COMPARATIVE CHLOROPLAST GENOMIC ANALYSES REVEALED EXTENSIVE GENOMIC ARRANGEMENT IN SOME CORE AND NON-CORE CARYOPHYLLALES

M. AJMAL ALI

Department of Botany and Microbiology, College of Science, King Saud University, Riyadh-11451, Saudi Arabia

Keywords: Caryophyllales; cp genome; Phylogenomics; mVISTA; MAUVE.

Abstract

The order Caryophyllales exhibit diverse diversity in morphology to molecules, which leads to taxonomic complexities in circumscribing especially to its families. The comparative analysis of the available chloroplast genome to detect pattern of genomic arrangement and variation is lacking; hence, the alignment pattern and genomic rearrangement across the Caryophyllales were detected, and the phylogenetic relationship among the families of the Caryophyllales based on maximum cp genes were inferred. The comparison of the Caryophyllales cp genomes based on representatives of 10 families with Taxillus chinensis as reference genome revealed that coding region were more conserved than the non-coding region; however, clpP, rpl16 and ycf15 were the most divergent coding region among all taxa. Further, the genomic rearrangement occurred in gene organization of the taxa among different families of Caryophyllales, the extensive rearrangement were observed in Amaranthaceae, Caryophyllaceae, Chenopodiaceae, Droseraceae and Cactaceae.

Introduction

The order Caryophyllales (-the core eudicots) is a diverse clade of angiosperms that includes c. 12,500 species under c.749 genera and c. 40 families [viz. Achatocarpaceae, Agdestidaceae, Aizoaceae, Amaranthaceae, Anacampserotaceae, Ancistrocladaceae, Asteropeiaceae, Barbeuiaceae, Basellaceae, Cactaceae, Caryophyllaceae, Chenopodiaceae, Corbichoniaceae, Didiereaceae, Dioncophyllaceae, Droseraceae, Drosophyllaceae, Frankeniacaeae, Gisekiaceae, Halophytaceae, Limeaceae, Lophiocarpaceae, Macarthuriaceae, Microteaceae, Molluginaceae, Montiaceae, Nepenthaceae, Nyctaginaceae, Petiveriaceae, Physenaceae, Phytolaccaceae, Plumbaginaceae, Polygonaceae, Portulacaceae, Rhabdodendraceae, Sarcobataceae, Simmondsiaceae, Stenoparmataceae, Talinaceae, Tamaricaceae] (APG, 2016; Walker et al., 2018; Yao et al., 2019). The members of the order Caryophyllales exhibit diverse diversity in morphology to molecules (Hernández-Ledesma et al., 2015; Smith et al., 2018) which leads to taxonomic complexities in circumscribing especially at the family level, and even at the generic and specific level too; hence, investigating the relationship at different taxonomic level was always remained great interest in the era of pre-phylogenetic (Behnke, 1976) to phylogeny-based classification (Giannasi, 1992; APG 1998, 2003, 2009, 2016; Cuénoud et al., 2002, Brockington et al., 2009; Schäferhoff et al., 2009; Arakaki et al., 2011; Crawley and Hilu, 2012a,b; Ruhfel et al., 2014; Yang et al., 2015, 2018). As a result the identification and description of new taxa at all the taxonomic levels are done and the circumscription of the order Caryophyllales are radically changed now (Hernández-Ledesma et al., 2015; Liu et al., 2015; Walker et al., 2018; Yao et al., 2019). Despite it, many of the relationships among families of Caryophyllales still remain

1E-mail: majmalali@rediffmail.com, ajmalpdr@gmail.com, alimohammad@ksu.edu.sa
uncertain, and a comparative analysis of the available chloroplast genome (cp) to detect pattern of genomic arrangement and variation is lacking. Hence the present study has been undertaken to infer the alignment and genomic rearrangement across the selected families of the order Caryophyllales, and phylogenetic relationship among these families based on cp genes.

Materials and Methods

Data source

The chloroplast genome sequences of c. 37 taxa under 10 out of 40 families of the order Caryophyllales are available in the NCBI GenBank. Out of these, a total of 19 representative taxa under 10 families (viz. Aizoaceae, Amaranthaceae, Cactaceae, Caryophyllaceae, Chenopodiaceae, Droseraceae, Montiaceae, Polygonaceae, Portulacaceae and Talinaceae) of the order Caryophyllales, and three outgroup taxa [Taxillus chinensis (Loranthaceae), T. sutchuenensis (Loranthaceae) and, Erythropalum scandens (Erythropalaceae)] from the order Santalales were retrieved for the comparative analysis (Table 1).

Comparative analysis of cp genome

The retrieved cp genome of the representatives families of Caryophyllales were compared with one of the out group taxon T. chinensis (GenBankNC_036306.1) from the order Santalales as reference genome using the mVISTA program in Shuffle-LAGAN mode (Brudno et al., 2003; Frazer et al., 2004), and the genomic rearrangements were detected using MAUVE (Darling et al., 2004; Fig. 2).

Molecular phylogenetic analyses

The coding regions of 39 plastid-coding genes (Table 2) were extracted from the retrieved assembled cp genome, and aligned using CLUSTAL X (Thompson et al., 1997). The Maximum Parsimony (MP) analysis (Eck and Dayhoff, 1996; Nei and Kumar, 2000), using bootstrap method (Felsenstein, 1985), and the Maximum Likelihood (ML) analysis using maximum composite likelihood method (Tamura et al., 2004) were used to conduct the molecular phylogenetic analyses using the software MEGA X (Kumar et al., 2018). Taxillus chinensis (Loranthaceae), T. sutchuenensis (Loranthaceae), Erythropalum scandens (Erythropalaceae) from the order Santalales were used as outgroup in the phylogenetic analyses.

Results and Discussion

Comparison of Caryophyllales chloroplast genomes

The genomic features (viz, total cp genome size base pair (bp), gene size (bp), spacer size (bp), total number of genes, number of tRNA genes, number of protein encoding genes, number of rRNA genes and total GC content (%)) of the selected sequences included in the present analysis were compared (Table 1). The total cp genome size ranged from 113064 bp in Carnegiea gigantea (Cactaceae) to 161541 bp in Rheum palmatum (Polygonaceae). The coding gene size was varied from 68877 bp in Carnegiea gigantea (Cactaceae) to114159 bp in R. palmatum (Polygonaceae). The spacer size was found to be 41173 bp in Dionaea muscipula (Droseraceae) to 76337 bp in Amaranthus hypochondriacus (Amaranthaceae). Further, except the number of rRNA genes which were found in all the analyzed four taxa; the total number of genes, number of tRNA genes, number of protein encoding genes, and total GC content (%) ranges were 98-113, 20-30, 67-80, and 36-37%, respectively. Despite the constancy of genetic content, structures and organization of chloroplast genomes of flowering plants, enormous variation have also been noted especially in the total cp genome coding size, spacer size, total number of genes, number of tRNA genes and
Table 1. The representative genome sequences of Caryophyllales retrieved from GenBank for comparative analysis. *, Included in ML analysis. **used as reference genome for mVISTA/MAUVE analysis.

| Family        | Taxon                                | Accession Number | Total cp genome size (bp) | Gene size (bp) | Spacer size (bp) | Total no. of genes | Number of tRNA genes | Number of protein encoding genes | Total GC content (%) | Included in ML; mVISTA/MAUVE analysis |
|---------------|--------------------------------------|------------------|---------------------------|----------------|------------------|-------------------|---------------------|-------------------------------|-------------------|-----------------------------------|
| Caryophyllales|                                      |                  |                           |                |                  |                   |                     |                               |                   |                                   |
| Aizoaceae     | 1. Mesembryanthemum crystallinum L.  | NC_029049.1      | 153831                    | 104957         | 48874            | 113               | 29                  | 80                            | 37                | 1/2/*                             |
|               | 2. Tetragonia tetragonoides (Pall.) Kuntze | NC_036991.1      | 149506                    | 100768         | 48738            | 110               | 29                  | 77                            | 37                | 2/3/*                             |
| Amaranthaceae | 3. Amaranthus hypochondriacus L.     | NC_030770.1      | 150518                    | 74181          | 76337            | 98                | 25                  | 69                            | 36                | 3/4/*                             |
| Cactaceae     | 4. Carnegiea gigantea (Engelm.) Britton & Rose | NC_027618.1      | 113064                    | 68877          | 44187            | 99                | 28                  | 67                            | 36                | 4/5/*                             |
| Caryophyllaceae| 5. Agrostemma githago L.             | NC_023357.1      | 151733                    | 104985         | 46748            | 111               | 30                  | 77                            | 36                | 5/6/*                             |
|               | 6. Colobanthus apetalus (Labiil.) Druce | NC_036424.1      | 151228                    | 103997         | 47231            | 111               | 30                  | 77                            | 36                | 6/8/*                             |
|               | 7. Gymnocarpus pravulskii Bunge ex Maxim. | NC_036812.1      | 150636                    | 106337         | 44299            | 111               | 30                  | 77                            | 36                | 7/9/*                             |
| Chenopodiaceae| 8. Silene capitata Kom.              | NC_035226.1      | 150224                    | 107168         | 43056            | 111               | 29                  | 78                            | 36                | 8/7/*                             |
|               | 9. Haloxylon persicum Bunge          | NC_027669.1      | 151586                    | 106818         | 44768            | 113               | 29                  | 80                            | 36                | 9/11/*                            |
|               | 10. Salicornia bigelovii Torr.       | NC_027226.1      | 153076                    | 107538         | 45538            | 100               | 20                  | 76                            | 36                | 10/10/*                            |
| Table 1 (contd.) |
|------------------|
| **Droseraceae**  | **Montiaceae** |
| 11. *Aldrovandra vesiculosa* L. | **Cistanthe longiscapa** (Barnéoud) Carolinex M.A. Hershkovitz |
| **Nc_035416.1** | **Nc_035415.1** |
| 141568          | 136810         |
| 92985           | 89342          |
| 48583           | 47468          |
| 101             | 101            |
| 30              | 30             |
| 67              | 67             |
| 36              | 37             |
| 11/14/*         | 13/12/*        |
| **Polygonaceae** |                  |
| 15. *Fagopyrum dibotrys* (D.Don) H.Hara |                  |
| **Nc_037705.1** |                  |
| 159320          |                  |
| 113778          |                  |
| 45542           |                  |
| 113             |                  |
| 30              |                  |
| 79              |                  |
| 37              |                  |
| 15/18/*         |                  |
| **Portulacaceae** |                  |
| 18. *Portulaca oleracea* L. |                  |
| **Nc_036236.1** |                  |
| 156533          |                  |
| 110988          |                  |
| 45545           |                  |
| 113             |                  |
| 30              |                  |
| 79              |                  |
| 36              |                  |
| 18/19/*         |                  |
| **Talinaceae**  |                  |
| 19. *Talinum paniculatum* (Jacq.) Gaertn. |                  |
| **Nc_037748.1** |                  |
| 156929          |                  |
| 110265          |                  |
| 46664           |                  |
| 112             |                  |
| 30              |                  |
| 78              |                  |
| 36              |                  |
| 19/20/*         |                  |
| **OUT GROUP**   |                  |
| **Santalales**  |                  |
| **Loranthaceae** |                  |
| 20. *Taxillus chinensis* (DC.) Danser |                  |
| **Nc_036306.1** |                  |
| 121363          |                  |
| 79489           |                  |
| 41874           |                  |
| 89              |                  |
| 23              |                  |
| 62              |                  |
| 37              |                  |
| */1/*           |                  |
| 21. *T. suichuenensis* (Locomte) Danser |                  |
| **Nc_036307.1** |                  |
| 122562          |                  |
| 79471           |                  |
| 43091           |                  |
| 89              |                  |
| 23              |                  |
| 62              |                  |
| 37              |                  |
| */1/*           |                  |
| **Erythropalaceae** |                  |
| 22. *Erythropsis scandens* Blume |                  |
| **Nc_036759.1** |                  |
| 156154          |                  |
| 110131          |                  |
| 46023           |                  |
| 112             |                  |
| 29              |                  |
| 79              |                  |
| 37              |                  |
| */1/*           |                  |
number of protein encoding genes (Simpson and Stern, 2002; Raubeson and Jansen, 2005; Daniell et al., 2016) which could be due to genomic duplications or fractionation (Wendel et al., 2016).

The comparative genomic analysis revealed that coding region was more conserved than the non-coding region; however, clpP, rpl16 and ycf15 were the most divergent coding region among all taxa (Fig. 1). Further, the genomic rearrangement occurred in gene organization of taxa among different families of Caryophyllales, the extensive rearrangement were observed in the representatives of the families Amaranthaceae, Caryophyllaceae, Chenopodiaceae, Droseraceae and Cactaceae (Fig. 2). The majority of the loss of introns within protein-coding genes have also previously been observed in specific plant groups or species such as in Hordeum vulgare (Saski et al., 2007), Manihot esculenta (Daniell et al., 2008), Cicer arietinum (Jansen et al., 2008) and Bambusa sp. (Wu et al., 2009). Moreover, intron loss (such as that in clpP) occurs in diverse angiosperms including Poaceae, Onagraceae and Oleaceae (Jansen et al., 2007). The extensive rearrangement could be due to loss of introns, IR expansion and contraction (Daniell et al., 2016).

Table 2. List of the genes included in the molecular phylogenetic analyses.

| Gene product                     | Genes                                      |
|----------------------------------|--------------------------------------------|
| Photosystem I                    | psaA, psaB, psaC, psaJ, ycf4               |
| Photosystem II                   | psbA, psbC, psbE, psbH, psbI, psbK, psbN, psbT |
| Cytochrome b6/f                  | petA, petG, petN                           |
| ATP synthase                     | atpF*, atpH, atpL, atpA, atpB, atpE        |
| Rubisco                          | rbcL                                      |
| Large subunit ribosomal proteins | rpl14*, rpl2*, rpl20                      |
| Small subunit ribosomal proteins | rps14, rps18, rps2, rps3, rps4, rps7, rps8 |
| RNA polymerase subunit           | rpoB, rpoC2, rpoC1*                       |
| Other proteins                   | Envelope membrane Protein cemA            |
|                                  | c-type cytochrome synthesis gene ccsA     |

Phylogenetic analysis

The molecular phylogenetic analysis of aligned combined sequences data matrix had 32374 positions, resulted into most parsimonious tree with the length 20970 (CI: 0.592, RI: 0.700), and the ML tree (with the highest log likelihood -182780.57) whose topology was congruent to MPT (Fig 3). The molecular phylogenetic relationships among the major clades/families of the order Caryophyllales were well resolved and seem to be strongly supported in the present ML analyses, and were found congruent with the previous recent phylogenomic (Yao et al., 2019) and phylotranscriptomic (Walker et al., 2018) analyses of Caryophyllales. The analysis also inferred strong support for the carnivorous clade Droseraceae (100% BS) as sister to a clade Polygonaceae, and Caryophyllaceae as sister to Amaranthaceae and Chenopodiaceae (100% BS). The molecular phylogenetic studies based on chloroplast markers and extensive sampling (Kadereit et al., 2003, 2012) as well as morphological similarities [petaloid tepals, filament tubes, 2-locular anthers; compare with Table 5 of Kadereit et al. (2003)] place the family Caryophyllaceae closer to the Amaranthaceae s.s., while in terms of habitat preferences they are more like many members of the Chenopodiaceae. The family Montiaceae and Talinaceae resolved as a grade, and as sister to the family Talinaceae, a clade was recovered in which the family Cactaceae was sister to a clade of Portulacaceae. The placements of all families of the order seem to be strongly supported.
Fig. 1. Percent identity plot for comparison of 19 Caryophyllales chloroplast genome with *Taxillus chinensis* as reference. *Taxillus chinensis* (Loranthaceae). Alignment lane 1. *Mesembryanthemum crystallinum* (Aizoaceae), 2. *Tetragonia tetragonioides* (Aizoaceae), 3. *Amaranthus hypochondriacus* (Amaranthaceae), 4. *Carnegia gigantea* (Cactaceae), 5. *Agrostemma githago* (Caryophyllaceae), 6. *Colobanthus apetalus* (Caryophyllaceae), 7. *Gymnocarpus przewalskii* (Caryophyllaceae), 8. *Silene capitata* (Caryophyllaceae), 9. *Haloxylon persicum* (Chenopodiaceae), 10. *Salicornia bigelovii* (Chenopodiaceae), 11. *Aldrovanda vesiculosa* (Droseraceae), 12. *Dionaea muscipula* (Droseraceae), 13. *Drosera regia* (Droseraceae), 14. *Cistanthe longiscapa* (Montiaceae), 15. *Fagopyrum dibotrys* (Polygonaceae), 16. *Oxyria sinensis* (Polygonaceae), 17. *Rheum palmatum* (Polygonaceae), 18. *Portulaca oleracea* (Portulacaceae), 19. *Talinum paniculatum* (Talinaceae).
COMPARATIVE CHLOROPLAST GENOMIC ANALYSES REVEALED

Fig. 2. MAUVE alignment of representative of 19 Caryophyllales chloroplast genomes. The *T. chinensis* genome is shown at top as the reference. Within each of the alignment, local collinear blocks are represented by blocks of the same color connected by lines [1. *Taxillus chinensis* (Loranthaceae), 2. *Mesembryanthemum crystallinum* (Aizoaceae), 3. *Tetragonia tetragonioides* (Aizoaceae), 4. *Amaranthus hypochondriacus* (Amaranthaceae), 5. *Carnegiea gigantea* (Cactaceae), 6. *Agrostemma githago* (Caryophyllaceae), 7. *Silene capitata* (Caryophyllaceae), 8. *Colobanthus apetalus* (Caryophyllaceae), 9. *Gymnocalycium przewalskii* (Caryophyllaceae), 10. *Salicornia bigelovii* (Chenopodiaceae), 11. *Haloxylon persicum* (Chenopodiaceae), 12. *Drosera regia* (Droseraceae), 13. *Dionaea muscipula* (Droseraceae), 14. *Aldrovanda vesiculosa* (Droseraceae), 15. *Cistanthe longiscapa* (Montiaceae), 16. *Rheum palmatum* (Polygonaceae), 17. *Oxyria sinensis* (Polygonaceae), 18. *Fagopyrum dibotrys* (Polygonaceae), 19. *Portulaca oleracea* (Portulacaceae), 20. *Talinum paniculatum* (Talinaceae)].
Moreover, the monophyly of all major clades within the order (e.g., Centrospermae, the carnivorous clade, the FTPP clade, the globular inclusion clade, and the Portulacineae clade) seem to be supported (Fig. 3).

Additionally, in Amaranthaceae clade, Caryophyllaceae clade and Chenopodiaceae clade extensive genomic rearrangement were also observed (Fig. 3). Moreover, the rearrangement and gene/intron loss were correlated with ML tree. The protein-coding gene loss, intron loss, intron inversion, pseudogene formation, IR contraction, expansion and loss have also been previously reported in Caryophyllales (Yao et al., 2019).

Fig. 3. Relationships among the families of the Caryophyllales inferred using Maximum Likelihood analysis of 39 chloroplast coding genes.

Acknowledgments
This research was supported by the King Saud University, Deanship of Scientific Research, College of Science, Research Center.

References
APG (Angiosperm Phylogeny Group). 1998. An ordinal classification for the families of flowering plants. Ann. Mo. Bot. Gard. 85(4): 531–553.

APG II (Angiosperm Phylogeny Group). 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Bot. J. Linn. Soc. 141(4): 399–436.

APG III (Angiosperm Phylogeny Group). 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Bot. J. Linn. Soc. 161: 105–121.
COMPARATIVE CHLOROPLAST GENOMIC ANALYSES REVEALED

APG IV (Angiosperm Phylogeny Group). 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Bot. J. Linn. Soc. 181: 1–20.

Arakaki, M., Christin, P.A., Nyffeler, R., Lendel, A., Eggli, U., Ogburn, R.M., Spriggs, E., Moore, M.J. and Edwards, E.A. 2011. Contemporaneous and recent radiations of the world’s major succulent plant lineages. Proc. Natl. Acad. Sci. USA. 108: 8379–8384

Behnke, H.D. 1976. Ultrastructure of sieve-element plastids in Caryophyllales (Centrospermae), evidence for the delimitation and classification of the order. Plant Syst. Evol. 126: 31–54.

Brockington, S.F., Alexandre, R., Ramdial, J., Moore, M.J., Crawley, S., Dhingra, A., Hilu, K., Soltis, D.E. and Soltis, P.S. 2009. Phylogeny of the Caryophyllales sensu lato: revisiting hypotheses on pollination biology and perianth differentiation in the core Caryophyllales. Int. J. Plant Sci. 170: 627–643.

Brudno, M., Malde, S., Poliakov, A., Do, C.B., Couronne, O., Dubchak, I., and Batzoglou, S. 2003. Global alignment: finding rearrangements during alignment. Bioinformatics 19S1: 154–162.

Crawley, S.S. and Hilu, K.W. 2012a. Caryophyllales: evaluating phylogenetic signal in trnK intron versus matK. J. Syst. Evol. 50: 387–410.

Crawley, S.S. and Hilu, K.W. 2012b. Impact of missing data, gene choice, and taxon sampling on phylogenetic reconstruction: the Caryophyllales (angiosperms). Plant Syst. Evol. 298: 297–312.

Cuénoud, P., Savolainen, V., Chatrou, L.W., Powell, M., Graye, R.J. and Chase, M.W. 2002. Molecular phylogenetics of Caryophyllales based on nuclear 18S rDNA and plastid rbcL, atpB, and matK DNA sequences. Amer. J. Bot. 89: 132–144.

Daniell, H., Lin, C.S., Yu, M. and Chang, W.J. 2016. Chloroplast genomes: diversity, evolution, and applications in genetic engineering. Genome Biol. 217(1):1–34.

Daniell, H., Wurdack, K.J., Kanagaraj, A., Lee, S.B., Sasaki, C. and Jansen, R.K. 2008. The complete nucleotide sequence of the cassava (Manihot esculenta) chloroplast genome and the evolution of atpF in Malpighiales: RNA editing and multiple losses of a group II intron. Theor. Appl. Genet. 116: 723–737.

Darling, A.C., Mau, B., Blatter, F.R. and Perna, N.T. 2004. Mauve: multiple alignment of conserved genomic sequence with rearrangements. Genome Res. 14(7): 1394–1403.

Eck, R.V. and Dayhoff, M.O. 1996. Atlas of Protein Sequence and Structure. National Biomedical Research Foundation, Silver Springs, Maryland, USA.

Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39: 783–791.

Frazer, K.A., Pachter, L., Poliakov, A., Rubin, E.M. and Dubchak, I. 2004. VISTA: computational tools for comparative genomics. Nucleic Acids Res. 32(suppl. 2): 273–279.

Giannasi, D.E. 1992. Evolutionary relationships of the Caryophyllidae based on comparative rbcL sequences. Syst. Biol. 17: 1–15

Hernández-Ledesma P., Berendsohn, W.G., Borsch, T., Mering, S.V., Akhani, H., Arias, S., Castañeda-Noa, I., Eggli, U., Eriksson, R., Flores-Olvera, H., Fuentes-Bazán, S., Kadereit, G., Klak, C., Korotkova, N., Nyffeler, R., Ocampo, G., Ochoterena, H., Oxelman, B., Sanchez, R.K.R.A., Schlumpberger, B.O. and Uotila, P. 2015. A taxonomic backbone for the global synthesis of species diversity in the angiosperm order Caryophyllales. Willdenowia 45: 281–383.

Jansen, R.K., Cai, Z., Raubeson, L.A., Daniell, H., Leebens-Mack, J., Müller, K.F. Gisinger-Bellian, M., Haberle, R.C., Hansen, A.K., Chumley, T.W., Lee, S.B., Peery, R., McNeal, J.R., Kuehl, J.V. and Boore J.L. 2007. Analysis of 81 genes from 64 plastid genomes resolves relationships in angiosperms and identifies genome-scale evolutionary patterns. Proc. Natl. Acad. Sci. USA 104:19369–19374.

Jansen, R.K., Wojciechowski, M.F., Sanniyasi, E., Lee, S.B. and Daniell, H. 2008. Complete plastid genome sequence of the chickpea (Cicer arietinum) and the phylogenetic distribution of rps12 and clpP intron losses among legumes (Leguminosae). Mol. Phylogenet. Evol. 48:1204–1217.

Kadereit, G., Ackerly, D. and Pirie, M.D. 2012. A broader model for C4 photosynthesis evolution in plants inferred from the goosefoot family (Chenopodiaceae s.s.). Proc. Biol. Sci. 279(1741): 3304–3311.

Kadereit, G., Borsch, T., Weising, K. and Freitag, H. 2003. Phylogeny of Amaranthaceae and Chenopodiaceae and the evolution of C4 photosynthesis. Int. J. Plant Sci. 164: 959–986.
Kumar, S., Stecher, G., Li, M., Knyaz, C. and Tamura, K. 2018. MEGA X: Molecular evolutionary genetics analysis across computing platforms. Mol. Biol. Evol. 35(6): 1547–1549.

Liu, B., Ye, J., Liu, S., Wang, Y., Yang, Y., Lai, Y., Zeng, G. and Lin, Q. 2015. Families and genera of Chinese angiosperms: a synoptic classification Biod. Sci. 23: 225–231.

Nei, M. and Kumar, S. 2000. Molecular Evolution and Phylogenetics. Oxford University Press, New York.

Raubeson, L.A. and Jansen, R.K. 2005. Chloroplast genomes of plants. In: Henry, R.J. (Ed.), Plant Diversity and Evolution: Genotypic and Phenotypic Variation in Higher Plants. CAB International, Wallingford, UK.

Ruhfel, B.R., Gitzendamer, M.A., Soltis, P.S., Soltis, D.E. and Burleigh, J.G. 2014. From algae to angiosperms – inferring the phylogeny of green plants (Viridiplantae) from 360 plastid genomes. BMC Evol. Biol. 14: 1–23.

Sasaki, C., Lee, S.B., Fjellheim, S., Guda, C., Jansen, R.K., Luo, H., Tomkins, J., Rognli, O.A., Daniell and H., Clarke, J.L. 2007. Complete chloroplast genome sequences of Hordeum vulgare, Sorghum bicolor and Agrostis stolonifera, and comparative analyses with other grass genomes. Theor. Appl. Genet. 115: 571–590.

Schäferhoff, B., Müller, K.F. and Borsch, T. 2009. Caryophyllales phylogenetics: disentangling Phytolaccaceae and Molluginaceae and description of Microteaceae as a new isolated family. Willdenowia 39: 209–228.

Simpson, C.L. and Stern, D.B. 2002. The treasure trove of algal plastid genomes. Surprises in architecture and gene content, and their functional implications. Plant Physiol. 129: 957–966.

Smith, S.A., Brown, J.W., Yang, Y., Bruenn, R., Drummond, C.P., Brockington, S.F., Walker, J.F., Last, N., Douglas, N.A. and Moore, M.J. 2018. Disparity, diversity and duplications in the Caryophyllales. New Phytol. 217: 836–854.

Tamura, K., Nei, M. and Kumar, S. 2004. Prospects for inferring very large phylogenies by using the neighbor-joining method. Proc. Nat. Acad. Sci. (USA) 101: 11030–11035.

Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F. and Higgins, D.G. 1997. The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res. 25: 4876-4882.

Walker, J.F., Yang, Y., Feng, T., Timoneda, A., Mikenas, J., Hutchinson, V., Edwards, C., Wang, N., Ahluwalia, S., Olivier, J., Walker-Hale, N., Majure, L.C., Puente, R., Kadereit, G., Lauterbach, M., Eggl, U., Flores-Olvera, H., Ochoterena, H., Brockington, S.F., Moore, M.J. and Smith S.A. 2018. From cacti to carnivores: Improved phylotranscriptomic sampling and hierarchical homology inference provide further insight to the evolution of Caryophyllales. Am. J. Bot. 105: 446–462.

Wendel, J.F. Jackson, S.A., Meyers, B.C. and Wing, R.A. 2016. Evolution of plant genome architecture. Genome Biol. 17: 37. Wu, F.H., Kan, D.P., Lee, S.B., Daniell, H., Lee, Y.W., Lin, C.C., Lin, N.S. and Lin C.S. 2009. Complete nucleotide sequence of Dendrocalamus latiflorus and Bambusa oldhamii chloroplast genomes. Tree Physiol. 29: 847–56.

Yang, Y., Moore, M.J., Brockington, S.F., Soltis, D.E., Wong, G.K.S., Carpenter, E.J., Zhang, Y., Chen, L., Yan, Z., Xie, Y., Sage, R.F., Covshoff, S., Hibberd, J.M., Nelson, M.N. and Smith, S.A. 2015. Dissecting molecular evolution in the highly diverse plant clade Caryophyllales using transcriptome sequencing. Mol. Biol. Evol. 32: 2001–2014.

Yang, Y., Moore, M.J., Brockington, S.F., Mikenas, J., Olivier, J., Walker, J.F. and Smith, S.A. 2018. Improved transcriptome sampling pinpoints 26 ancient and more recent polyploidy event in Caryophyllales, including two allopolyploidy event. New Phytol. 217: 855–870.

Yao, G., Jin, J.J., Li, H.T., Yang, J.B., Mandala, V.S., Croy, M., Mostow, R., Douglas, N.A., Chase, M.W., Christenhusz, M.J.M., Soltis, D.E., Soltis, P.S., Smith, S.A., Brockington, S.F., Moore, M.J., Yi, T.S. and Li, D.Z. 2019. Plastid phylogenomic insights into the evolution of Caryophyllales. Mol. Phylogenet. Evol. 134: 74–86.

(Manuscript received on 13 February 2019; revised on 16 April 2019)