Karyotypic Changes through Dysploidy Persist Longer over Evolutionary Time than Polyploid Changes

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Abstract

Chromosome evolution has been demonstrated to have profound effects on diversification rates and speciation in angiosperms. While polyploidy has predated some major radiations in plants, it has also been related to decreased diversification rates. There has been comparatively little attention to the evolutionary role of gains and losses of single chromosomes, which may or not entail changes in the DNA content (then called aneuploidy or dysploidy, respectively). In this study we investigate the role of chromosome number transitions and of possible associated genome size changes in angiosperm evolution. We model the tempo and mode of chromosome number evolution and its possible correlation with patterns of cladogenesis in 15 angiosperm clades. Inferred polyploid transitions are distributed more frequently towards recent times than single chromosome gains and losses. This is likely because the latter events do not entail changes in DNA content and are probably due to fission or fusion events (dysploidy), as revealed by an analysis of the relationship between genome size and chromosome number. Our results support the general pattern that recently originated polyploids fail to persist, and suggest that dysploidy may have comparatively longer-term persistence than polyploidy. Changes in chromosome number associated with dysploidy were typically observed across the phylogenies based on a chi-square analysis, consistent with these changes being neutral with respect to diversification.

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Introduction

While variation in chromosome number is widespread among plants, its role in species diversification has long been debated [1–3]. Transitions in chromosome number comprise the multiplication of a whole chromosome set (which may entail a whole genome duplication, WGD), or an increase by half of the genome, demiploidy, which can occur when one homoeologous set of chromosomes is duplicated in an already existing polyploid [4], and changes in single chromosome number (resulting from fission, fusion, duplication or deletion of single or few chromosomes; [5]). Demiploidy is thought to occur through the crossing of gametes of different ploidy levels (e.g., a tetraploid crossed with a diploid, followed or preceded by a doubling of the genome, yields a hexaploid, which is inferred as a 4× to 6× demiploidy transition). Researchers have long argued about the prevalence of polyploidy in flowering plants as well as its evolutionary and genomic consequences [3]. Recent works have demonstrated that polyploidy is ubiquitous in angiosperms and has played an important role in many lineages, with evidence of several rounds of both ancient and recent polyploidizations [6–11]. The terms paleo- and neopolyploid have been loosely used to describe the relative time of the polyploidy event - either as ancient (paleo) or recent (neo). However, what is ancient and recent varies among authors (e.g., neopolyploidy may be defined as a polyploidization event within a genus or within a species; [12]). In addition, there are still conflicting opinions on whether there is a positive or negative relationship between ancient polyploid events and diversification rates. Whereas polyploids have traditionally been regarded as evolutionary dead ends [1,13–14], recent studies have suggested correspondence between polyploid events and diversification of some of the most species-rich angiosperm lineages [3,15]. Polyploidizations are rather frequent, but newly formed polyploid lineages generally fail to persist, which would explain their low diversification rates and the biased distribution of polyploidy towards terminal branches of the plant tree of life [10,17]. Whereas neopolyploids are widespread among angiosperms (an estimated ca. 30% of extant species have polyploidized since their genus arose [8,10]), paleoploidyization events are comparatively very rare [9,11,17]. Thus, although polyploidy may initiate...
Phylogenetic sampling

In this study, we consider gains and losses of single chromosomes as processes that entail (i) change in DNA content (aneuploidy: duplication or losses of chromosomes), or (ii) little or negligible change in DNA content (dysploidy: fission and/or fusion); Supporting Information S1). Despite the prevalence of gains and losses of single chromosomes among angiosperms [27], the evolutionary role of these chromosome number transitions has received far less attention than that of polyploidy. Some studies have suggested an important role of gains and losses of single chromosomes in species diversification [28–33], but there has been no formal test of this role.

A central issue in the study of chromosome number evolution concerns the relative importance of polyploid transitions versus gains and losses of single chromosomes [24]. While polyploidy takes shape as a more dramatic transition – one that involves the whole genome – in practice, the persistence of polyploid lineages is widely believed to be higher compared to aneuploid ones [24]. In contrast, to our knowledge, the evolutionary persistence of lineages affected by dysploidy has not been studied.

Here, we perform a phylogenetic comparative analysis of chromosome evolution and lineage diversification in 15 flowering plant clades to estimate the relative importance of polyploidy and gains and losses of single chromosomes in the evolution of angiosperms. The particular aims of this study are to evaluate (i) previous hypotheses about the role of polyploidy in angiosperm diversification; (ii) the persistence of gains and losses of single chromosomes (including a priori aneuploidy and dysploidy) along angiosperm evolution; and (iii) the relative distribution and timing of polyploidy and gains and losses of single chromosomes across angiosperm phylogenies.

Materials and Methods

Phylogenetic sampling

We used molecular phylogenies from 15 angiosperm groups (Supporting Information S1; Material S1) belonging to both dicots (10) and monocots (5), and displaying both monocentric and holocentric chromosomes (Table 1; Supporting Information S1). The four Cyperaceae datasets included in this study were treated independently: the Cariceae dataset represents the main lineages of the tribe and comprised 1–2 species per each Carex section, whereas the three Carex sections (Oaules, Phacocystis, and Spirastocthen) included a high percentage of the extant species of each of those sections. Each co-author provided 1–2 datasets for which they were experts, and which had a reliable published phylogeny, information to calculate absolute times of divergence and chromosome number variation (Supporting Information S1; Material S1). Taxonomic level of the phylogenies was heterogeneous, comprising families (two), tribes (three), genera (five) and sections (five). Molecular phylogenies with branch lengths scaled to the number of nucleotide substitutions were obtained from the authors of the original published studies (Supporting Information S1; Material S1). The trees were rooted using outgroup species or clades as specified in the original studies and dated using the penalized likelihood method [34] as implemented in the APE R package [35–36]. The most appropriate smoothing parameter was chosen based on an initial cross-validation run and calibration points were included to transform trees from relative to absolute times. For the Orchidinae dataset, an ultrametric tree previously generated using BEAST [37] was directly obtained from the study author (Supporting Information S1; Material S1). Chromosome counts (used for the reconstruction of chromosome number transitions) were obtained for each group from different sources (Supporting Information S1; Material S1). Tips of the phylogeny without available chromosome counts were pruned. All our datasets had: (i) sequence data for at least 12 species (maximum 100 species); (ii) chromosome counts available for at least 75% of the species sampled in the phylogeny, and (iii) variation in chromosome numbers among the species remaining in the phylogeny (Table 1).

Tempo and mode of chromosome evolution

Given the dated molecular phylogenies and the assignments of chromosome numbers to the tips, we aimed to infer the location of chromosome number transitions using the ChromEvol methodology [4]. This likelihood-based method assesses the fit of several models that allow for various types of chromosome number change along the phylogenies and infers the type of each transition in chromosome number (WGD, demipolyploidy, increase and decrease in a single chromosome; Table 2) along the branches of the tree. We ran all eight available models and used the Akaike information criterion (AIC [38]) to select the best model for each dataset. Models of chromosome evolution in ChromEvol are based on two (gain and loss of a single chromosome) to six parameters (polyploidy, demipolyploidy, gain and loss of a single chromosome and gain and loss of a single chromosome proportional to the current chromosome number) representing chromosome transitions (Table 2). The expected numbers of polyploidy events and gains and losses of single chromosomes along each branch of the phylogeny were recorded based on the best-fitting model.

Using the ChromEvol software (evaluatePPDist option), we calculated the observed chromosome number transitions per unit of time that occurred relatively recently (four temporal strategies: tip branches, from present to 10% of total time, from present to 25% of total time and from present to 50% of total time) and those that occurred deeper in time (the rest of the tree). We calculated the expected number of each type of chromosome number transition (polyploidizations plus demipolyploidizations and gains plus losses of single chromosomes) along the tree assuming that they occur homogeneously over time as the null hypothesis (total number of events inferred along the tree divided by the total time). Then chi-square was used to test whether the number of observed transitions along external and internal branches for each temporal level is significantly different than the number of transitions under the expectation of constant transition rate along the tree (null hypothesis). P values smaller than 0.002 were considered significant to reject the null hypothesis. We selected this conservative P-value because our tests are two-tailed and because we did multiple tests and therefore Bonferroni correction is required. Nevertheless, P-values smaller than 0.025 were considered as marginal support to reject the null hypothesis.

Study of gains and losses of single chromosomes

Gains and losses of single chromosomes encompass different phenomena with various expected outcomes: 1) Aneuploidy:
Table 1. Main features of the datasets analysed in this study.

| Focal group (order, family) | Species richness | Sphy* | Scounts* | 2n-range* | Centromerotype |
|-----------------------------|-----------------|--------|----------|-----------|----------------|
| Hedera (Arales, Araliaceae) | 12              | 12     | 12       | 24 – 96   | Monocentric    |
| Orchidinae (Asparagales, Orchidaceae) | ca. 1800 | 103    | 73       | 10–82     | Monocentric    |
| Bellis, Bellium, Bellidstrum (Asterales, Asteraceae) | 21 | 19     | 18       | 9 – 45    | Monocentric    |
| Helianthus (Asterales, Asteraceae) | 49 | 47     | 47       | 17 – 51   | Monocentric    |
| Resedaceae (Brassicales) | ca. 85 | 66     | 35       | 6 – 40    | Monocentric    |
| Arenaria sect. Plinthine (Caryophyllales, Caryophyllaceae) | 14 | 14     | 14       | 9 – 70    | Monocentric    |
| Erodium (Geraniaceae, Geraniaceae) | ca. 74 | 66     | 55       | 8 – 80    | Monocentric    |
| Antirrhineae (Lamiales, Plantaginaceae) | ca. 326 | 44     | 36       | 6 – 18    | Monocentric    |
| Passiflora (Malphigiales, Passifloraceae) | ca. 530 | 61     | 56       | 6 – 12    | Monocentric    |
| Cistaceae (Malvales) | ca. 180        | 47     | 45       | 5 – 24    | Monocentric    |
| Cariceae (Poales, Cyperaceae) | ca. 2000 | 135    | 100      | 6 – 57    | Holocentric    |
| Carex sect. Ovales (Poales, Cyperaceae) | ca. 90 | 57     | 57       | 26 – 43   | Holocentric    |
| Carex sect. Phacocyrtis (Poales, Cyperaceae) | ca. 70 | 35     | 21       | 30 – 46   | Holocentric    |
| Carex sect. Spirostachya (Poales, Cyperaceae) | ca. 70 | 38     | 25       | 30 – 42   | Holocentric    |
| Saxifraga sect. Saxifraga (Saxifragales, Saxifragaceae) | ca. 70 | 56     | 50       | 8 – 110   | Monocentric    |

*Sphy: number of species sampled in the phylogeny; Scounts: number of species sampled in the phylogeny with known chromosome counts; 2n-range: observed range of chromosome numbers.

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duplication or loss of a chromosome including its DNA content, and 2) Dysploidy; chromosome fusion/fission that do not result in changes in DNA content. In addition, losing chromosomes after polyploidization has a different outcome than when there is not previous polyploidization (in the first case, although genes may be lost, there are extra copies of the genes). In order to differentiate between different patterns of gains and losses of single chromosomes for lineages for which these transitions were inferred, we gathered genome size values from the Plant DNA C-values database (data.kew.org/cvalues/) and references therein. We then performed for lineages with holocentric chromosomes (Cariceae) displayed marginal support for the latter pattern (but Figures S1–S6 in Supporting Information S2). Therefore, dysploid transitions occurring in these groups would mostly correspond to fissions, fusions and genome rearrangements without changes in DNA content (Table 2, Supporting Information S1). For the remaining two datasets (Arenaria and Erodium) we cannot differentiate between dysploidy and aneuploidy.

Results

The studied groups comprise a high cytogenetic variability, with chromosome numbers ranging from \( n = 5 \) to \( n = 110 \) (Table 1). ChromEvol analyses (Table 2, Table S1 in Supporting Information S2) reveal that models of chromosome evolution including polyploidy (12 groups) are more frequent than those which do not (three groups). Interestingly, demipolyploidization, associated with hybridization between different ploidy levels and allopolyploidization processes [4], is inferred in seven of them. Gains and losses of single chromosomes are inferred in 12 groups: 10 of them are affected by single chromosome gains, nine by losses and seven by both events. Rates of gains and losses of single chromosomes are independent of the current chromosome number except for four groups (see inferred models in Table 2). We have found a high heterogeneity in chromosome transition rates both for gains and losses of single chromosomes (0.0013–80.9440 #transitions per million year (my\(^{-1}\)) and polyploid transitions (0.0013–0.7888 #transitions my\(^{-1}\)) (Supporting Information S1). The absolute number of chromosome gain and loss events inferred by our analyses is much higher than that of polyploidy for all groups with both types of transitions, with the exception of Passiflora, Erodium and Cistaceae datasets (Table 2).

Our analyses (at four different temporal levels) comparing the expected and the observed number of transitions per time reveal similar results: First, the number of polyploid transitions towards the tips of the trees is significantly higher than expected under the null hypothesis (constant polyploidization rate through time) in four of the 12 datasets with polyploidy, in two data sets there is marginal support to reject the null hypothesis whereas for the remaining six data sets the results were congruent with it (Table 2). Second, gains and losses of single chromosomes were in general distributed much more evenly across the trees, with ten of the 12 datasets exhibiting a distribution of gains and losses of single chromosomes statistically indistinguishable from expectation under the null hypothesis (constant chromosome gains and losses transition rate), whereas one exhibited a significantly higher number of these events towards the tips (Erodium, Table 2) and one (Cariceae) displayed marginal support for the latter pattern (but with opposite results when comparing separately gains and losses; results not shown). Correlation analyses between genome size and chromosome numbers (6 of 12 datasets; Tables S2–S7 and Figures S1–S6 in Supporting Information S2) and previous studies for the Cyperaceae revealed that gains and losses of single chromosomes are probably due to dysploidy for at least 10 of the 12 datasets for which this kind of transition was inferred (Table 2, Tables S2–S7 and Figures S1–S6 in Supporting Information S2). Therefore, dysploid transitions occurring in these groups would mostly correspond to fissions, fusions and genome rearrangements without changes in DNA content (Table 2, Supporting Information S1).
Table 2. Best-fitting model of chromosome number evolution, basic chromosome number (x) at the root of the tree with its probability (in brackets), and inferred number of chromosome gains, losses, polyploidy (PP), and demipolyploidy (Demi-PP) events for each dataset.

| Focal group (order, family) | Best supported model* | x (P>0.05) | Gains | Losses | PP | Demi-PP | P value from Chi-square for Polyploidy** | P value from Chi-square for gains and losses of single chromosomes** | Type of gains and losses of single chromosomes |
|-----------------------------|----------------------|------------|-------|--------|----|---------|------------------------------------------|---------------------------------------------------|-----------------------------------------------|
| Hedera (Apirales, Araliaceae) | CRD | 24 (0.92) | 0 | 0 | 2 | 5 | 0.2255 (obs recent > exp recent, obs ancient < exp ancient) | | |
| Orchidinae (Asparagales, Orchidaceae) | CRD | 21 (0.88), 22 (0.11) | 1 | 32 | 3 | 1 | 0.0084 (obs recent > exp recent, obs ancient < exp ancient) | 0.3477 (obs recent > exp recent, obs ancient < exp ancient) | Dysploidy |
| Bellis, Bellium, Bellidstrum (Asterales, Asteraceae) | CRDE | 9 (0.99) | 0 | 0 | 6 | 0 | 0.0028 (obs recent > exp recent, obs ancient < exp ancient) | | |
| Helianthus (Asterales, Asteraceae) | CRD | 17 (0.96) | 0 | 0 | 11 | 11 | 0.0001 (obs recent > exp recent, obs ancient < exp ancient) | | |
| Resedaceae (Brassicales) | CRDE | 3 (0.256), 4 (0.25), 20 (0.20), 5 (0.15), 1 (0.08), 6 (0.05) | 21 | 0 | 10 | 1 | 0.3140 (obs recent > exp recent, obs ancient < exp ancient) | 0.7685 (obs recent < exp recent, obs ancient < exp ancient) | Dysploidy |
| Arenaria sect. Plinthine (Caryophyllales, Caryophyllaceae) | LR | None P>0.05 | 920 | 1270 | 46 | 0 | 0.0004 (obs recent > exp recent, obs ancient < exp ancient) | 0.7384 (obs recent > exp recent, obs ancient < exp ancient) | Undetermined |
| Erodium (Geraniales, Geraniaceae) | CRDE | 10 (0.45), 9 (0.36), 5 (0.10) | 2 | 3 | 9 | 1 | 0.0001 (obs recent > exp recent, obs ancient < exp ancient) | 0.0001 (obs recent > exp recent, obs ancient < exp ancient) | Undetermined |
| Antirrhineae (Lamiales, Plantaginaceae) | LRDE | 9 (0.96) | 0 | 14 | 6 | 1 | 0.5354 (obs recent < exp recent, obs ancient > exp ancient) | 0.5866 (obs recent < exp recent, obs ancient < exp ancient) | Dysploidy |
| Passiflora (Malphigiales, Passifloraceae) | CR | 6 (0.99) | 1 | 0 | 4 | 2 | 0.3355 (obs recent < exp recent, obs ancient > exp ancient) | 0.7407 (obs recent > exp recent, obs ancient < exp ancient) | Dysploidy |
| Cistaceae (Malvales) | CR | 4 (0.87), 2 (0.08) | 7 | 0 | 9 | 0 | 0.1743 (obs recent > exp recent, obs ancient < exp ancient) | 0.3006 (obs recent > exp recent, obs ancient < exp ancient) | Dysploidy |
| Cariceae (Poales, Cyperaceae) | LR | None P>0.05 | 3480 | 3699 | 3 | 0 | 0.0001 (obs recent > exp recent, obs ancient < exp ancient) | 0.0269 (obs recent > exp recent, obs ancient < exp ancient) | Dysploidy |
| Carex sect. Ovales (Poales, Cyperaceae) | LRND | None P>0.05 | 1176 | 1086 | 0 | 0 | - | 0.9765 (obs recent > exp recent, obs ancient < exp ancient) | Dysploidy |
| Carex sect. Phacocystis (Poales, Cyperaceae) | CRND | 38 (0.32), 37 (0.23), 39 (0.23), 36 (0.09), 40 (0.08) | 74 | 101 | 0 | 0 | - | 0.2936 (obs recent > exp recent, obs ancient < exp ancient) | Dysploidy |
| Carex sect. Spirostachyae (Poales, Cyperaceae) | CRND | 38 (0.27), 39 (0.24), 37 (0.19), 40 (0.13), 36 (0.08) | 12 | 34 | 0 | 0 | - | 0.3439 (obs recent > exp recent, obs ancient < exp ancient) | Dysploidy |
Table 2. Cont.

| Focal group (order, family) | Best supported model* | Gains | Losses | PP | Demi-PP | P value from Chi-square for Polyploidy** | P value from Chi-square for gains and losses of single chromosomes** | Type of gains and losses of single chromosomes |
|----------------------------|-----------------------|-------|--------|----|--------|----------------------------------------|-------------------------------------------------------------------|--------------------------------------------------|
| *CR = Constant_Rate, three parameters: gains and losses of single chromosomes and polyploidy; CRD = Constant_Rate_Demi, three parameters: gains and losses of single chromosomes and one for polyploidy and demipolyploidy; CRDE = Constant_Rate_Demi_Est, four parameters: gains and losses of single chromosomes, polyploidy and demipolyploidy; CRND = Constant_Rate_No_Dupli, two parameters: gains and losses of single chromosomes; LR = Linear_Rate, five parameters: gains and losses of single chromosomes, gains and losses of single chromosomes proportional to chromosome number, and polyploidy; LRD = Linear_Rate_Demi, five parameters: gains and losses of single chromosomes, gains and losses of single chromosomes proportional to chromosome number, and one for polyploidy and demipolyploidy; LRDE = Linear_Rate_Demi_Est, six parameters: gains and losses of single chromosomes, gains and losses of single chromosomes proportional to chromosome number, polyploidy and demipolyploidy; and LRND = Linear_Rate_No_Dupli, four parameters: gains and losses of single chromosomes and gains and losses of single chromosomes proportional to chromosome number. **Alternatives analyses (internal vs. external branches of the phylogeny, present to 25% of total time vs. rest of the chronogram tree, and present to 50% of total time vs. rest of the chronogram tree) reveal identical conclusions. |
| Saxifraga sect. Saxifraga Saxifragales, Saxifragaceae | CRD | 25 (0.08), 24 (0.08), 26 (0.08), 23 (0.08), 27 (0.07), 22 (0.07), 28 (0.06), 21 (0.06), 29 (0.05), 20 (0.05) | 216 | 29 | 0 | 0.4278 (obs recent > exp recent, obs ancient < exp ancient) | 0.1471 (obs recent > exp recent, obs ancient < exp ancient) | Dysploidy |

Significant P values from the Chi-square analyses for the present to 10% of total time ("recent" times) vs. rest of the chronogram tree ("ancient" times) temporal level are shown, comparing the number of observed (inferred by ChromEvol analysis) vs. expected (under the null hypothesis of constant transition rate through time) polyploidy and gains/losses transitions. The type of gains and losses of single chromosomes has been inferred from the bibliography (Supporting Information S1 Notes S2) and from the results of the analysis of the relationship between chromosome number and genome size (Supporting Information S2). Significant P values from the Chi-square analyses for the present to 10% of total time ("recent" times) vs. rest of the chronogram tree ("ancient" times) temporal level are shown, comparing the number of observed (inferred by ChromEvol analysis) vs. expected (under the null hypothesis of constant transition rate through time) polyploidy and gains/losses transitions. The type of gains and losses of single chromosomes has been inferred from the bibliography (Supporting Information S1 Notes S2) and from the results of the analysis of the relationship between chromosome number and genome size (Supporting Information S2).
centromere [41]. Moreover, structural changes from fission and fusion are expected not to be underdominant [40]. Our results are in line with this hypothesis for the four datasets with holocentric chromosomes as we cannot reject the null hypothesis for any of them (Table 2). Additional studies are required to compare diversification patterns of organisms having different kinds of chromosomes (holocentric vs. monocentric chromosomes; Supporting Information S1).

To sum up, our results support the hypothesis that dysploidy is less disadvantageous than polyploidy in terms of generating long term persisting lineages [17]. This is most likely because the inferred dysploid transitions typically do not necessarily entail changes in DNA content but only genome structural rearrangements (Supporting Information S1).

Supporting Information

Supporting Information S1  A. Glossary of cytogenetic terms used throughout the article. B. Results and discussion concerning Table S6. Species, diploid chromosome number (2n) and genome size (2C, pg) for Cistaceae. Table S3. Species, diploid chromosome number (2n) and genome size (2C, pg) for Saxifraga sect. Saxifraga. Figure S1. Linear model for the correlation between diploid chromosome number (2n) and genome size (2C, pg) in Resedaceae. Figure S2. Linear model for the correlation between diploid chromosome number (2n) and genome size (2C, pg) in Antirrhineae. Figure S3. Linear model for the correlation between diploid chromosome number (2n) and genome size (2C, pg) in Saxifraga sect. Saxifraga. Figure S4. Linear model for the correlation between diploid chromosome number (2n) and genome size (2C, pg) in Orchidinae. Figure S5. Linear model for the correlation between diploid chromosome number (2n) and genome size (2C, pg) in Passiflora.

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Conceived and designed the experiments: ME SMB IM. Performed the experiments: ME SMB. Analyzed the data: ME SMB. Contributed reagents/materials/analysis tools: ME SMB IM MM MP PJM

Materials

Supporting Information S1 Zip file with graphs of phylogenetic trees with haploid chromosome numbers in the tips and phylogenetic trees in parenthetical format from chromEvol analyses with inferred mutation events.

ZPI

Supporting Information S2 Table S1. Parameters of the best supported model inferred for each group with ChromEvol. Table S2. Species, diploid chromosome number (2n) and genome size (2C, pg) for Cistaceae. Table S3. Species, diploid chromosome number (2n) and genome size (2C, pg) for Antirrhineae. Table S4. Species, diploid chromosome number (2n) and genome size (2C, pg) for Saxifraga sect. Saxifraga. Table S5. Species, diploid chromosome number (2n) and genome size (2C, pg) for Orchidinae. Table S6. Species, diploid chromosome number (2n) and genome size (2C, pg) for Resedaceae. Table S7. Species, diploid chromosome number (2n) and genome size (2C, pg) for Passiflora.

Material S1 Zip file with graphs of phylogenetic trees with haploid chromosome numbers in the tips and phylogenetic trees in parenthetical format from chromEvol analyses with inferred mutation events.

ZIP

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