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Chromosome diversity and evolution in the genus *Gagea* (*Liliaceae*)

Abstract

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Based on literature survey, chromosome numbers for 12 *Gagea* sections and 97 accepted species (for a total of 270 accessions) were obtained. Early branching lineages are all composed by diploids, while the widest range of ploidy level variation occurs in species-rich sections *Gagea* and *Didymobulbos*. Data on basic chromosome number, ploidy level, chromosome total haploid length (THL) and measures of karyotype asymmetry (calculated for 8 *Gagea* sections, 42 species and a total of 60 accessions) were included in a data set. Combining the large amount of data enabled mean karyotypes to be produced, highlighting differences in karyotype structure between sections. Further differences were noted when parameters for analysing karyotype asymmetry were assessed and superimposed onto a phylogenetic framework. DA recognized correctly the 8 considered sections in 100% of cases, and the same happened within section *Gagea* (series *Solenarium*, *Gagea*, *Helenaeanae* and *Monticolae*) and within section *Didymobulbos* (series *Saxatiles*, *Occidentales*, *Arvenses* and *Chrysanthae*). Despite massive genome size reduction is a noticeable feature of *Gagea* respect to other *Lilioideae* taxa, also in this genus there is a slight tendency to increase again the chromosome size, especially in late branching sections (e.g. *Bulbiferae*, *Platyspermum*, *Minimae*, *Didymobulbos*). Hence, the relatively high CV_{CL} values occurring in *Gagea* sections (except the early branching sect. *Anthericoides*) seemingly originated through chromosome rearrangements towards a bimodal karyotype, without significant genome size variation.

Introduction

Gagea Salisb. (incl. *Lloydia* Salisb. ex Rchb.) is one of the 15 genera presently included in the family *Liliaceae* (tribe *Tulipeae*) and has a Boreal distribution. According to Peruzzi & al. (2009a, and literature cited therein) it is the sister group of all the other Tulipeae genera (*Amana* Honda, *Erythronium* L., *Tulipa* L.). Among *Liliaceae*, *Gagea* is the genus with the highest number of species (ca. 280), a diversity that is presumably due to frequent occurrence of polyploidy and hybridization combined with propensity for vegetative propagation (Peruzzi 2008a; Peterson & al. 2009).

Recent studies in the molecular systematics of the genus (Peterson & al. 2004, 2008; Peruzzi & al. 2008a-b; Zarrei & al. 2009) have led to an improved understanding of its phylogeny, mostly confirming the sectional classification of Levichev (Peterson & al. 2008). For the purpose of the present study, we accept a subdivision of *Gagea* into at least 14 sectional units, 12 of which are represented among the materi-

al on which our results are based. They are (included species for which data are available are listed in Appendix 1):

sect. *Anthericoides* A. Terracc.
sect. *Lloydia* (Salisb.) Peruzzi, J.-M. Tison, A. Peterson & J. Peterson
sect. *Triflorae ined.*
sect. *Plecostigma* (Turcz.) Pascher
sect. *Gagea*
sect. *Bulbiferae* Levichev
sect. *Platyspermum* Boiss. (incl. sect. *Graminifoliae* Levichev)
sect. *Minimae* (Pascher) M.T. Davlianidze
sect. *Persicae* (Levichev *pro ser.*) *ined.*
sect. *Stipitatae* (Pascher) M.T. Davlianidze (incl. sect. *Dschungaricae* Levichev)
sect. *Spathaceae* Levichev
sect. *Didymobulbos* (K. Koch) Boiss. (incl. sect. *Fistulosae* (Pascher) M.T. Davlianidze)

The basic chromosome number, as in the whole *Lilioideae* (*Lilieae* + *Tulipeae*), is $x = 12$. According to Fedorov (1969), Peruzzi (2003, 2008b), Gutiérrez Esteban & al. (2009), Gutiérrez & Vázquez (2010) and IPCN series (Missouri Botanical Garden), for 97 accepted *Gagea* species it is known a least one chromosome counting, i.e. ca. 35% of the presumed total number of existing species. Chromosome number ranges from $2n = (18)\ 24$ ($2x$) to $2n = 132$ ($11x$).

According to Peruzzi & al. (2009a), polyploidy is very rare in the tribe *Lilieae* (1.54%), while is very common in the tribe *Tulipeae* (40.7%) and especially in *Gagea*. Mean 1Cx genome size in *Gagea* is very close to the inferred ancestral value for *Liliaceae* (6.67 pg, according to Leitch & al., 2007), but the study of karyotype structure variation, together with the phylogenetic position of *Gagea* suggest a secondary reduction from larger genomes (Peruzzi & al. 2009a). According to the latter authors, the karyotype in *Gagea* is typically bimodal, with comparatively high CV_{CL} and moderate CV_{CI} values. Previous studies show that *Tulipeae* as a whole follow an equal pattern of DNA addition/subtraction (i.e. the same amount of DNA is added to each chromosome arm regardless of its size), although they originated in a family where an unequal pattern (the amount of DNA added varies between longer and shorter chromosome arms unequally leading to an overall increase in karyotype asymmetry with genome size) is dominant. In the evolution of the genus *Gagea* as a whole, a massive reduction in genome size (0.3-0.5 fold) was accompained by an increase in interchromosomal asymmetry (CV_{CL}), leaving the intrachromosomal asymmetry (CV_{CI}) almost unchanged.

Within this framework, aim of this paper is to answer to the following questions: a) are the polyploids equally distributed among *Gagea* sections? b) is the karyotype structure different among *Gagea* sections? c) did genome size reduction continued to play a role also in infrageneric evolution of *Gagea*? d) what is the variation pattern of karyotype asymmetry among *Gagea* sections? e) have karyotype features a possible taxonomic value in *Gagea*?

Material and Methods

Source of karyotype data

Chromosome number and karyotype information were derived from Fedorov (1969), Peruzzi (2003, 2008b), Peruzzi & Aquaro (2005), Gutiérrez Esteban & al. (2009), Gutiérrez & Vázquez (2010), IPCN series (Missouri Botanical Garden) and literature cited therein. In total, karyotype data were collected for 270 accessions of *Gagea*, concerning chromosome counts, and for 60 accessions concerning karyotype structure. Taken together data were available for 97 and 42 species respectively, and included representatives of all sections with exception of sect. *Tricholloydia* and sect. *Incrustatae*. For karyotyping purposes, only literature with published idiograms and/or karyotype measurements and/or good metaphase plates with magnification or scale-bar indicated were considered. When 2*n* mitotic metaphase plates were measured, the graphic method proposed by Plummer & al. (2003) was used to match homologous chromosomes. This involves plotting the relative length of each chromosome [(= length of individual chromosome/total length of all chromosomes)/100] against its arm ratio, in order to pair chromosomes. Karyotype features for other *Tulipeae* genera (i.e. *Amana* + *Erythronium* + *Tulipa*) were taken from the dataset published by Peruzzi & al. (2009a).

Karyotype analysis

A data matrix comprising 52 karyotype features (Table 1) was assembled. The matrix file is available at request to the author. For analysis of karyotype asymmetry, according to the

Table 1. 52 karyological parameters used in this study. LA = long arm; SA = short arm; TL = total length; R = ratio long arm/short arm; THL = total haploid length.

CV_{CI}				
CV_{CL}				
THL				
ploidy level				
I	LA	SA	TL	R
II	LA	SA	TL	R
III	LA	SA	TL	R
IV	LA	SA	TL	R
V	LA	SA	TL	R
VI	LA	SA	TL	R
VII	LA	SA	TL	R
VIII	LA	SA	TL	R
IX	LA	SA	TL	R
X	LA	SA	TL	R
XI	LA	SA	TL	R
XII	LA	SA	TL	R

considerations in Paszko (2006) and Peruzzi et al. (2009a), two coefficients of variation (CV) were found to be particularly informative measures of asymmetry. The CV_{CI} index evaluates differences in centromere position for each chromosome in the karyotype and provides a measure of intrachromosmal asymmetry. In contrast the CV_{CL} gives a measure of interchromosomal asymmetry as it reflects how variable the chromosome sizes are in the karyotype. In both cases, the larger the value the greater the asymmetry in the karyotype. For each section a mean haploid idiogram was built as follows. Using karyotype data for each species, chromosome pairs were arranged into decreasing lengths, then the absolute length of the long and short arms of each chromosome pair were taken. The data were then pooled to produce a mean length of each chromosome pair for a section (e.g. the data for the longest chromosome pair of all *Gagea* sect. *Gagea* species were pooled to give the mean value for sect. *Gagea* chromosome pair I). It is noted that since the study was based exclusively on measurements of Feulgen-stained chromosomes, there was no possibility of identifying and analyzing homeologous chromosomes between taxa. Instead the "mean karyotype" of each genus refers only to the shape of the haploid karyotype.

According to Levin (2002 and literature cited therein), the correlation between total haploid chromosome length (THL) and 1C values typically exceeds $r = 0.85$ within species and between species in related genera, thus THL has been considered to be a good proxy for genome size. This was shown to be correct also for family *Liliaceae* (Peruzzi & al., 2009a). For this reason, we used directly THL values as relative genome size proxy.

Correlations

For continuous quantitative data Pearson's correlation coefficient was used, whereas for mixed scalar and ordinal data Spearman's rho coefficient was calculated. Correlations were considered as weak (up to 0.3), average (up to 0.5), good (up to 0.80) and high (above 0.80). Only correlations significant at the 1% level or stronger are discussed.

Phylogenetic framework and inferred basic chromosome numbers

The phylogenetic framework for *Gagea* used in this study was derived from the works of Peterson & al. (2004, 2008); Peruzzi & al. (2008a-b); Zarrei & al. (2009). All nodes for which bootstrap support was too low were collapsed (see also Fig. 1).

Discriminant Analysis

A classificatory discriminant analysis (DA), an identification optimization procedure based on probability of identification (e.g., Geisser's classification probabilities) was performed on the dataset (52 variables, see Table 1 x 60 accessions) using *a priori* classifications (Henderson, 2006). DA was used to test if sectional circumscriptions fit with karyological data. This model assumes each taxon is discrete. The discriminant analysis developed predictive discriminant functions for the groups, which were applied to single accessions in each assigned group. The 52 predictor variables were entered simultaneously using the different infrageneric taxa as the grouping variables. The model used *a priori* probability calibrated on group size, when classifying accessions.

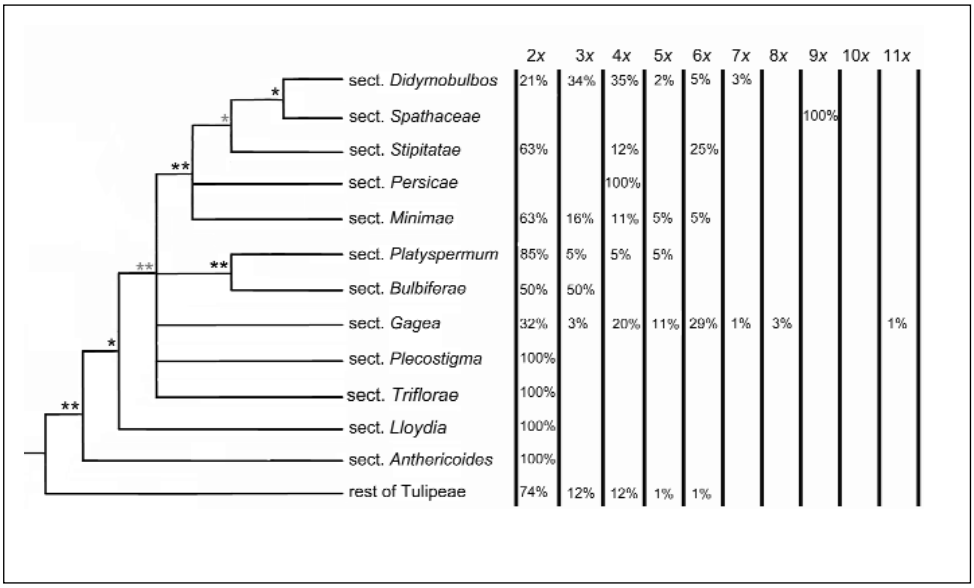

Fig. 1. Distribution (%) of ploidy levels among *Gagea* sections and lineages, superimposed onto a phylogenetic framework. Number of chromosome count accessions: 92 (*Didymobulbos*), 4 (*Spathaceae*), 14 (*Stipitatae*), 2 (*Persicae*), 6 (*Minimae*), 23 (*Platyspermum*), 2 (*Bulbiferae*), 104 (*Gagea*), 4 (*Plecostigma*), 1 ("*Triflorae*"), 16 (*Lloydia*), 2 (*Anthericoides*). The strength of the clades (* = supported by one molecular marker only; ** = supported by two molecular markers; grey = BS 70-90%; black = BS above 90%) is given. See Materials and Methods for the source of phylogenetic framework including bootstrap values.

Results

Figure 1 summarizes the distribution of ploidy levels among *Gagea* sections. No chromosome data are presently available for the sections *Tricholloydia* and *Incrustatae*. It is apparent how early branching lineages are all composed by diploids, and that the widest range of ploidy level variation occurs in sections *Gagea* and *Didymobulbos*. Sections *Persicae* and *Spathaceae* are instead composed by polyploids only. It is noteworthy also the presence of dysploids with $2n = 18$ across the sections *Gagea* and *Stipitatae* (2 and 3 species, respectively).

Data on karyotype structure resulted available only for the following 8 sections: *Anthericoides, Lloydia, Plecostigma, Gagea, Bulbiferae, Platyspermum, Minimae, Didymobulbos.* Fig. 2 shows mean haploid idiograms for all those sections, superimposed onto the consensus phylogenetic framework of *Gagea*. The different sizes of the karyotypes largely reflect the patterns evidenced by the boxplots in Fig. 3, with the relatively small chromosomes of *Gagea* compared with other Tulipeae. An average negative correlation resulted between ploidy level and THL (r = - 0.353).

By the analysis of Fig. 4, summarizing the karyotype asymmetry variation among *Gagea* sections, it is evident how sect. *Anthericoides* shows an inverted proportion of the

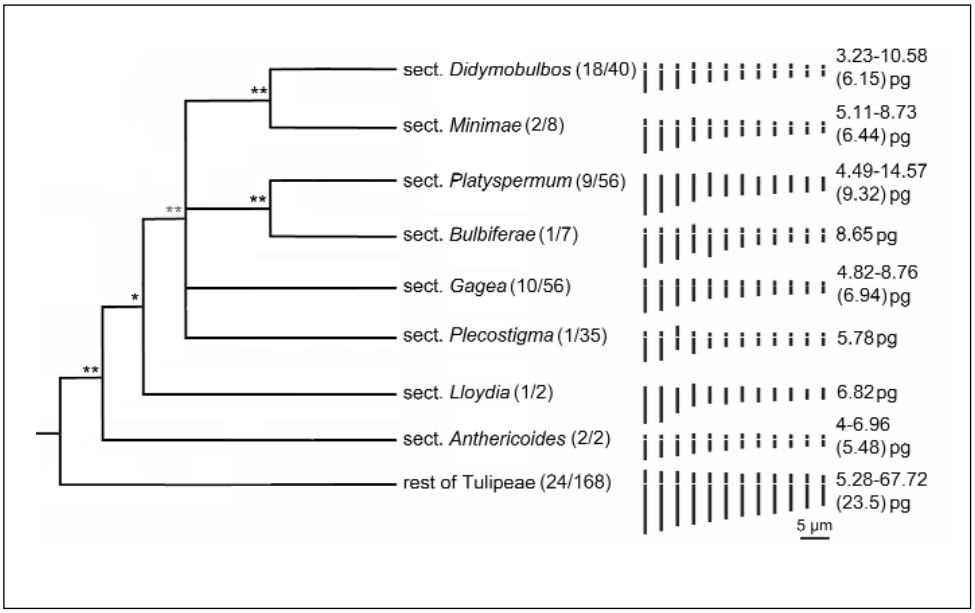

Fig. 2. Mean haploid idiograms among *Gagea* sections, superimposed onto a phylogenetic framework. For each section, the number in brackets corresponds to the number of species studied karyologically followed by the total number of species considered to comprise the section. For more information see caption of Fig. 1.

two CVs, respect to others. By calculating the ratio CV_{CI}/CV_{CL} for each accession, it results that sect. *Anthericoides* has indeed values above 1 (1.18 ± 0.05), as in the rest of Tulipeae (1.20 ± 0.38), while all other sections show values under that value (data not shown). No correlation was found among THL and CV_{CL}, while an average positive correlation was evidenced between THL and CV_{CI} (r = 0.331).

DA recognized correctly the 8 considered sections in 100% of cases. The same happened with the 4 considered series within section *Gagea* (*Solenarium*, *Gagea*, *Helenaeanae*, *Monticolae*) and with the 4 considered series within section *Didymobulbos* (*Saxatiles*, *Occidentales*, *Arvenses*, *Chrysanthae*).

Discussion

According to our data, polyploidy started to play an important role in the evolution of *Gagea* only relatively late, probably together with hybridization attitude. Ability for vegetative propagation, which occurs in all *Gagea* species and also in other *Tulipeae* (e.g. *Tulipa sylvestris*) resulted in an useful pre-adaption, favoring the spread of partially or totally sterile offspring (e.g. perissoploids). All *Gagea* sections share similar basic karyotype structure, but some difference is apparent in terms of karyotype asymmetry and chromosome size variation. Despite massive genome size reduction is a noticeable feature

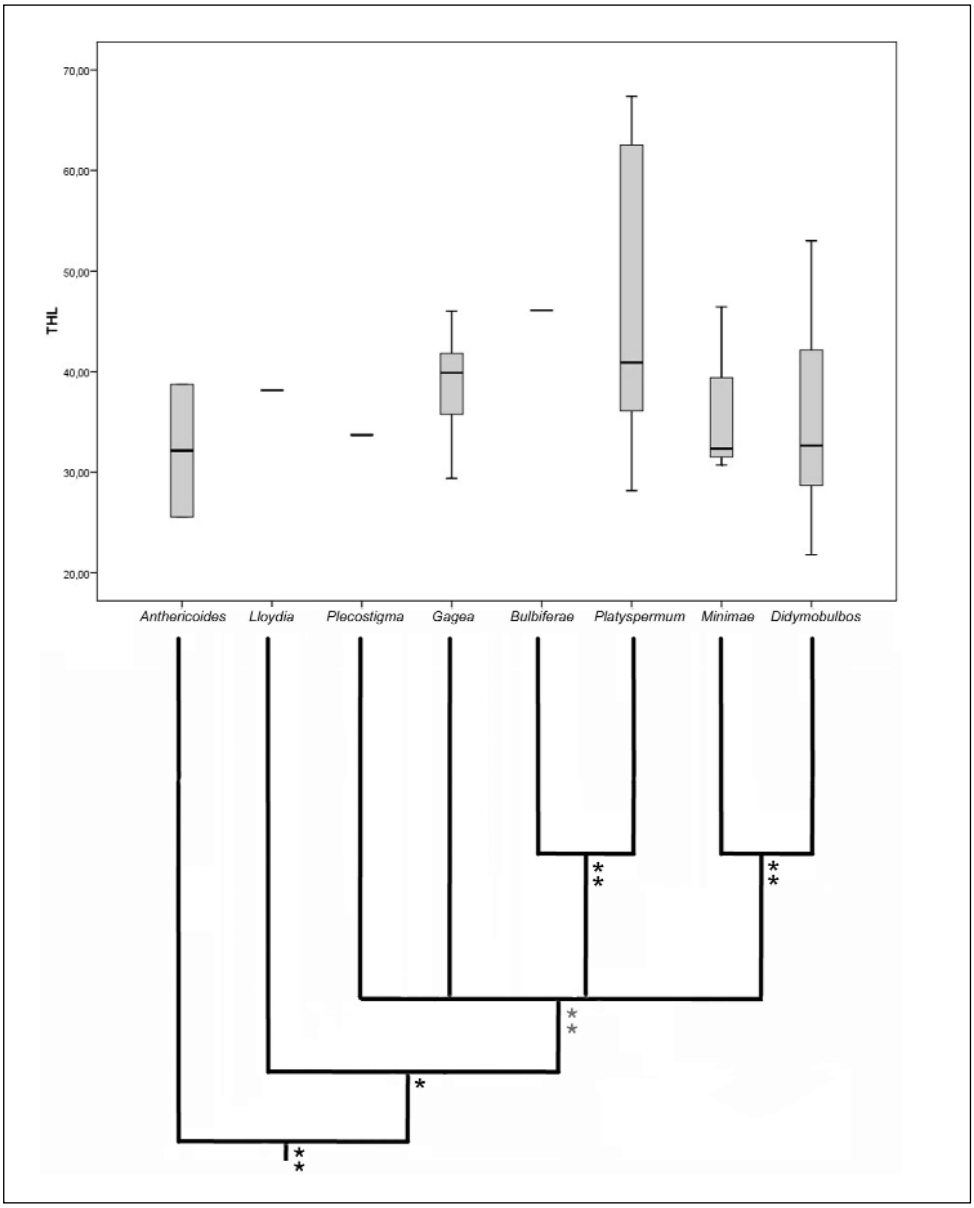

Fig. 3. Boxplots illustrating the variability of THL. The outlined central box depicts the middle 50% of the data extending from upper to lower quartile; the horizontal bar is at the median. The ends of the vertical lines ("whiskers") indicate the minimum and maximum data values, unless outliers are present in which case the whiskers extend to a maximum of 1.5 times the inter-quartile range. Circles indicate outliers, unless extreme outliers are present in which case the circles extend to a maximum of three times the inter-quartile range and the extreme outliers are indicated as asterisks. Taxa are ordered by phylogenetic grouping (according to the phylogenetic tree on the bottom of the graph, taken from Fig. 2).

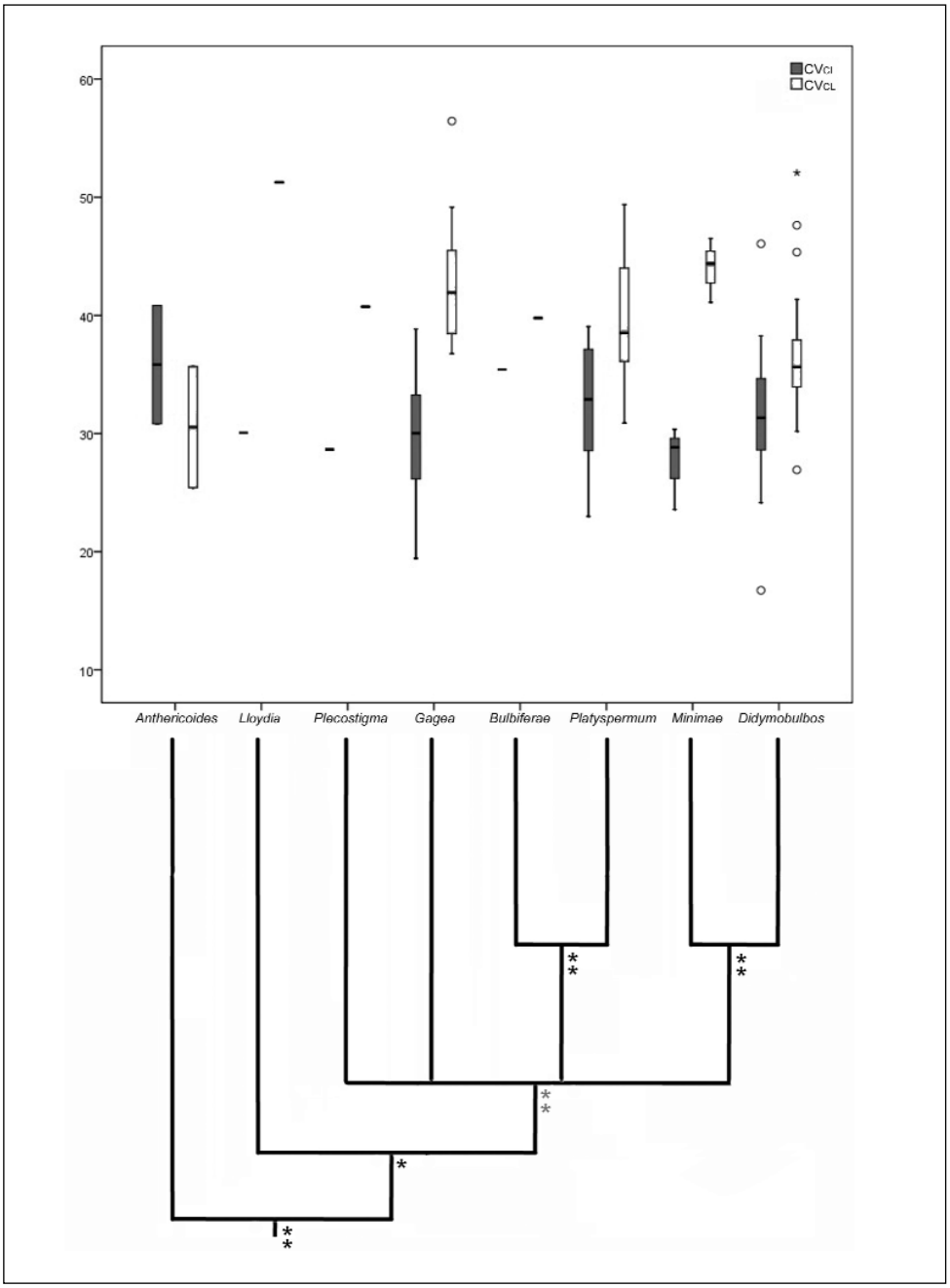

Fig. 4. Clustered boxplots illustrating the variability of both the coefficient of variation (CV) of the centromeric index (CV_{CI}) and chromosome length (CV_{CL}) (See Fig. 3 for more explanations concerning the boxplots). Taxa are ordered by phylogenetic grouping (according to the phylogenetic tree on the bottom of the graph, taken from Fig. 2).

of *Gagea* respect to other *Lilioideae* taxa, also in this genus there is a slight tendency to increase again the chromosome size, especially in late branching sections (e.g. *Bulbiferae*, *Platyspermum*, *Minimae*, *Didymobulbos*). Although *Tulipeae* as a whole were shown to follow an "equal" pattern (Peruzzi & al. 2009), actually within *Gagea* the "unequal" pattern of DNA increase (typical of many other *Liliaceae*) played again a role. Hence, the relatively high CV_{CL} values occurring in almost all *Gagea* sections (except the early branching sect. *Anthericoides*) seemingly originated through chromosome rearrangements towards a bimodal karyotype, without significant genome size variation. Finally, karyotype features resulted good (even if not definitive) taxonomic markers for the considered *Gagea* sections and series.

Possible future perspectives on karyological *Gagea* studies: a) extend the karyological investigations to cover the missing taxa (especially in those sections which are poorly sampled or completely unknown by a karyological point of view); b) start molecular cytogenetic study (i.e. FISH, GISH, chromosome painting) in order to clarify the relationships among *Gagea* sections and among small-sized *Gagea* chromosomes and large-sized (often over-sized, see Ambrozova & al. 2009) chromosomes of other *Lilioideae*.

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Appendix 1. included species for which karyological data are available (Fedorov 1969; Peruzzi 2003, 2008b; Gutiérrez Esteban & al. 2009; Gutiérrez & Vázquez 2010 and IPCN series [Missouri Botanical Garden]). Asterisks indicate those species for which also idiogram information was available.

sect. *Anthericoides* A. Terracc.
**G. graeca* (L.) Irmisch
**G. trinervia* (Viv.) Greuter

sect. *Lloydia* (Salisb.) Peruzzi, J.-M. Tison, A. Peterson & J. Peterson
**G. serotina* (L.) Ker Gawl. = *Lloydia serotina* (L.) Rchb.

sect. *Triflorae ined.*
G. triflora (Ledeb.) Schult. & Schult. f. = *Lloydia triflora* (Ledeb.) Baker

sect. *Plecostigma* (Turcz.) Pascher
G. calantha Levichev
**G. chlorantha* (M. Bieb.) Schult. & Schult. f.
G. villosula Vved.

sect. *Gagea*
G. aipetriensis Levichev
G. artemczukii A. Krasnova
G. brevistolonifera Levichev (= *G. carinata* Levichev *nom. nud.*)
G. calyptrifolia Levichev
G. capusii A. Terracc.
**G. chanae* Grossh. (ser. *Monticolae* Levichev)
**G. charadzeae* M.T. Davlianidze (ser. *Gagea*)
G. davlianidzeae Levichev
G. elegans Wall. ex D. Don
G. erubescens (Bess.) Schult. & Schult. f.
G. fedschenkoana Pascher
**G. germainae* Grossh. (ser. *Gagea*)
**G. helenae* Grossh. (ser. *Helenaeanae* M.T. Davlianidze)
G. longiscapa Grossh.
**G. lutea* (L.) Ker Gawl. (ser. *Solenarium* (Dulac) Peruzzi & J.-M. Tison)
G. megapolitana Henker
**G. paczkoskii* (Zapal.) Grossh. (ser. *Gagea*)
G. pineticola Klok. (= *G. praeciosa* Klok.)
G. podolica Schult. & Schult. f.
G. pomeranica Ruthe
G. praemixta Vved.
**G. pratensis* (Pers.) Dumort. (ser. *Gagea*)
G. protraeta Levichev *nom. nud.*
**G. pusilla* (F. W. Schmidt) Sweet (ser. *Gagea)*
**G. reverchoni* Degen (ser. *Helenaeanae* M.T. Davlianidze)
G. rubicunda Meinsh.
G. terraccianoana Pascher
G. tribulbilla Levichev *nom. nud.*
**G. tisoniana* Peruzzi, Bartolucci, Frignani & Minutillo (ser. *Gagea*)
G. transversalis Steven
G. turkestanica Pascher

sect. *Bulbiferae* Levichev
**G. bulbifera* (Pall.) Salisb.

sect. *Platyspermum* Boiss. (incl. sect. *Graminifoliae* Levichev)
**G. alexeenkoana* Miscz.
**G. caroli-kochii* Grossh.
**G. commutata* K. Koch
G. dayana Chodat & Beauv.
G. graminifolia Vved.
G. kamelinii Levichev
G. ludmilae Levichev
**G. reticulata* (Pall.) Schult. & Schult. f. (= *G. tenuifolia* (Boiss.) Fom.)
**G. rigida* Boiss. & Spruner
**G. sarmentosa* K. Koch
**G. taurica* Stev.
G. vegeta Vved.

sect. *Minimae* (Pascher) Davlianidze
**G. confusa* A. Terracc.
G. filiformis (Ledeb.) Kar. & Kir. (= *Gagea heteroantha* Levichev *nom. nud.*)
G. granulosa Turcz.
**G. minima* (L.) Ker Gawl.
G. nakaiana Kitag.

sect. *Persicae* (Levichev *pro ser.*) *ined.*
G. gageoides (Zucc.) Vved. (= *G. persica* Boiss.)

sect. *Stipitatae* (Pascher) Davlianidze (incl. sect. *Dschungaricae* Levichev)

G. aberrans Levichev *nom. nud.*
G. caelestis Levichev
G. chomutovae Pascher
G. dschungarica Regel
G. ferganica Levichev
G. juniperina Levicehv *nom. nud.*
G. minutiflora Regel
G. ova Stapf
G. paniculata Levichev
G. popovii Vved.
G. reinhardii Levichev (= *G. pamiroalaica* Levichev *nom. nud.*)
G. schachimardanica Levichev
G. stipitata Merckl.
G. subtilis Vved.

sect. *Spathaceae* Levichev
G. spathacea (Hayne) Salisb.

sect. *Didymobulbos* (K. Koch) Boiss. (incl. sect. *Fistulosae* (Pascher) M. T. Davlianidze)
G. amblyopetala Boiss. & Heldr.
**G. bohemica* (Zauschn.) Schult. & Schult. f. (ser. *Saxatiles* (A. Terracc.) Peruzzi & J.-M. Tison)
**G. chaberti* A. Terracc. (ser. *Occidentales* (A. Terracc.) Peruzzi & J.-M. Tison
G. chrysantha Schult. & Schult. f.
**G. dubia* A. Terracc. (ser. *Saxatiles* (A. Terracc.) Peruzzi & J.-M. Tison)
**G. durieui* Parl. (ser. *Occidentales* (A. Terracc.) Peruzzi & J.-M. Tison)
**G. foliosa* (J. & C. Presl) Schult. & Schult f. (ser. *Occidentales* (A. Terracc.) Peruzzi & J.-M. Tison)
**G. fragifera* (Vill.) Ehr. Bayer & G. López (= *G. anisanthos* K. Koch) (ser. *Arvenses* M.T. Davlianidze)
**G. glacialis* K. Koch. (ser. *Arvenses* M.T. Davlianidze)
**G. granatellii* (Parl.) Parl. (ser. *Occidentales* (A. Terracc.) Peruzzi & J.-M. Tison)
**G. joannis* Grossh. (ser. *Arvenses* M.T. Davlianidze)
**G. lacaitae* A. Terracc. (ser. *Occidentales* (A. Terracc.) Peruzzi & J.-M. Tison)
G. luberonensis J.-M. Tison
**G. mauritanica* Durieu (ser. *Occidentales* (A. Terracc.) Peruzzi & J.-M. Tison)
G. micrantha (Boiss.) Pascher
G. nevadensis Boiss.
**G. lojaconoi* Peruzzi (ser. *Chrysanthae* (Pascher) Levichev)
**G. peduncularis* (J. & C. Presl) Pascher (ser. *Saxatiles* (A. Terracc.) Peruzzi & J.-M. Tison)
G. polidorii J.-M. Tison
**G. sicula* Lojac. (ser. *Chrysanthae* (Pascher) Levichev)
**G. soleirolii* F. W. Schultz (ser. *Occidentales* (A. Terracc.) Peruzzi & J.-M. Tison)
**G. sulfurea* Miscz. (ser. *Arvenses* M.T. Davlianidze)
G. tenera Pascher
G. testudina Levichev
**G. villosa* (M. Bieb.) Sweet (ser. *Arvenses* M.T. Davlianidze)