



**PAN-PLASTOMES OR CON-PLASTOMES – A NOVEL SIGHT ON THE GENETIC DIVERSITY OF CHLOROPLAST GENOMES OF HIGHER PLANTS FOR PHYLOGENETIC INVESTIGATIONS**

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**Resume**

The first review of plant pan-plastomes has been prepared. While complete chloroplast genomes have already been sequenced for several thousand species, there are currently only about three dozens of presented pan-plastomes. There are publications though, in which the term "pan-plastome" was not used, but in fact the pan-approach was applied to the sequenced multiple chloroplast genomes. The importance of the use of pan-plastomes for phylogenetic studies is noted, since in this case intraspecific differences are taken into account. The need for the compilation and use of consensus plastomes or con-plastomes, which contain only the most frequently occurring major mutations compared to the reference chloroplast genome, is emphasized, as this can lead to a more accurate inference of evolutionary events. Some attention is paid to the terminology used, including historical aspects. A point of view is expressed that more attention should be paid to the sequencing and compilation of plant pan-plastomes.

**Keywords:** plastome, pan-plastome, chloroplast genome, chloroplast pangenome, sequencing, higher plants, phylogeny

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**Brief history of plastid terms**

The subject of this review requires a brief consideration of the terms used. Thus, in 1920, the term "genome" was proposed to denote the hereditary information contained in the nucleus in a haploid set of chromosomes, but the adjacent protoplasm was also mentioned [Winkler, 1920]. Even at that time, there was an understanding of the hereditary role of the cytoplasm, which, as is now known, contains the genetic material in mitochondria and chloroplasts. In 1926, the term "plasmon" was proposed for the cytoplasmic hereditary material [von Wettstein, 1926]. Later, an attempt was made to separate chloroplasts from the plasmon and the term "plastidome" arose, and then "plastome" [Renner, 1934]. Twenty years later, P. Michaelis presented a diagram of the genetic components of the cell, in which he separated the Genome (Chromosomes, nuclear genes)

from plasmagenes contained in the plasmon and consisting of the plastome, chondriosomes, cytoplasmon and yet unidentified components<sup>1</sup> [Michaelis, 1954].

Currently, the terms plastome and plastid/chloroplast genome are synonymous and used widely. The prefix "pan" for chloroplast genomes appeared relatively recently [Starkenburger et al., 2014] and is used to denote a group of plastomes with known complete nucleotide sequences belonging to the same plant species. In one of the articles [Magdy et al., 2019], chloroplast pangenome of pepper species was designated as supra-plastome.

Thus, the pan-plastome combines all the diversity of chloroplast genome nucleotide sequence variants in a particular plant species, and contains information on both

<sup>1</sup> "?" in the original article [Michaelis, 1954]

major and rarer minor mutations. Con-plastomes (consensus plastomes) contain information only on the most frequently occurring major mutations compared to the reference chloroplast genome of a particular species; they are mentioned much less frequently, but they may find their own niche, including phylogenetic studies.

### Plastid genome structure

The first reports that chloroplasts contain nucleic acids appeared in the middle of the previous century. By that time, it had already become known that DNA is the substance of heredity. At the cytological level, DNA and RNA in chloroplasts of several plant species were discovered in 1951 [Chiba, 1951], and biochemically, DNA was isolated from chloroplasts of spinach and tobacco leaves in 1954, and in larger quantities - in 1957 [Jagendorf, Wildman, 1954; Chiba, Sugahara, 1957]. However, three decades passed before the first complete chloroplast genomes were sequenced in 1986 - those of *marchantia* [Ohyama et al., 1986] and tobacco [Shinozaki et al., 1986], which confirmed plastome's quadripartite structure, consisting of Large Single-Copy (LSC) and Small Single-Copy (SSC) regions, separated by two identical (or near identical) inverted repeats IRa and IRb, and arranged in the order LSC-IRb-SSC-IRa. The advent of next-generation DNA sequencing methods essentially put genome skimming on stream, and now complete chloroplast genomes have been sequenced and annotated for tens of thousands of plant species, whereas before 2005 only fifty plastomes had been sequenced using the Sanger method, and by the beginning of the current century there were only ten.

In chloroplasts, genomes are generally represented by a large number of copies (i.e., they are essentially polyploids) and are organized into monomeric and multimeric circular and linear (including branching) forms [Lilly et al., 2001; see also the review by Ruhlman and Jansen, 2012]. Monomers are usually 120 to 180 thousand bases long, although there are examples of smaller and larger sizes, and plastomes without IRs are also known. Plastomes usually contain 100 to 140 genes, involved mostly in (but not restricted with) photosynthesis and gene expression. Plastomes are characterized by a relatively low GC content, varying within 34-39%.

The use of differences in the nucleotide sequences of plastomes has long been widely used in phylogenetic studies [Palmer et al., 1988], including the establishment of the maternal form by comparing the nucleotide sequences of complete plastomes in amphidiploids [Yukawa et al., 2006]. Thus, with the advent of the ability to sequence complete chloroplast genomes at low cost, such studies have moved to a new level and have further prospects, which were discussed in a recent review [Qu et al., 2023]. It should be noted though, that pan-plastomes were not mentioned by Qu et

al., and it is they (together with con-plastomes) that can provide much more information about plant evolution, including the ability to better separate closely related species and establish cytoplasm donors in hybrid forms. In another recent review [Wang et al., 2024a], it was noted that pan-organellar genomes have provided new evolutionary insights.

### Pan-plastomes of higher plants

Pan-plastomes were first mentioned in 2014 during the analysis of chloroplast genomes of two algae species, *Nannochloropsis salina* and *N. oculata* [Starkenburger et al., 2014]. Since then, not many papers have appeared that used either this term or "chloroplast pan-genome" or "pangenomic analysis of plastome". However, there are still a number of publications that did not use any of these terms, but, in fact, did conduct pangenomic analysis of complete plastomes. We considered it possible to include such papers in the table with information on pan-plastomes, marking them with an asterisk. It should be noted that the information we collected on multiple chloroplast genomes of individual plant species, referred as not mentioning pan-plastomes, can hardly claim to be exhaustive.

The relatively weak interest in pan-plastomes of plants is explained by the fact that chloroplast genomes are considered to be highly conserved in evolution, and after sequencing such a genome for one representative of one species, it was compared with the genomes of other species, including closely related ones. The differences revealed in such comparison are interpreted as interspecific, without taking into account possible intraspecific polymorphism of plastomes. For example, the plastome of common wheat *Triticum aestivum* cv. Chinese Spring was the eighth sequenced plastome and only the fifth for higher plants [Ogihara et al., 2000]. Its size was determined to be 134,540 bp. Two years later, the same authors re-sequenced the plastome of common wheat (which had already become the eleventh by that time) and determined that its size was 5 bp larger – 134,545 bp [Ogihara et al., 2002], considering that the plastome had been previously incorrectly defined, although this may not have been the case. For a number of other wheat varieties complete plastomes have recently been sequenced, with sizes ranging from 135,900 to 135,909 bp [Cho et al., 2022]. In this regard, it is worth paying attention to the article by other authors [Wu et al., 2015], in which the authors applied different strategies for sequencing and assembling the chloroplast genomes of two *Oryza australiensis* samples, and they found the assemblies were not identical. Wu et al. [2015] attributed the observed differences to errors, although in fact they may have revealed DNA polymorphism. But times are changing, and interest in plant pan-plastomes is growing, which we will try to demonstrate in this article.

Table

Taxon	Accessions	Sizes (total)	LSC sizes	SSC sizes	IR-A/B sizes	Gene number	References
2004							
<i>Oryza sativa</i> *	2	134,496; 134,551					Tang et al., 2004
2015							
<i>Echinochloa crus-galli</i> *	3	139,846–139,860	81,833-81,844	12,517-12,520	22,748	131	Nah et al., 2015
<i>Panax ginseng</i> *	11	156,241–156,425					Kim et al., 2015
2016							
<i>Populus tremula</i> *	2	156,067–156,641	84,367	16,670	27,509-28,133	130	Kersten et al., 2016
2017							
<i>Landoltia punctata</i> *	4	170,994-171,152	92,721-92,742	14,635-14,473	31,894-31,900	116	Ding et al., 2017
<i>Landoltia japonica</i> *	2	165,436; 166,424	88,635; 89,277	13,866; 14,005	31,468; 31,571		
<i>Larix gmelini var. japonica</i> *	3	122,553–122,598	65,598	56,128	436	111	Ishizuka et al., 2017
2018							
<i>Brachypodium distachyon</i>	53	134,991–135,214				133	
<i>B. hybridum</i>	3	136,326–136,330					Sancho et al., 2018
<i>B. stacei</i>	1						
2019							
<i>Astelia pumila</i> *	5	158,215-158,221	85,981-85,983	18,182-18,186	27,026	113	Pfanzelt et al., 2019
<i>Capsicum</i> spp. ( <i>C. baccatum</i> ; <i>C. b.</i> var. <i>baccatum</i> ; <i>C. b.</i> var. <i>pendulum</i> ; <i>C. chacoense</i> ; <i>C. annuum</i> var. <i>annuum</i> ; <i>C. a.</i> var. <i>glabriusculum</i> ; <i>C. chinense</i> ; <i>C. frutescens</i> )	321	156,879±166	87,216–87,901	17,840–17,996	25,735–26,160	117	Magdy et al., 2019
<i>Larix gmelini</i> *	12	122,581–122,5983	57,664	56,387	306	111	Zimmermann et al., 2019
<i>Larix cajanderi</i>	7						
<i>Lindera megaphylla</i> *	2	152,741	93,691-93,726	18,882-18,914	20,067-20,068	128	Jiang et al., 2019
<i>Silene vulgaris</i> *	6	151,463-151,583	82,180-82,258	17,303-17,350	25,693-26,008		Krüger et al., 2019

		2020				2021				2022				2023			
<i>Aegilops tauschii</i> *	17	135,551-136,009	79,723-80,142	12,732-12,771	21,548	124									Su et al., 2020		
<i>Agrostis tef</i> *	32	134,349-134,437	79,726-79,798	12,580-12,600	21,021-21,022	112									Teshome et al., 2020		
<i>Oryza</i> sp.*																	
<i>O. rufipogon</i> (295)	1,330	134,158-134,695	80,321-80,740	11,972-12,385	20,738-20,809										He et al., 2021		
<i>O. sativa</i> (1,135) + 22 specieses)																	
<i>Phyllostachis edulis</i>	412	154,478 (pan-)													Wang et al., 2021		
<i>Populus</i> spp.	39	155,096-158,591													Zhou et al., 2021		
<i>Solanum melongena</i>	32	155,534-155,655	86,183-86,250	18,492-18,570	25,416-25,444	112											
<i>S. incanum</i>	3	155,592-155,657	86,197-86,276	18,503-18,539	25,420-25,446	112(113)									Barchi et al., 2021		
<i>S. insanum</i>	2	155,534; 155,592	86,202; 86,240	18,498; 18,500	25,416	113											
<i>Zea mays</i> *	34	140,452-140,464	82,830-82,455	12,527-12,541	22,766	111									López et al., 2021		
<i>Beta</i> sp.*																	
<i>Beta vulgaris</i>	4	149,723-150,222	83,107-83,610	17,793-17,797	24,409-24,410												
<i>B. nana</i>	2	150,478; 152,816	83,427; 85,772	18,101; 18,118	24,463; 24,475												
<i>B. intermedia</i>	2	150,150; 150,154	83,203; 83,208	18,046; 18,047	24,450												
<i>B. corolliflora</i>	2	150,159; 150,175	83,213; 83,229	18,046	24,450										Sielenmann et al., 2022		
<i>B. macrohiza</i>	2	150,168; 150,271	83,242; 83,315	18,040; 18,068	24,443; 24,444												
<i>Patellifolia patellaris</i>	2	151,798; 151,800	83,834; 83,836	17,756	25,194												
<i>Brassica napus</i>	1,579	153,797 (pan-)				135									Liu et al., 2022		
<i>Nelumbo nucifera</i>	316	163,457-163,672	91,746-91,914	19,605-19,639	26,053-26,071										Wang et al., 2022		
<i>Triticum aestivum</i> *	7	135,900-135,909	80,005-80,014	12,791	21,552	131									Cho et al., 2022		
<i>Chrysanthemum</i> sp.*																	
<i>Chrysanthemum indicum</i> *	3	151,033-151,053				109									Liu et al., 2023		
(2x, 4x, var. <i>aromaticum</i> )																	
<i>Cucumis sativus</i>	50	156,616-157,641	86,339-88,883	18,069-18,363	25,166-25,797										Xia et al., 2023		
<i>Curcuma alismatifolia</i>	56	162,139-164,111	86,860-88,364	15,692-15,863	29,855-30,255										Wang et al., 2023		
<i>Dioscorea alata</i>	52	153,114-153,161	83,351-83,415	18,815-18,836	25,464										Lu et al., 2023		
<i>Fagopyrum tataricum</i>	513	159,253-159,576	84,249-84,875	13,176-13,414	30,685-30,852										Zhou et al., 2023		
<i>Fragaria</i> sp.*	165	155,493-155,809													Song et al., 2023		
(21 species)		155,644 (avr.)															

<i>Malus baccata</i> *	12	160,024–160,295	88,134–88,409	19,175–19,188	26,353–26,354	110–112	Wang et al., 2023a
<i>Paeonia</i> * (16 species)	63	152,741±301	84,402±277	17,016±69	25,662±247	111	Chen et al., 2023
<i>Pueraria montana</i> *	24	153,391–153,419	84,082–84,139	17,986–18,005	25,632–25,641	130	Zhou et al., 2023a
<i>Pulsatilla patens</i> *	16	161,836–161,930				113	Szandar et al., 2023
<i>Solanum tuberosum</i> *	6	155,296–155,562	85,737–86,003	18,364–18,376	25,592–25,593	133	Goryunova et al., 2023
<i>Sorghum bicolor</i> *	5	140,753–140,820	82,684–82,740	12,705–12,706	22,681–22,687	123	Zhang et al., 2023
			2024				
<i>Aquilaria</i> * ( <i>A. sinensis</i> , <i>A. rugosa</i> , <i>A. crassna</i> )	22	174,804–175,046	87,355	3347	42,103	142	Kan et al., 2024
<i>Costus</i> * (10 species)	13	160,360–168–966	90,802–92,189	18,363–20,124	27,982–29,903	111–113	Li et al., 2024
<i>Elymus sibirica</i>	175	114,176–114,370**	80,598–80,795	12,708–12,912	20,782–20,819		Xiong et al., 2024
<i>Euphorbia</i> * (9 species)	18	162,172–164,773	90,514–91,373	17,578–18,602	25,954–27,704	129–133	Lee et al., 2024
<i>Entrema japonicum</i> *	9	153,794–153,852	83,889–84,006	17,790–17,812	26,016–26,017	131	Yang et al., 2024
<i>Firmiana danxiaensis</i> *	4	160,832–161,206	89,737–90,135	20,027–20,067	25,522–25,523	129	Li et al., 2024a
<i>Gastrodia elata</i>	24	35,113–35,447			–	28	Li et al., 2024
<i>Gossypium</i> * (12 species)	336	160,231–161,041	88,650–89,046	20,205–20,360	25,592–25,651	129	Yan et al., 2024
<i>Hemerocallis citrina</i>	65	156,048–156,263	84,492–84,798	18,428–18,548	26,364–26,407	112	Jia et al., 2024
<i>Hibiscus syriaca</i>	95	160,231–161,041				113	Go et al., 2024
<i>Medicago ruthenica</i>	61	127,233–127,998				108	Zhang et al., 2024a
<i>Medicago sativa</i>	231	125,192–126,105				109	Zhang et al., 2024
<i>Pisum</i> ( <i>P. sativum</i> , <i>P. fulvum</i> , <i>P. abyssinicum</i> )	145	120,826–122,547				110	Kan et al., 2024
<i>Prunus mume</i>	322	157,871–158,213	86,102–86,412	18,963–19,011	26,387–26,400	112	Wang et al., 2024
			2025				
<i>Aegilops aucheri</i> *	5	135,666–135,668	79,774–79,775	12,787–12,788	21,552–21,553	132	Kuluev et al., 2025
<i>Ginkgo biloba</i> *	227	156,910–157,047	99,179–99,272	22,254–22,320	17,733–17,735	119	Nie et al., 2025
<i>Peucedanum harry-smithii</i> *	2	147,143–147,197	92,400–92,469	17,521–17,522	18,576	113	Song et al., 2025

\* - chloroplast genomes without mentioning the term pan-plastome by the authors of the articles

\*\* - these sizes with single IR region

In our other article in this issue of *Biomics* [Kuluev et al., 2025], dedicated to nuclear pangenomes of plants, we touched on the history of the introduction of the pan-approach into genomic research in some detail and will not dwell on it here. Although it should be noted, that for nuclear genomes with much larger number of genes (varying within the range of 20 to 35 thousand per haploid genome or per separate haplosubgenome in the case of a polyploid species), it is the nuclear pangenome that gives an idea of the entire gene pool specific for a particular plant species at any ploidy level. All these nuclear genes are divided into several categories: core genes - inherent in all accessions, softcore genes - inherent in most accessions, dispensable genes - present in several samples, private genes - present in one or a few samples. In the case of the plastome, such a division is impossible due to the too small number of genes and the importance of the overwhelming majority of them. On the other hand, such information on gene categories is not of particular interest for phylogeny, unlike nuclear genomes, whose differences should be used in the selection process during creation of high-yielding varieties. But major and minor differences between plastomes within a species should be taken into account, and therefore it is necessary to also operate with the concept of con-plastome with its only major mutations. That is, a combination of information on pan-plastomes and con-plastomes can provide new important information on evolution in the plant kingdom. But so far, consensus plastomes are rarely found in the literature.

Returning to the above mentioned table, it should be noted that it contains data only from published articles in peer-reviewed journals as provided by the authors, for a particular plant species or their groups. But since not all authors focused on different quantitative indicators, only those that can be found in the original articles (including supplementary information) are given. At the same time, even different sizes of the entire plastome or its regions within one plant species can display the existing diversity of plastomes within every species.

To more clearly show the changing attitude towards pan-plastomes, the information in the table is ordered by year, and within each year - according to the Latin names of the objects.

In recent years, only 20 articles have been published that specifically mention plant pan-plastomes: 2018 – 1 article; 2019 – 1; 2020 – 0; 2021 – 4; 2022 – 3; 2023 – 5; and 7 articles were published in 2024.

As can be seen from the table, in some species, despite a fairly large number of sequenced samples, the sizes of plastomes do not differ greatly. Thus, in two rice species, among more than a thousand plastomes, the differences reach only 537 bp. In *Elymus sibirica*, among 175 samples, the difference in plastome sizes was 194 bp. In eggplant, among 32 samples, the differences in plastome size were 121 bp. Even smaller differences are

characteristic of *Dioscorea alata* - among 52 samples, only 47 bp, and in maize, among 34 samples, the plastomes differ in size by only 12 bp. At the same time, other plant species showed more pronounced differences in plastome length. Thus, in different poplar species they reach 3.5 kb, in turmeric - almost 2 kb, in cucumber – a little more than 1 kb, and in alfalfa – a little less than 1 kb.

Various length of the plastome compartments (LSC, SSC, and IR) may arise as a result of two different processes (separately or in a combination) - duplications/insertions/deletions and inverted repeat boundary shifts ("ebb and flow", [Goulding et al., 1996]).

But the greatest interest is not so much in the variations in the sizes of plastomes, but in the presence of substitutions in their nucleotide sequences, which made it possible to compile groups of haplotypes in a number of articles. Thus, 175 plastomes of *E.sibirica* formed 34 haplotypes, which formed 5 clusters [Xiong et al., 2024]. 521 plastomes of buckwheat were divided into 10 clusters with 53 haplotypes [Zhou et al., 2023]. A total of 52 plastomes of *D.alata* fit into four haplotypes [Lu et al., 2023]. 50 cucumber plastomes were divided into 23 groups [Xia et al., 2023]. 65 sequenced plastomes of *Hemerocallis citrina* were divided into 21 haplotypes [Jia et al., 2024]. 322 plastomes of *Prunus mume* formed 16 groups with 46 haplotypes [et al., 2024a]. High plastome diversity was found in *Medicago ruthenica* – 61 sequenced samples formed 56 haplotypes [Zhang et al., 2024a], while another species *M. sativa* formed 57 haplotypes based on 231 plastomes [Zhang et al., 2024].

Despite the fact that in the article devoted to the sequencing and analysis of 1464 plastomes of several rice species (*O.sativa*, *O.rhizomatis*, *O.coarctata*, *O.eichingeri*, *O.latifolia*, *O.meyeriana*, *O.alta*, *O.grandiglumis*, *O.longiglumis*, *O.ridleyi*, *O.meyeriana*, *O.nivara*, *O.rufipogon*, *O.glaberrima*, *O.barthii*, *O.glumipatula*, *O.meridionalis*, *O.longistaminata*, *O.punctata*, *O.minuta*, *O.officinalis*, *O.australiensis*, *O.branchyantha*, *O.granulata*), pan-plastomes were not compiled explicitly, the authors were able to divide all the studied chloroplast genomes into 12 well supported genetic clusters plus 1 mixed genetic cluster and into 266 haplotypes [He et al., 2021]. Given that plastomes of a number of rice species were involved in this analysis, the resulting plastome can be considered a super-panplastome by analogy with nuclear pangenomes [Khan et al., 2020]. The *Fragaria* plastome, composed of 165 samples of 21 strawberry species (*F.iinumae*, *F.nubicola*, *F.nipponica*, *F.pentaphylla*, *F.daltoniana*, *F.chinensis*, *F.nilgerrens*, *F.viridis*, *F.bucharica*, *F.mandschurica*, *F.vesca*, *F. × bifera*, *F.moupinensis*, *F.tibetica*, *F.gracilis*, *F.corymbosa*, *F.orientalis*, *F.moschata*, *F.iinumae*, *F.nubicola*, *F.nipponica*, *F.pentaphylla*, *F.daltoniana*, *F.chinensis*, *F.nilgerrens*, *F.viridis*, *F.bucharica*, *F.mandschurica*, *F.vesca*, *F. × bifera*, *F.moupinensis*, *F.tibetica*, *F.gracilis*,

*F.corymbosa*, *F.orientalis*, *F.moschata*, *F.virginiana*, *F. × ananassa*, *F.virginiana*, *F.chiloensis*), among which the largest number of samples belonged to the last three octaploid species – 38, 30 and 22 samples, respectively, – also may be considered as the super-panplastome. Comparative analysis of the plastomes of these species made it possible to divide them into five groups. However, the authors did not use the term pan-plastome. Another super-panplastome was compiled for 12 species of cotton (*Gossypium hirsutum* (168 accessions), *G.barbadense* (104 accessions), *G.arboreum* (25 accessions), *G.herbaceum* (19 accessions), *G.tomentosum* (5 accessions), *G.mustelium*, *G.darwinii*, *G.ekmanium*, *G.stephensii* (3 accessions for each), *G.davidsonii*, *G.raimondii*, *G.anomalum* (1 accession for each).

Returning to the issue of terms, it should be noted that in one article, a Pan-CpGenome with Core Sequence was assembled based on 412 plastomes of bamboo *Phyllostachis edulis* [Wang et al., 2021]. Also, it is worth noting that a consensus pan-plastome was compiled for *Capsicum* spp.

The fact deserving attention is for *Brassica napus* not only a pan-plastome but also a mitochondrial pangene has been compiled; the size of pan-mitogenome turned out to be 222,076 bp [Liu et al., 2022]. Notably, 2,092 variants were found in the pan-plastome, while there were only 326 variants in the pan-mitogenome.

### Conclusion

In one of the recent works, based on the analysis of 197 known complete plastomes of plants of different families, a pattern-cladistic analysis was proposed, which, in the opinion of the authors, significantly simplifies the handling of data when constructing phylogenetic trees based on the nucleotide sequences of complete chloroplast genomes due to their rather large length [Mavrodiev, Madorsky, 2023]. However, the authors (although, as many others) took into analyses single complete plastomes of individual plant species, and this approach, taking into account the information on the intraspecific diversity of nucleotide sequences of plastomes above, can lead to the loss of significant phylogenetic information, though this may be acceptable for an initial rough assessment.

To clarify the relationship of species and genera within a family or other taxa, researchers still reconstruct phylogenetic trees based on complete chloroplast genomes, one for each species, and this is undoubtedly important information, especially in cases where such sequences were previously unknown. Thus, in particular, 20 plastomes of 19 species of the genus *Crataegus* and one species *Mespilus germanica*, belonging to a sister genus, were recently sequenced, which made it possible to clarify their relationship and form two clades for the genus *Crataegus* [Meng et al., 2025]. It can be assumed that determination of the complete chloroplast genomes of

several samples for each of these species will make it possible to clarify their phylogeny even more accurately. We can address the same wish to our works, in which the phylogenetic tree was constructed on the basis of single samples of several species of the wheat-*Aegilops* alliance [Kuluev et al., 2024]. As a whole, based on their high evolutionary conservatism, a tendency to rely on single plastome sequences for individual species has a right to exist; it is used widely and, in particular, has been recently applied to the study of the tribe Triticeae (including wheat and *Aegilops*), leading to the reconstruction of a phylogenetic tree based on 34 plastomes of 34 species from 18 genera [Chen et al., 2021]. Meanwhile, we assembled complete plastomes of several representatives of *Aegilops aucheri* of different geographic origin with certain differences in nucleotide sequences (including the length difference), they formed independent branches on the phylogenetic tree [Kuluev et al., 2025], and we intend to develop such a pan/con approach for studying plastomes, since it seems very promising. Earlier, 17 chloroplast genomes of *Aegilops tauschii* from different geographic origins also formed three distinct clades on the phylogenetic tree [Su et al., 2020].

When discussing con-plastomes, it is important to note the following feature of organelle genomes. It is quite possible that similar to heteroplasmy (according to which, as an example, a human can have different types of mitochondrial genomes), some heteroplasmy can also be inherent in plants, when one sample can even contain nonidentical plastomes in one cell, especially since their number in one cell reaches several thousand and they are physically separated due to their location in different chloroplasts [Sabir et al., 2014]. Among the modern freshwater cyanobacteria, that share a common ancestor with chloroplasts, there are oligoploid and polyploid species, and the genomic heterogeneity of polyploids is important for rapid adaptation to environmental changes [Scarampi et al., 2025]. Highly likely different variants of plastomes coexist and have an adaptive value. Experiments with transplastomic plants and their characteristic hetero-/homoplastomic status demonstrated that the homoplastomic state can only be achieved by antibiotic-assisted selection [Swiatek et al., 2003]. It is quite possible experimenters already assemble and analyze an individual con-plastome for the sample under study, but for phylogenetic constructions it is also necessary to use species' con-plastomes compiled using several accessions, this will allow to level out insignificant differences and improve our understanding of evolutionary events. Unfortunately, detection of heteroplasmy today is significantly complicated by the fact that extended fragments of plastomes are identified in nuclear and mitochondrial genomes [Yoshida et al., 2014]. On the one hand, such “findings” might be the result of erroneous assembly of nuclear genomes, but on the other hand, there

is an evolutionary mechanism for the gradual transfer of chloroplast genes to the nucleus, acting for millions of years but in some groups of plants it may not yet be complete, given the large variation in plastome sizes. Such plastid fragments of the nuclear genome accumulate substitutions independently of plastomes, and it is not yet possible to distinguish these substitutions from plastome heterogeneity using short reads of good quality or long reads of low quality. Assemblies based on the long reads of high quality seem to be more promising in this regard, but their use in studies of chloroplast genomes is still extremely rare [Scheunert et al., 2020; Tomasello et al., 2024].

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