect. *Gireoudia*, 111 species are currently described, and chromosome data are available for 43 of these (39% of the section); and for *Begonia* sect. *Platycentrum*, 211 species are currently described and there are chromosome data for 54 of these (26% of the section). By contrast, the very large and phylogenetically unresolved Asian section *Begonia*

sect. *Petermannia* has 455 species, and chromosome numbers have been reported for only 11 of these (i.e. 2.4% of the section); section-specific phylogenetic, taxonomic and cytological research is clearly required for this inadequately studied section.

Also presented in this paper are genome size data obtained from various sources (e.g. Dewitte *et al.*, 2009; Du *et al.*, 2018; and the Plant DNA C-values database, Pellicer & Leitch, 2020), as well as some previously unpublished *Begonia* C-values (see [Supplementary table 2](#)). The species were grouped into sections and clades and paired with their chromosome count, if available (the full dataset is presented in [Supplementary table 2](#)). In total, 84 genome size estimates were collected, 80 of *Begonia* species and one of *Hillebrandia sandwicensis*. The phylogenetic distribution of the data by clade and section is shown in [Table 1](#) and [Supplementary table 2](#).

A total of 21 newly generated and unpublished genome sizes are included, as well as another 63 obtained from existing sources. Our dataset includes genome size data for four African species, 32 Neotropical species, and 33 Asian species. As previously described by Dewitte *et al.* (2009), high levels of variation are found in *Begonia* genome size data. Our compiled C-value data range from 245 Mbp/1C in *Begonia ulmifolia* Willd. ($n = 15$, *Begonia* sect. *Donaldia*, Neotropical clade 1) to 2497 Mbp/1C in *B. formosana* (Hayata) Masam. ($n = 30$, *Begonia* sect. *Platycentrum*, Asian clade C). This represents a 2-fold difference in chromosome number but more than a 10-fold difference in genome size, and suggests that much of the variation observed in nuclear DNA content in *Begonia* arises from changes in the amount of repetitive DNA. These changes are the result of the activity of transposable elements, as well as changes in copy number and length of repetitive DNA regions via unequal recombination (e.g. Schubert & Vu, 2016).

Chromosome number variation in Begonia

Although there is variation throughout the family, within each *Begonia* clade many species share a similar haploid chromosome number (e.g. $n = 14$ in Neotropical clade 2-i; [Figure 1](#)), and most sections identified in the Moonlight *et al.* (2018) classification have conserved basic chromosome numbers with a variable number of outliers. These findings highlight that there is phylogenetic signal at section level in *Begonia* chromosome numbers and supports Moonlight and colleagues' natural sectional classification. [Table 2](#) summarises the range of chromosome numbers found in each clade and section, as well as the most common haploid numbers.

The number of sections with polyploid species was observed to be higher in Asian clades C and D, as well as in the Neotropical clades, compared with other clades. This could be due to the presence of more speciose sections in these clades, although such ploidy variation was not found to be associated with higher species numbers in sections within the Neotropical clades. Asian sections are generally larger, and the presence of polyploid species and within-species chromosome number variation in some of them is

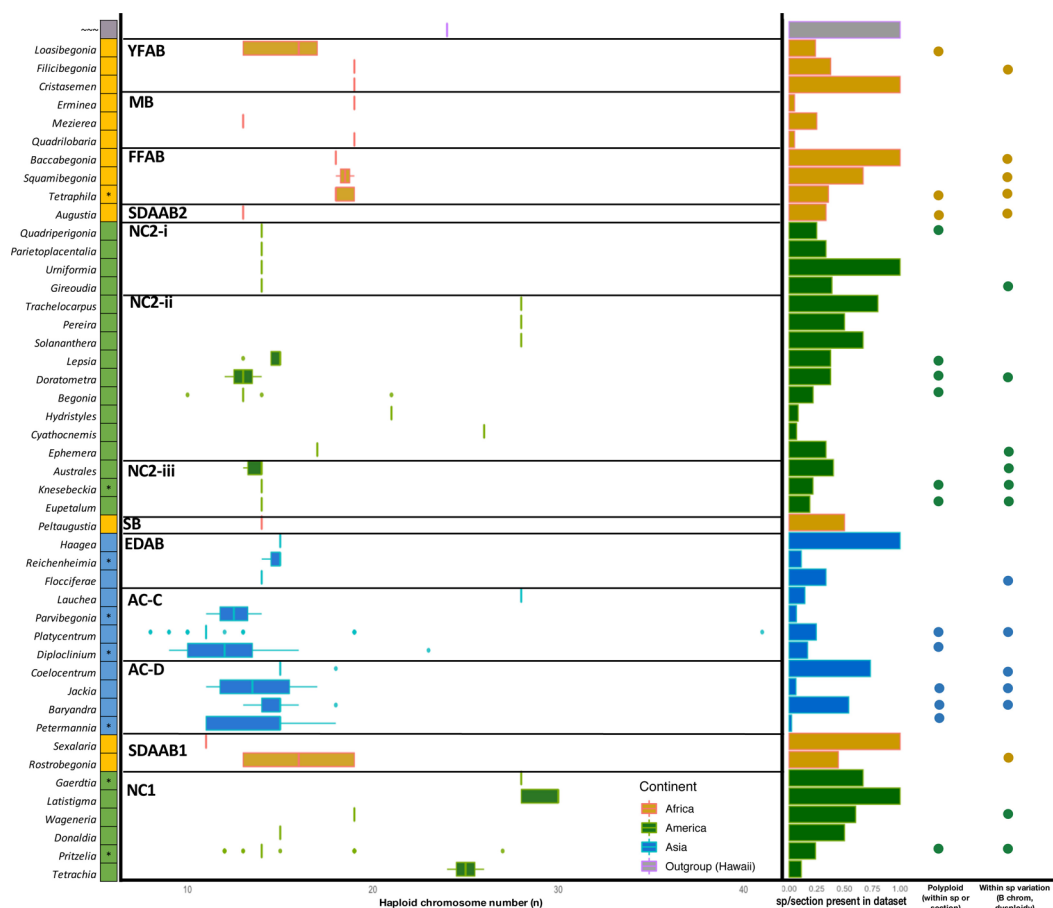


Figure 1. Variation in haploid chromosome number across the *Begonia* sections recognised by Moonlight et al. (2018) and their chromosome data. Boxes in the box plot are grouped by clade. The colours indicate the continent where these sections are found. Bar charts indicate the proportion of the section with known chromosome counts. Dots indicate sections with polyploid species or with species with known interspecific chromosome number variation (including B chromosomes). AC-C, Asian clade C; AC-D, Asian clade D; EDAB, early diverging Asian *Begonia*; FFAB, fleshy-fruited African *Begonia*; MB, Malagasy *Begonia*; NC1, Neotropical clade 1; NC2-i, Neotropical clade 2-i; NC2-ii, Neotropical clade 2-ii; NC2-iii, Neotropical clade 2-iii; SB, Socotran *Begonia*; SDAAB1, seasonally dry adapted African *Begonia* 1; SDAAB2, seasonally dry adapted African *Begonia* 2; YFAB, yellow-flowered African *Begonia*. * Unresolved or polyphyletic in the phylogeny of Moonlight et al. (2018).

striking compared with other larger sections. Among the five largest *Begonia* sections (with more than 100 species), three of them are Asian (*Begonia* sections *Petermannia*, *Platycentrum* and *Diploclinium*) and two are Neotropical (*Begonia* sections *Pritzelia* and *Gireoudia*).

Table 2. Chromosome number ranges and most common values per clade and section of *Begonia*^a

| Continent and <i>Begonia</i> clade | n range | Commonest n | <i>Begonia</i> section | n range | Commonest n | | | |
|---|---------|-------------|--------------------------|---------|-------------|---------------------------|---|----|
| Africa | | | | | | | | |
| Fleshy-fruited African <i>Begonia</i> | 13–19 | 19 | <i>Erminea</i> | – | 19 | | | |
| | | | <i>Mezierea</i> | – | 13 | | | |
| | | | <i>Muscibegonia</i> | – | – | | | |
| | | | <i>Nervioplacentaria</i> | – | – | | | |
| | | | <i>Quadrilobaria</i> | – | 19 | | | |
| Malagasy <i>Begonia</i> | 18–19 | 19 | <i>Baccabegonia</i> | – | 18 | | | |
| | | | <i>Squamibegonia</i> | – | 19 | | | |
| | | | <i>Tetraphila</i> | 18–19 | 19 | | | |
| | | | <i>Peltaugustia</i> | – | 14 | | | |
| Socotran <i>Begonia</i> | – | 14 | | | | | | |
| Seasonally dry adapted African <i>Begonia</i> 1 | 11–19 | 13, 19 | <i>Rostrobegonia</i> | 13–19 | 13, 19 | | | |
| | | | <i>Sexalaria</i> | – | 11 | | | |
| Seasonally dry adapted African <i>Begonia</i> 2 | – | 13 | | | | | | |
| Yellow-flowered African <i>Begonia</i> | 13–19 | 19 | <i>Chasmophila</i> | – | – | | | |
| | | | <i>Cristasemen</i> | – | 19 | | | |
| | | | <i>Exalabegonia</i> | – | – | | | |
| | | | <i>Filicibegonia</i> | – | 19 | | | |
| | | | <i>Loasibegonia</i> | 13–17 | 13, 17 | | | |
| <i>Scutobegonia</i> | – | – | | | | | | |
| America | | | | | | | | |
| Neotropical clade 1 | 12–30 | 28 | <i>Donaldia</i> | – | 15 | | | |
| | | | <i>Gaerdtia</i> | – | 28 | | | |
| | | | <i>Kollmannia</i> | – | – | | | |
| | | | <i>Latistigma</i> | 28–30 | 30 | | | |
| | | | <i>Pritzelia</i> | 12–27 | 14 | | | |
| | | | <i>Stellandrea</i> | – | – | | | |
| | | | <i>Tetrachia</i> | 24–26 | 24, 26 | | | |
| | | | <i>Wageneria</i> | – | 19 | | | |
| | | | Neotropical clade 2-i | – | 14 | <i>Gireoudia</i> | – | 14 |
| | | | | | | <i>Parietoplacentaria</i> | – | 14 |
| <i>Quadriperigonia</i> | – | 14 | | | | | | |
| <i>Urniformia</i> | – | 14 | | | | | | |
| Neotropical clade 2-ii | 11–28 | 13, 28 | <i>Astrothrix</i> | – | – | | | |
| | | | <i>Begonia</i> | 10–21 | 13 | | | |
| | | | <i>Casparya</i> | – | – | | | |
| | | | <i>Cyathocnemis</i> | – | 26 | | | |
| | | | <i>Doratometra</i> | 12–14 | 12, 13, 14 | | | |
| | | | <i>Ephemeria</i> | – | 17 | | | |
| | | | <i>Hydristyles</i> | – | 21 | | | |
| | | | <i>Lepsia</i> | 13–15 | 15 | | | |
| | | | <i>Microtuberosa</i> | – | – | | | |
| | | | <i>Pereira</i> | – | 28 | | | |
| | | | <i>Pilderia</i> | – | – | | | |
| | | | <i>Rossmannia</i> | – | – | | | |
| | | | <i>Ruizopavonia</i> | – | – | | | |
| | | | <i>Solananthera</i> | – | 28 | | | |
| <i>Trachelocarpus</i> | – | 28 | | | | | | |
| <i>Warburgina</i> | – | – | | | | | | |

Table 2. (Continued)

| Continent and <i>Begonia</i> clade | n range | Commonest n | <i>Begonia</i> section | n range | Commonest n |
|------------------------------------|---------|-------------|------------------------|---------|----------------|
| Neotropical clade 2-iii | 13–16 | 14 | <i>Australes</i> | 13–14 | 14 |
| | | | <i>Barya</i> | – | – |
| | | | <i>Eupetalum</i> | – | 14 |
| | | | <i>Gobenia</i> | – | – |
| | | | <i>Knesebeckia</i> | – | 14 |
| Asia | 14–15 | 15 | <i>Flocciferae</i> | – | 15 |
| | | | <i>Haagea</i> | – | 15 |
| | | | <i>Reichenheimia</i> | 14–15 | 15 |
| Asian clade C | 8–41 | 11 | <i>Alicida</i> | – | – |
| | | | <i>Apterobegonia</i> | – | – |
| | | | <i>Diploclinium</i> | 9–23 | 9, 12 |
| | | | <i>Lauchea</i> | – | 28 |
| | | | <i>Monophyllon</i> | – | – |
| | | | <i>Parvibegonia</i> | 11–14 | 11, 14 |
| | | | <i>Platycentrum</i> | 8–19 | 11 |
| | | | <i>Putzeysia</i> | – | – |
| | | | <i>Baryandra</i> | 13–18 | 15 |
| Asian clade D | 11–18 | 15 | <i>Bracteibegonia</i> | – | – |
| | | | <i>Coelocentrum</i> | 15–18 | 15 |
| | | | <i>Jackia</i> | 11–17 | 11, 12, 15, 17 |
| | | | <i>Oligandrae</i> | – | – |
| | | | <i>Petermannia</i> | 11–18 | 15 |
| | | | <i>Ridleyella</i> | – | – |
| | | | <i>Symbegonia</i> | – | – |

^a Groups for which no variation or cytological data were found are indicated by an en rule (–).

The available chromosome count data for *Begonia* sect. *Petermannia* are not representative enough to allow comparisons with other sections (11/455 species); however, the other two Asian sections were found to have a wider range of chromosome numbers, and larger chromosome number variation, compared with the larger Neotropical sections (see [Figure 1](#)). Whether the more highly dynamic karyotypes in Asian *Begonia* are associated with higher speciation rates is difficult to tell from the available data. More cytological data, as well as further studies to explore the frequency of hybridisation and polyploidisation events in the highly speciose sections in these clades, are required to help address this question. Moreover, dynamic karyotypes are probably not the only driver of speciation in Asian *Begonia*, because other large sections, such as *Begonia* sect. *Coelocentrum*, present more stable chromosome numbers but large variation in genome size.

Fewer polyploidy events within sections are found in Neotropical clade 1 than in Neotropical clade 2. Although chromosome numbers across the Neotropical clades are generally variable ($n = 12–30$, [Table 2](#)), two of the most common numbers in our dataset are $n = 14$ and $n = 28$, and therefore we suggest $x = 14$ as the basic number for Neotropical *Begonia* as a whole. There are two clades, Neotropical clade 1 and Neotropical clade 2-ii,

that have sections with haploid number $n = 28$ ($x = 14$), which probably implicates polyploidy events across Neotropical *Begonia*. The evolutionary history of these clades indicates that they arise from two different *Begonia* dispersal events from Africa to the Neotropics (Moonlight *et al.*, 2015, 2018), which suggests that these clades have not only different levels of dysploidy (hence the variation of $n = 14$ or $28 \pm 1/2/3$ across Neotropical sections such as *Begonia* sect. *Latistigma* [$n = 28, 30$], *Begonia* sect. *Begonia* [$n = 13, 14$], *Begonia* sect. *Doratometra* [$n = 12, 13, 15$] and *Begonia* sect. *Australes* [$n = 13, 14, 17$]) but also different independent polyploidisation events.

Neotropical clades 1 and 2-ii were also found to have larger chromosome count variation (Table 2), which could indicate that polyploidy events were in many cases followed by dysploidy, mainly chromosome loss and/or genome reduction. This is documented as a common phenomenon after polyploidisation (Mandáková & Lysak, 2018). From these two clades, only a few sections, such as *Begonia* sect. *Latistigma*, *Pritzelia*, *Begonia* and *Australes*, have enough chromosome counts to enable exploration of their distribution on a species-level phylogenetic tree (Moonlight *et al.*, 2018; Supplementary figure 1). These data suggest a high number of polyploidy events in *Begonia* sect. *Begonia*, as well as some phylogenetic signal in the chromosome numbers of sections *Pritzelia* and *Latistigma*. Although most studied species were reported to have $2n = 56$, *Begonia* sect. *Pritzelia* is the largest Neotropical section, and therefore a more complete understanding of phylogenetic relationships between species as well as more cytological data would help shed light on chromosome evolution within this group.

The range of chromosome numbers in African *Begonia* is considerably narrower than the ranges in the Neotropical and Asian clades (see Figure 1). There are three common karyotypes observed in African *Begonia*: (i) $n = 13$ (in nine species belonging to the clades of seasonally dry adapted African *Begonia* [SDAAB] 1 and 2, yellow-flowered African *Begonia* [YFAB] and fleshy-fruited African *Begonia* [FFAB]); (ii) $n = 18$ (in 10 species from the Malagasy *Begonia* [MB] clade); and (iii) $n = 19$ (in 13 species in the FFAB, MB, SDAAB1 and YFAB clades). Despite within-section variation in African *Begonia* being rare, there does not seem to be one single basic chromosome number for all African *Begonia* species; $n = 19$ is most frequent in the early diverging clades, $n = 13$ is most abundant in the sister clades of the larger Asian clade and Neotropical clade 1 (*Begonia* sections *Augustia*, *Sexalaria* and *Rostrobegonia*), and $n = 14$ in the sister clade to Neotropical clade 2 (*Begonia* sect. *Peltaugustia*).

Two African sections were found to have within-section chromosome number variation: *Begonia* sect. *Tetraphila* and *Begonia* sect. *Rostrobegonia*. For these sections, further cytogenetic data are clearly needed to elucidate their basic chromosome numbers. A *Begonia* sect. *Tetraphila* phylogeny (Moonlight *et al.*, 2018) with chromosome numbers mapped onto it is shown in Supplementary figure 2. This indicates at least two different chromosome loss-or-gain events between $n = 36$ and $n = 38$.

Chromosome count variation is larger in Asian *Begonia* clades than in other *Begonia* clades. These include some very species-rich, taxonomically complex and non-monophyletic

sections (Moonlight *et al.*, 2018). Although the sample sizes are different and there are outliers, the early diverging Asian *Begonia* (EDAB) clade and the Asian clades C and D have $n = 11$ and $n = 15$ as their most common haploid chromosome numbers, respectively (see Table 2 and Figure 1). There is large variation within Asian clades C and D, but 46% and 76% of the species analysed in these respective clades retained these karyotypes. However, it must be acknowledged that these may be only considered basic number candidates, because our dataset is biased by over-representation in sections such as *Begonia* sect. *Coelocentrum* (84 species) and *Begonia* sect. *Baryandra* (79 species) in Asian clade D (which have $n = 15$ in 44 and 23 of the species, respectively), and *Begonia* sect. *Platycentrum* (196 species) in Asian clade C ($n = 11$ in 54 species).

By contrast, other large Asian sections, such as *Petermannia* (451 species) and *Jackia* (60 species), were found to have much wider variation in chromosome number but with much lower sampling. Greater and more phylogenetically balanced sampling will be needed to determine whether $n = 11$ and $n = 15$ are the basic chromosome numbers of these *Begonia* clades. Moreover, the high number of outliers in these clades also indicates that dysploidy is frequent in some Asian *Begonia* sections. Species-level data could be explored in a phylogenetic context only for sections *Platycentrum* and *Petermannia* (Supplementary figure 3), again showing some phylogenetic signal in chromosome number distributions.

Although some variation can be found in most of the main Asian *Begonia* sections, in sections *Jackia*, *Diploclinium* and *Petermannia* the variation was found to be larger, but this may be for different reasons in different sections. *Begonia* sect. *Jackia* is composed of 60 species, but we have chromosome data for only eight species, and these were variable ($n = 12, 15, 17$ and 22). Because chromosome counts have been reported for only 13% of the species in this section, additional data for this section could help resolve its karyotype evolutionary history and confirm or refute the idea that the more limited chromosome number variation in *Begonia* sect. *Jackia* compared with *Begonia* sect. *Diploclinium* and *Begonia* sect. *Petermannia* is only due to limited data availability.

Chromosome data for *Begonia* sect. *Diploclinium* are available for nearly 20% of the 113 species in this section and show that they vary extensively (i.e. $n = 9, 11, 12, 13, 14, 15, 16$ and 23). Although the species in this section are morphologically similar, this group is not a “natural” taxon (as discussed in Moonlight *et al.*, 2018). This section could, however, have abnormally high rates of chromosomal change. For *Begonia* sect. *Petermannia* (the largest section, having 455 species), chromosome data were available for just 11 species (2% of the species) and show much less variation ($n = 11, 15$ and 18); however, the section is too under-sampled for any firm conclusions to be drawn from this finding. The phylogeny of Moonlight *et al.* (2018) indicates that *Begonia* sections *Diploclinium* and *Petermannia* are currently polyphyletic, and this is supported by chromosome data presented here. Additional morphological and molecular phylogenetic work is clearly needed to help recircumscribe these taxa into natural groups.

Asian *Begonia* species make up the largest and most species-diverse sections, and most of these are not fully resolved in Moonlight *et al.* (2018). However, recent research focused on chromosome count variation across selected Asian sections has provided complete datasets and phylogenies that allow analysis of the chromosome evolution of specific sections (e.g. *Begonia* sect. *Coelocentrum*, Kono *et al.*, 2020; *Baryandra*, Kono *et al.*, 2021a; *Diploclinium*, Kono *et al.*, 2021b). These studies provide a good overview of chromosome evolution throughout these sections, confirming that *Begonia* sect. *Coelocentrum* species have a stable haploid chromosome number of $n = 15$, whereas *Begonia* sections *Baryandra* and *Diploclinium* were found to have wider variation in chromosome counts, due to different chromosome gain-or-loss events across their evolutionary history. Other complex and large Asian *Begonia* sections, such as *Begonia* sections *Petermannia* and *Platycentrum*, would also benefit from such in-depth studies.

In most large plant genera, chromosome number information on 22% of the species and most clades and sections would be enough to shed light on their karyotype evolution and basic chromosome numbers. The large genus *Astragalus* L. was also found to have karyotype variation and high levels of dysploidy. Chromosome numbers from $n = 6$ to $n = 45$ have been described in 836 karyotyped species, representing 27% of the genus according to the Chromosome Counts Database (Rice *et al.*, 2015) and the Plants of the World Online database (POWO, 2022). However, a clear basic number is inferred from these data of $x = 8$, found in nearly the 80% of its karyotyped species. Regarding other examples of large genera, such as *Bulbophyllum* Thouars (2114 species in total, only 89 with chromosome numbers that oscillate between $n = 18$ and $n = 24$, but $n = 19$ has been reported for 85% of karyotyped species) and *Psychotria* L. (1641 species in total, only 30 with accepted chromosome numbers varying from $n = 11$ to $n = 66$, but 11 is the basic number in 85% of karyotyped species), karyotypes have been published for only 2–4% of their species (Rice *et al.*, 2015; POWO, 2022).

Other larger genera, such as *Carex* L. and *Euphorbia* L., are also examples of large and taxonomically complex plant groups that are similar to *Begonia* in this context. *Carex* has 2002 species, but chromosome counts are available for only 590 (30% of the genus; Rice *et al.*, 2015; POWO, 2022), and no basic chromosome number can be inferred for the whole genus. According to Więćław *et al.* (2020), this genus rarely presents a wide variation in chromosome counts at either the intraspecific or sectional level, but haploid numbers are variable between sections or subsections. In most cases this is similar to *Begonia*, in which we also see chromosome number stability within sections (see Figure 1). However, frequent within-species chromosome number variation has been previously described for *Begonia* (Dewitte *et al.*, 2009).

It must also be taken into account that *Carex* has holocentric chromosomes (Greilhuber, 1995). Holocentric chromosomes can stabilise chromosome fragments, which can facilitate karyotypic rearrangements (Escudero *et al.*, 2012). This chromosomal instability may

contribute to the lack of clarity and consensus in establishing a basic chromosome number for *Carex*. However, no holocentric chromosomes have previously been reported in *Begonia*, so its karyotypic variation cannot be attributed to this trait.

In the case of *Euphorbia*, which has 1976 species, 261 (13%) karyotypes have been published (Rice *et al.*, 2015; POWO, 2022). This genus was found to have a wide range of haploid chromosome numbers ($n = 6$ to $n = 100$), but there is no basic number or clear consensus on its karyotype evolution. Additionally, genome size variation in *Euphorbia* shows a 48-fold difference (342 to 140,800 Mbp, Pellicer & Leitch, 2020). There have not been many studies on the cause of this genomic variation, but previous research has established that although natural hybridisation is infrequent in *Euphorbia* (Sheidai *et al.*, 2010), aneuploidy and polyploidy have played a role in *Euphorbia* speciation (Perry, 1943).

Even for large genera such as *Carex* and *Euphorbia* with such variation in chromosome counts, it is rare to find in-depth, genus-level research. A genus-wide assessment of cytological data has been carried out for *Solanum* L. (Chiarini *et al.*, 2018), for which chromosome counts were reported for 506 species (52% of the genus). However, little variation is found, the basic number being $x = 12$ in 97% of the species for which cytological data are available. Comparison of Begoniaceae data with cytological data from other species-rich genera in other families (Rice *et al.*, 2015; POWO, 2022) suggests that it is very likely that *Begonia* cytology is not under-studied but rather that this genus has a more complex chromosome evolutionary history that is not found in most of the other megadiverse genera.

Genome size variation in *Begonia*

Of the 81 species for which genome size data are presented in this paper, chromosome counts are also available for 72 (Supplementary table 2). Figure 2 shows the relationship between their haploid genome size (Mbp) and haploid chromosome number. Our C-value dataset includes very few African species, and therefore little variation can be observed. The genomes of African *Begonia* species have sizes between 360 and 630 Mbp/1C, which is greater than for the *Hillebrandia sandwicensis* genome (332.6 Mbp/1C). Additional genome size data across African *Begonia* clades would provide a better overview of genome size evolution and stability in the early diverging *Begonia* clades.

Published data show no correlation ($R^2 = 0.02$, $p = 0.87$) between chromosome number and genome size in *Begonia*. Although C-value data are available for only a small number of species in the genus, this dataset indicates that sections with conserved chromosome numbers, such as *Platycentrum* (211 species), *Coelocentrum* (86 species), *Ephemer*a (15 species), *Gireoudia* (111 species), *Petermannia* (455 species) and *Pritzelia* (158 species), have variable genome sizes. This suggests that it is highly likely that these genome size differences are due to variation in repetitive elements. Most of these sections have the highest number of species and represent recent and rapid *Begonia* species radiations (Moonlight *et al.*, 2018); they are therefore good model groups with which to test the

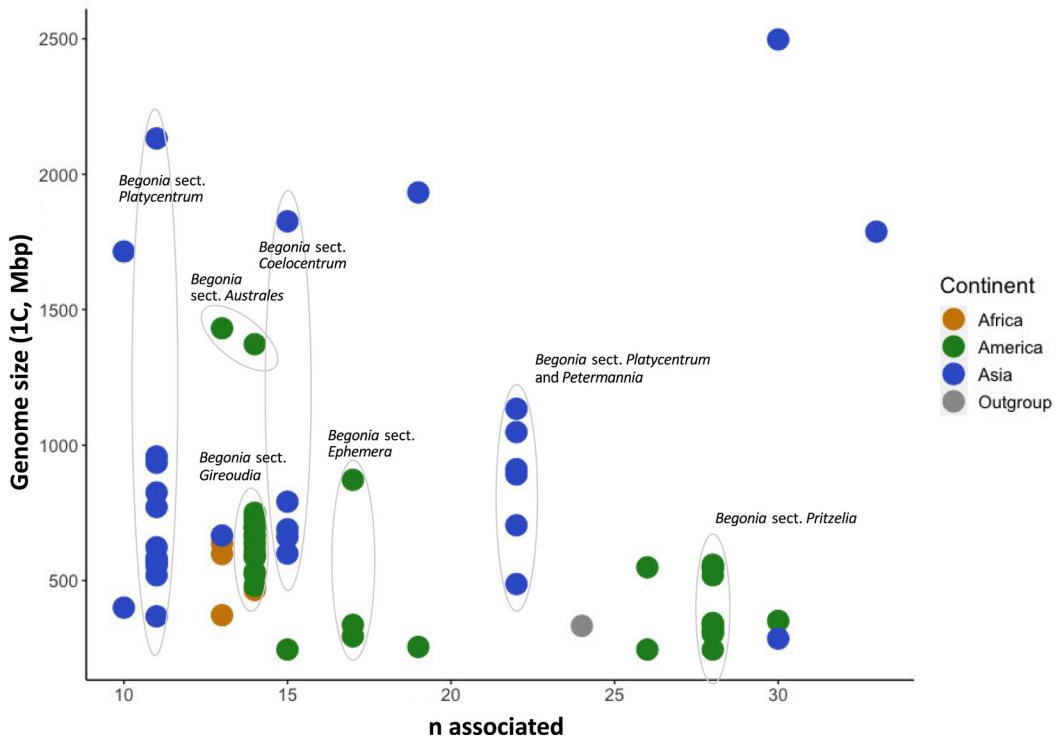


Figure 2. Genome sizes and chromosome numbers of 64 *Begonia* species and *Hillebrandia sandwicensis*. The sources of the data used to create this scatter plot are specified in [Supplementary table 2](#). Species in the same sections are enclosed within an ellipse. Colours indicate the continent where each species is found. The *Hillebrandia* data point is labelled as 'Outgroup'.

influence of repetitive DNA and transposable elements on *Begonia* speciation events. In-depth genomic studies are needed to address this question.

Whether Neotropical and Asian radiations were found to have wider variation in genome sizes because they have more variable repetitive fractions in their genomes or because of sampling bias is difficult to know. The uneven sampling throughout the genus means that sections such as *Platycentrum* highly over-represented, and therefore the variation observed in Asian species is probably wider. The Asian *Begonia* clade C has a range of C-values from 367 Mbp to 2497 Mbp and the greatest representation of species in our dataset (33% of the species included belong to this clade). The variation observed here could also be present in other clades but not yet observed because of the lower sampling; clearly, more C-value data are needed across the genus. Because chromosome number variation is also high in this clade, we can confirm that species in Asian clade C have undergone high levels of genome structural variation, such as chromosomal gain and loss and polyploidisation, as well as marked genome size dynamics.

Neotropical species, with the exception of species in *Begonia* sect. *Australes*, may be characterised by having smaller genomes than those of Asian species (see [Figure 2](#)). Genome sizes of Neotropical species also seem less variable than those of Asian species. This suggests that there may be some phylogenetic signal in genome size in Neotropical radiations. However, because genome size variation changes across the phylogeny, such changes do not overlap with changes in chromosome number.

Other events driving chromosome size variation must play a role in the genome evolution of these species. The Asian clades were found to have wider and overlapping ranges of DNA content, as well as higher chromosome numbers (see [Figure 1](#)), which suggests that large-scale genome changes were common early in Neotropical radiations but have been rarer since, and that across all the Asian radiations there have been more recent changes in their genome structure. However, genome size variation found at a smaller scale within sections with stable chromosome numbers also indicates levels of transposition and genome dynamics in Neotropical *Begonia*. Further repetitive DNA studies across large Neotropical and Asian radiations with stable chromosome numbers would help elucidate the nature of this genome size variation and aid our understanding of their potential role in these large species radiations.

Conclusions

Karyotype evolution in *Begonia* has previously been shown to be complex, and no consensus on a basic chromosome number has been established using the available data (Dewitte, [2010](#)). In this paper, we have presented an updated summary of all chromosome number data that have been published in the Begoniaceae to date, including *Begonia* haploid chromosome numbers that range from $n = 7$ to $n = 41$.

The variable levels of chromosome number variation across other large angiosperm groups suggest that chromosome and ploidy changes are not necessarily involved in large species radiations. In the case of *Begonia*, it seems that higher rates of ploidy or chromosome number changes could be present in some of the larger sections. However, this is not the case in all the larger or more recent radiations, and in-depth, section-specific studies that involve investigation of hybridisation patterns and interspecific chromosomal variation would be required to further understand the role of these events in the evolution of *Begonia* groups.

This paper provides an updated genus-wide cytological dataset of Begoniaceae, with chromosome count data representing almost 20% of the genus, and genome size data for 81 species (4% of all *Begonia* species). The phylogenetic distribution of these cytological data (based on the latest genus-wide sectional classification, Moonlight *et al.*, [2018](#)) supports the idea of many *Begonia* sections as natural groups. Moreover, although the available data are not evenly spread across the phylogeny or the geographical distribution of the genus, our results suggest that chromosome number variation may be less variable in African *Begonia* species, whereas different levels of variation are seen across and within

species belonging to the Neotropical and Asian *Begonia* sections. For most large *Begonia* sections (> 70 species), more in-depth phylogenetic and cytogenetic studies are needed to help disentangle the origin and evolution of the large chromosome number variation already apparent in some sections (e.g. *Begonia* sections *Pritzelia*, *Petermannia* and *Platycentrum*). For other large radiations, such as those in *Begonia* sections *Coelocentrum* and *Gireoudia*, chromosome numbers appear to be highly stable but genome sizes are variable, highlighting a potential role of repetitive DNA in recent *Begonia* radiations.

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Supplementary material

Supplementary material for this article is available from the *Edinburgh Journal of Botany* online portal.

Supplementary table 1. Chromosome counts dataset for *Begonia*: all chromosome numbers (2n) available for use in the present study and their sectional basic number. Each species is classified by section and clade. Each chromosome number record includes the original reference(s) in which the number was reported. The presence of polyploid species in the section, as well as dysploidy and B chromosomes reported, are also recorded. EDAB, early diverging Asian *Begonia*; FFAB, fleshy-fruited African *Begonia*; MB, Malagasy *Begonia*; NC1, Neotropical clade 1; NC2-i, Neotropical clade 2-i; NC2-ii, Neotropical clade 2-ii; NC2-iii, Neotropical clade 2-iii; SB, Socotran *Begonia*; SDAAB1, seasonally dry adapted African *Begonia* 1; SDAAB2, seasonally dry adapted African *Begonia* 2; YFAB, yellow-flowered African *Begonia*. * Represented in Figures 1 and 2, and Tables 1 and 2.

Supplementary table 2. Genome size dataset for *Begonia* and *Hillebrandia sandwicensis*. All genome size values (1C values) found in the literature, plus the original values reported in this paper for the first time ('Present study'). Species are classified by section and clade, and associated chromosome numbers are specified if present in [Supplementary table 1](#). EDAB, early diverging Asian *Begonia*; FFAB, fleshy-fruited African *Begonia*; MB, Malagasy *Begonia*; NC1, Neotropical clade 1; NC2-i, Neotropical

clade 2-i; NC2-ii, Neotropical clade 2-ii; NC2-iii, Neotropical clade 2-iii; SB, Socotran *Begonia*; SDAAB1, seasonally dry adapted African *Begonia* 1; SDAAB2, seasonally dry adapted African *Begonia* 2; YFAB, yellow-flowered African *Begonia*.

Supplementary table 3. *Begonia* sections and the proportion for which chromosome counts are available. EDAB, early diverging Asian *Begonia*; FFAB, fleshy-fruited African *Begonia*; MB, Malagasy *Begonia*; NC1, Neotropical clade 1; NC2-i, Neotropical clade 2-i; NC2-ii, Neotropical clade 2-ii; NC2-iii, Neotropical clade 2-iii; SB, Socotran *Begonia*; SDAAB1, seasonally dry adapted African *Begonia* 1; SDAAB2, seasonally dry adapted African *Begonia* 2; YFAB, yellow-flowered African *Begonia*. ^a As of September 2021.

Supplementary figure 1. Species-level phylogeny of Neotropical *Begonia* sections recognised by Moonlight et al. (2018): A, *Pritzelia*; B, *Australes*; and C, *Begonia*. Chromosome number values (2n) are placed next to each species for which data are available. The colours of the boxes indicate different chromosome number values.

Supplementary figure 2. Species-level phylogeny of African *Begonia* sect. *Tetraphila* recognised by Moonlight et al. (2018). Chromosome number values (2n) are placed next to each species for which data are available. The colours of the boxes indicate different chromosome number values.

Supplementary figure 3. Species-level phylogeny recognised by Moonlight et al. (2018) of Asian *Begonia* sections: A, *Platycentrum*; B, *Petermannia*. Chromosome number values (2n) are placed next to each species for which data are available. The colours of the boxes indicate different chromosome number values.

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