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

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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, Frankeniaceae, Gisekiaceae, Halophytaceae, Limeaceae, Lophiocarpaceae, Macarthuriaceae, Microteaceae, Molluginaceae, Montiaceae, Nepenthaceae, Nyctaginaceae, Petiveriaceae, Physenaceae, Phytolaccaceae, Plumbaginaceae, Polygonaceae, Portulacaceae, Rhabdodendraceae, Sarcobataceae, Simmondsiaceae, Stegnospermataceae, 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

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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
IN GROUP										
Caryophyllales										
Aizoaceae	1. *Mesembryanthemum crystallinum* L.	NC_029049.1	153831	104957	48874	113	29	80	37	1/2/*
	2. *Tetragonia tetragonioides* (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* (Labill.) Druce	NC_036424.1	151228	103997	47231	111	30	77	36	6/8/*
	7. *Gymnocarpos przewalskii* Bunge *ex* Maxim.	NC_036812.1	150636	106337	44299	111	30	77	36	7/9/*
	8. *Silene capitata* Kom.	NC_035226.1	150224	107168	43056	111	29	78	36.	8/7/*
Chenopodiaceae	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	11. *Aldrovanda vesiculosa* L.	NC_035416.1	141568	92985	48583	101	30	67	36	11/14/*
	12. *Dionaea muscipula* J.Ellis	NC_035417.1	117589	76416	41173	100	29	67	38	12/13/*
	13. *Drosera regia* Stephens	NC_035415.1	136810	89342	47468	101	30	67	37	13/12/*
Montiaceae	14. *Cistanthe longiscapa* (Barnéoud) Carolin*ex* M.A. Hershkovitz	NC_035140.1	156830	108469	48361	105	22	79	36	14/15/*
Polygonaceae	15. *Fagopyrum dibotrys* (D.Don) H.Hara	NC_037705.1	159320	113778	45542	113	30	79	37	15/18/*
	16. *Oxyria sinensis* Hemsl.	NC_032031.1	160404	113809	46595	109	28	77	37	16/17/*
	17. *Rheum palmatum* L.	NC_027728.1	161541	114159	47382	110	28	78	37	17/16/*
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. sutchuenensis* (Lecomte) Danser	NC_036307.1	122562	79471	43091	89	23	62	37	-/-/-
Erythropalaceae	22. *Erythropalum scandens* Blume	NC_036759.1	156154	110131	46023	112	29	79	37	-/-/-

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 loos 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, psbJ, psbK, psbN, psbT*	
Cytochrome b6/f	*petA, petG, petN*	
ATP synthase	*atpF*, atpH, atpI, 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 phylotranscrip-tomic (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.

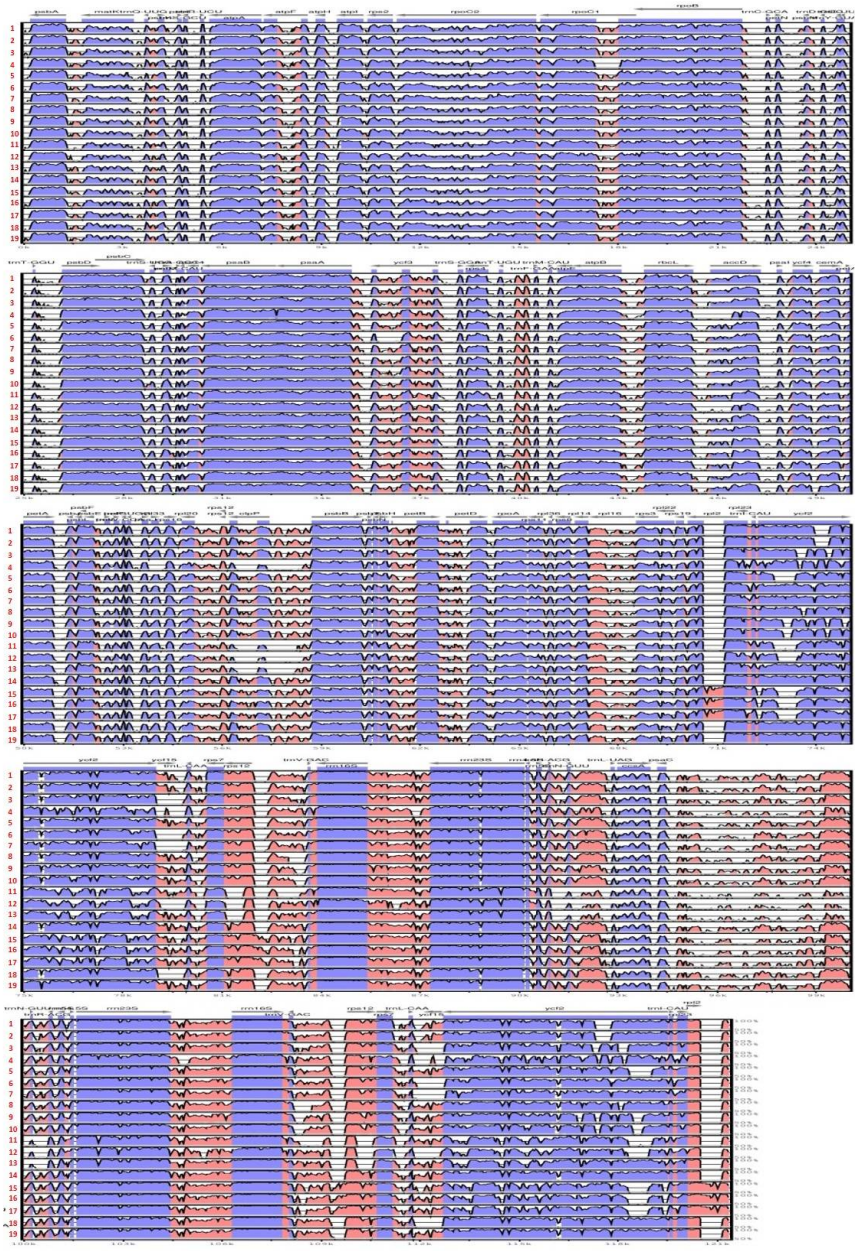

Fig. 1. Percent identity plot for comparison of 19 Caryophyllales chloroplast genome with *Taxillus chinensis* as reference *Taxillus chinensis* (Loranthaceae). Alignment lane 1. *Mesembryanthemum crystallinum* (Aizoaceae), 2. *Tetragonia tetragonioides* (Aizoaceae), 3. *Amaranthus hypochondriacus* (Amaranthaceae), 4. *Carnegiea gigantea* (Cactaceae), 5. *Agrostemma githago* (Caryophyllaceae), 6. *Colobanthus apetalus* (Caryophyllaceae), 7. *Gymnocarpos 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).

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. *Gymnocarpos 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 Caryophyllaes (Yao *et al*., 2019).

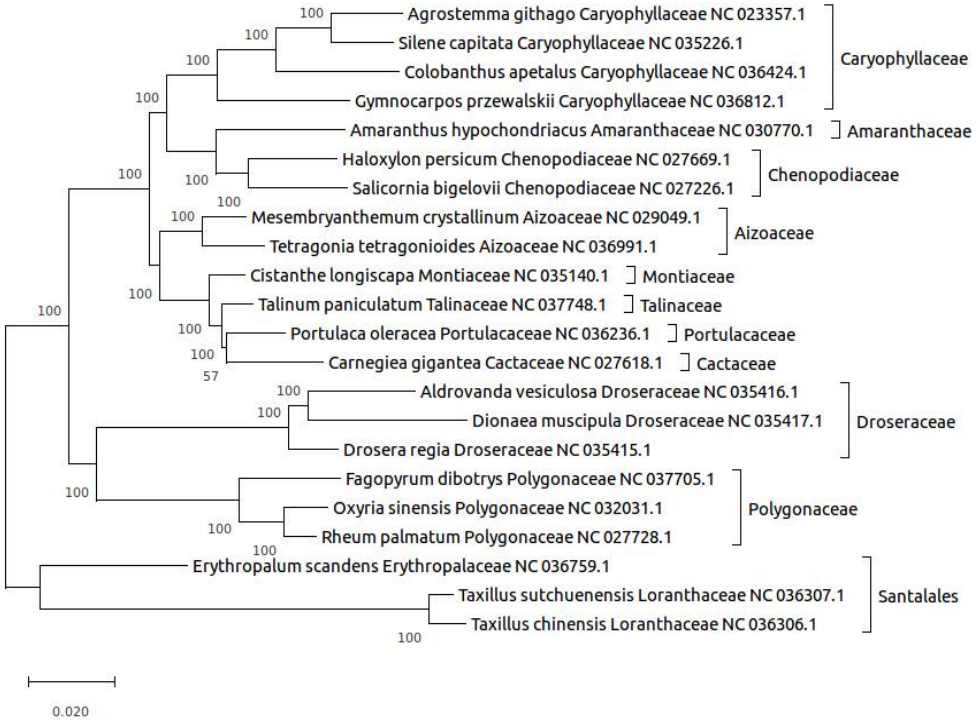

Fig. 3. Relationships among the families of the Caryophyllales inferred using Maximum Likelihood analysis of 39 chloroplast coding genes.

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