



## T2T GENOMES OF HIGHER PLANTS

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### Resume

In 2000, a major breakthrough occurred in plant genomics: an article was published reporting the sequencing of the first plant genome, which belonged to *Arabidopsis thaliana* and had a size of just over 100 million bp. Over the next quarter century, the era of DNA sequencing has yielded approximately 4 thousand genomes of different assembly levels for approximately 2 thousand plant species. Thus, due to the development of DNA sequencing technologies, genomes have begun to be assembled at the chromosomal level from "telomere to telomere," which is termed "T2T sequencing." More than 2 decades later, the *Arabidopsis* genome was assembled in T2T format, but earlier, similar T2T genomes had been assembled for rice *Oryza sativa* and banana *Musa acuminata*. A T2T genome of bread hexaploid wheat *Triticum aestivum*, with a size of 14.5 billion bp, more than 100 times the size of the *Arabidopsis* genome, was assembled recently. A total of 166 plant T2T genomes have already been sequenced for 108 plant species from 80 genera. At the same time, most T2T genomes are characterized by mosaic consensus assembly; therefore, T2T plant genomes with phased assembly by haplotypes and T2T pangenomes with similar phased assembly are of greater interest. This is because it is important to know all gene alleles of crossed or edited specimens for breeding and genomic editing.

**Keywords:** sequencing, genome, T2T genome, phased genome, genes, higher plants

**Citation:** Matniyazov R.T., Kuluev A.R., Baymiev An.Kh., Garafutdinov R.R., Kuluev B.R., Baymiev Al.Kh., Chemeris A.V. T2T genomes of higher plants. *Biomics*. 2025. V.17(1). P. 65 - 76. DOI: 10.31301/2221-6197.bmcs.2025-5

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#### Introduction

After the publication in December 2000 of an article reporting on the determination of the complete nucleotide sequence of the genome from the model plant *Arabidopsis thaliana* [Arabidopsis Genome Initiative, 2000], the era of sequencing of plant genomes began. Although the *Arabidopsis* genome is small, this result was a major breakthrough at the time. Prediction of genes in *Arabidopsis* then showed that 25.5 thousand genes are distributed over 115.5 million bp [Bevan et al., 2001]. In 2013, another miniature genome of a carnivorous plant, *Utricularia gibba*, was sequenced, with a size of 82 million bp and a slightly larger number of genes: 28.5 thousand [Ibarra-Laclette et al., 2013]. In the same year, the genome of European spruce *Picea abies* with a size of 19.6 billion

bp was sequenced [Nystedt et al., 2013], and the estimated number of genes was 28,354, which is not much more than that of *Arabidopsis* with a genome more than 100 times smaller in size. Later, other large genomes have been sequenced: in particular, Chinese pine *Pinus tabulaeformis* (25.6 billion bp with 80.5 thousand genes) [Niu et al., 2022] and evergreen sequoia *Sequoia sempervirens* (26.5 billion bp, carrying almost 119 thousand genes), but this species is a hexaploid [Neale et al., 2022]. Another hexaploid species is bread wheat *Triticum aestivum*, which carries more than 140,000 genes, and its genome, measuring 14.5 billion bp, was recently assembled in another format [Liu et al., 2025]. Thus, aside from the race for the size of plant genomes, considerable efforts have been expended to achieve the accuracy and completeness of genome assemblies. In

particular, in recent years, attention was given to the assembly of complete genomes, whose nucleotide sequences extend in each chromosome from one end to the other; this approach is called "T2T sequencing" or "from telomere to telomere." Many such genomes, including those of plants other than bread wheat, have already been assembled, which is what this article is about.

### Different plant genomes in terms of completeness of their assembly

Here, by different plant genomes we do not mean genomes of different species but assembly completeness levels, in which they differ quite significantly, just as in size. The main milestones in genomic sequencing need to be mentioned.

As mentioned above, the first plant genome to be sequenced was that of *Arabidopsis thaliana* (Arabidopsis Genome Initiative, 2000). This genome, as the first sequenced for this species, was designated and recognized as a reference. Actually, this happens with all newly sequenced genomes of certain species<sup>1</sup>; these genomes then turn into reference ones. After that, there is often a period of continuous improvement, because in fact, not a single genome of higher organisms, including humans, can be said to have been assembled without errors.

The next stage of genome assembly is not just the compilation of sets of contigs and scaffolds of a draft or even a reference genome, but determination of their distribution across chromosomes, resulting in so-called pseudo-chromosomes or pseudo-molecules. Long and ultra-long readings, coupled with shorter, more accurate reads, as well as the use of several other approaches, have made it possible to read an entire sequence of chromosomes—including centromeres that were difficult to read due to a multitude of repeats as well as telomeres—giving rise to the T2T (telomere-to-telomere) sequencing and assembly of genomic DNA. Even this approach, however, is not a high level of genome assembly because every higher organism that reproduces sexually contains two genomes in its nucleus<sup>2</sup>, inherited from its paternal and maternal forms. Although earlier it was believed that they are almost similar, then with the accumulation of sequencing data it has become obvious that they are very different. Nonetheless, the habitus of any such organism and its vitality are determined by a complete (not half) set of chromosomes. Therefore, the upper level of genome sequencing and assembly is likely

a phased diploid genome<sup>3</sup> with haplotyped assembly of the all chromosomes in T2T format without gaps; we have devoted another article to such genomes in this issue of the journal [Baymiev et al., 2025]. Nonetheless, this is still insufficient information about genomes of higher organisms, including plants, because it has turned out that a reference genome does not fully reflect the entire pool of genes inherent in a particular species, and this gene "repertoire" has to be known for breeding work. Therefore, the pangenome of a species, and then the super-pangenome of a genus, came onto the scene. We have also addressed this issue [Kuluev et al., 2025].

### T2T genomes of plants

In a 2020 review article, dedicated to the 20th anniversary of the sequencing of the first plant genome, information is provided from which it follows that by that time, complete nucleotide sequences of 1031 genomes of 788 plant species had already been determined [Sun et al., 2022]. Those authors noted that in the first decade, the main goal was to obtain reference genomes, primarily of agricultural crops, and only 26 genomes were sequenced. In the second decade, the number of such genomes increased 50-fold, and the emphasis shifted to the understanding of a physiological role of their nucleotide sequences. In that review [Sun et al., 2020], attention was also drawn to the assembly of diploid genomes and pangenomes, which represent new frontiers in genomic sequencing. As for T2T genomes of plants, it was literally stated about them that they are already visible on the horizon [Sun et al., 2020]. An article describing how to sequence and assemble T2T genomes, including their phased assembly by haplotypes, can be considered evidence of interest in this field of sequencing [Garg et al., 2024]. Relatively recently, it was reported that 3517 genomes of 1575 plant species have already been sequenced, and among them were ~50 plant genomes collected in T2T format as of autumn 2023 [Xie et al., 2024]. By now, as demonstrated below, the number of such genomes has tripled.

As readers can see in the table, 166 T2T genomes of higher plants have already been assembled, belonging to 108 plant species from 80 genera. It should be pointed out, however, that some genomes are only partially assembled in this form. For example, telomeric regions have been identified in only some chromosomes in certain species, but authors of the original articles emphasize, including in the titles of such articles, the assembly of genomes in T2T format. Therefore, there is no particular reason not to include these species (genomes) in the table in the present article. Moreover, so far, no genome of a higher organism has been assembled with exceptional accuracy.

<sup>1</sup> some of which initially remain in draft status for some time, especially when sequenced with relatively low coverage

<sup>2</sup> according to the current definition, a genome is all the nucleotide sequences of a haploid set of chromosomes

<sup>3</sup> this includes a polyploid organism that has undergone functional diploidization and is divided into separate subgenomes.

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Species	Ploidy	Genome size (Mb)	Predicted gene number	References
2021				
<i>Musa acuminata</i>	2n=3x=33	485	36979	Belser et al., 2021
<i>Oryza sativa</i> (2 genomes)	2n=2x=24	391; 395	51027; 50341	Song et al., 2021
2022				
<i>Arabidopsis thaliana</i>	2n=2x=10	133	27561	Hou et al., 2022
<i>Arabidopsis thaliana</i>	2n=2x=10	133	27583	Wang et al., 2022
<i>Oryza sativa</i> (4 genomes)	2n=2x=24	≈400	41090-43527	Zhang et al., 2022
<i>Citrullus lanatus</i>	2n=2x=22	369	24205	Deng et al., 2022
2023				
<i>Actinidia chinensis</i>	2n=2x=58	603	45500	Yue et al., 2023
<i>Actinidia chinensis</i>		608	38603	Han et al., 2023
<i>Actinidia latifolia</i>	2n=2x=58	640	37778	
<i>Actinidia eriantha</i>	2n=2x=58	615	45300	Wang et al., 2023
<i>Armoracia rusticana</i>	2n=4x=32	610	42025	Shen et al., 2023
<i>Brassica napus</i>	2n=4x=38	1005	124744	Li et al., 2023
<i>Brassica rapa</i>	2n=2x=16	424	47531	Zhang et al., 2023
<i>Cenchrus fungigraminus</i>	2n=4x=28	1967	68562	Zheng et al., 2023
<i>Chaenomeles specioza</i>	2n=2x=34	650	45515	He et al., 2023
<i>Cucumis melo</i>	2n=2x=24	379	32693	Wei et al., 2023
<i>Cucumis melo</i> ssp. <i>agrestis</i>	2n=2x=24	370	27500	Li et al., 2023
<i>Daucus carota</i>	2n=2x=18	430	36268	Wang et al., 2023
<i>Echinochloa phyllopogon</i>	2n=4x=36	1002	132212	Sato et al., 2023
<i>Fragaria vesca</i>	2n=2x=14	220	36173	Zhou et al., 2023
<i>Glycine max</i> (2 genomes)	2n=2x=40	1013; 1016	58287; 56725	Garg et al., 2023
<i>Glycine max</i>	2n=2x=40	1010	55498	Wang et al., 2023
<i>Glycine max</i>	2n=2x=40	1007	52157	Zhang et al., 2023
<i>Jasminum sambac</i>	2n=2x=26	537	39843	Xu et al., 2023
<i>Manihot esculentum</i>	2n=2x=36	664	37500	Xu et al., 2023
<i>Momordica charantia</i>	2n=2x=22	295	19895	Fu et al., 2023
<i>Morus notabilis</i>	2n=2x=12	410	27413	Ma et al., 2023
<i>Musa acuminata</i>	2n=3x=33	473	37000	Huang et al., 2023
<i>Musa acuminata</i>	2n=2x=22	470	39500	Liu et al., 2023
<i>Oryza sativa</i>	2n=2x=24	385	57359	Shang et al., 2023
<i>Populus tremula</i> × <i>P.alba</i>	2n=2x=38	398	32000	Zhou et al., 2023
<i>Pyrus pyrifolia</i>	2n=2x=34	501	41969	Sun et al., 2023
<i>Quercus variabilis</i>	2n=2x=24	778	36500	Wang et al., 2023
<i>Rhodomyrtus tomentosa</i>	2n=2x=22	470	33382	Li et al., 2023
<i>Scutellaria baicalensis</i>	2n=2x=18	384	28097	Pei et al., 2023
<i>Solanum tuberosum</i>	2n=2x=24	773	40155	Yang et al., 2023
<i>Vaccinium duclouxii</i>	2n=2x=24	573	41953	Zeng et al., 2023
<i>Vigna unguiculata</i> ssp. <i>sesquipedialis</i>	2n=2x=22	523	30594	Yang et al., 2023
<i>Vitis vinifera</i>	2n=2x=38	494	37534	Shi et al., 2023
<i>Vitis vinifera</i>	2n=2x=38	497	34925	Zhang et al., 2023
<i>Zea mays</i>	2n=2x=20	2178	42580	Chen et al., 2023

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2024					
<i>Aegilops umbellulata</i>	2n=2x=14	4280	78076		Singh et al., 2024
<i>Ananas comosus</i>	2n=2x=50	423	26000		Feng et al., 2024
<i>Brassica rapa</i> ssp. <i>chinensis</i>	2n=2x=20	441	49308		Zhou et al., 2024
<i>Brassica rapa</i> ssp. <i>purpuraria</i>		430	49243		
<i>Cananga odorata</i>	2n=2x=16	735	26449		Zheng et al., 2024
<i>Capsicum annuum</i>	2n=2x=24	3103	34428		Chen et al., 2024
<i>Capsicum rhomboideum</i>	2n=2x=26	1707	33512		
<i>Castanea mollissima</i>	2n=2x=24	740	35008		Li et al., 2024
<i>Chionanthus retusus</i>	2n=2x=46	685	42864		Wang et al., 2024
<i>Citrullus amarus</i> (5 genomes)		377-381	23551-24897		Zhang et al., 2024
<i>Citrullus colocynthis</i> (4 genomes)		361-380	24081-24208		
<i>Citrullus ecirrhosus</i>		402	24101		
<i>Citrullus lanatus</i> (13 genomes)	2n=2x=22	368-373	23825-25562		
<i>Citrullus mucosospermus</i> (2 genomes)		370-371	25232-25530		
<i>Citrullus naidinianus</i>		364	25277		
<i>Citrullus rehmii</i>		413	26969		
<i>Citrus chinensis</i> (2 genomes)	2n=2x=18	340; 346	31456; 30021		
<i>Cucumis melo</i> ssp. <i>chito</i>	2n=2x=24	375	31556		Mo et al., 2024
<i>Daucus carota</i>	2n=2x=18	451	33207		Liu et al., 2024
<i>Dianthus caryophyllus</i>	2n=2x=30	565	41000		Lan et al., 2024
<i>Eleocharis dulcis</i>	111	493	33493		Chen et al., 2024
<i>Eucalyptus regnans</i>	2n=2x=22	514	63000		Ferguson et al., 2024
<i>Fallopia multiflora</i>	2n=2x=18	1458	84768		Zeng et al., 2024
<i>Fallopia multiflora</i> var. <i>angulata</i>		1174	69100		
<i>Ficus cuspidata</i>	2n=2x=28	371	26642		Liao et al., 2024
<i>Firmiana kwangsiensis</i>	2n=2x=40	1160	33500		Wang et al., 2024
<i>Forsythia illuminates</i>	2n=2x=28	688	33932		Cui et al., 2024
<i>Gossypium raimondii</i>	2n=2x=26	460	53167		Huang et al., 2024
<i>Gymnostemma pentaphyllum</i>	2n=2x=22	599	26003		Yun et al., 2024
<i>Glycine max</i>	2n=2x=40	1020	53508		Jia et al., 2024
<i>Glycine soja</i>		1030	53495		
<i>Isodon rubescens</i> f. <i>lushanensis</i>	2n=2x=24	349	34865		Yang et al., 2024
<i>Lactuca sativa</i>	2n=2x=18	2593	45507		Wang et al., 2024
<i>Lactuca sativa</i> var. <i>crispa</i>	2n=2x=18	2590	41375		Zhang et al., 2024
<i>Malus domestica</i>	2n=2x=34	663	44300		Su et al., 2024
<i>Mentha suaveolens</i>	2n=2x=24	414	31251		Yang et al., 2024
<i>Musella lasiocarpa</i>	2n=2x=18	509	34361		Zhao et al., 2024
<i>Myrciaria cauliflora</i>	2n=2x=22	351	31235		Zhao et al., 2024
<i>Myrica rubra</i>	2n=2x=16	292	28345		Zhang et al., 2024
<i>Oldenlandia diffusa</i>	2n=2x=32	499	49701		Gao et al., 2024
<i>Olea europea</i>	2n=2x=46	1280	70138		Lv et al., 2024
<i>Panax ginseng</i>	2n=2x=48	3450	77266		Song et al., 2024
<i>Panicum miliaceum</i>	2n=2x=36	834	63678		Wang et al., 2024
<i>Penthorum chinense</i>	2n=2x=18	257	24617		Wang et al., 2024
<i>Persea americana</i>	2n=2x=24	841	40629		Yang et al., 2024
<i>Peucedanum praeruptorum</i>	2n=2x=22	1798	44468		Bai et al., 2024
<i>Phragmites australis</i> (3 genomes)	2n=2x=48	922; 814; 1217	40688; 40969; 40124		Wang et al., 2024

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<i>Populus ussuriensis</i>	2n=2x=38	412	34953	Liu et al., 2024
<i>Prunus salicina</i>	2n=2x=16	251	28500	Yang et al., 2024
<i>Pyrus bretschneideri</i>	2n=2x=34	510	46394	Qi et al., 2024
<i>Pyrus communis</i>		510	44702	
<i>Pyrus</i> hybrid (2 genomes)	2n=2x=34	523; 527	49238; 46848	Li et al., 2024
<i>Rosa gigantea</i>	2n=2x=14	549	52796	Zhou et al., 2024
<i>Salix cheilophila</i>	2n=2x=38	343	26397	Gao et al., 2024
<i>Santalum album</i>	2n=2x=20	218	24171	Peng et al., 2024
<i>Sesbania cannabina</i>	2n=4x=24	2087	89970	Luo et al., 2024
<i>Setaria italica</i>	2n=2x=18	422	43210	He et al., 2024
<i>Solanum commersonii</i>	2n=2x=24	710	38500	Feng et al., 2024
<i>Sorghum bicolor</i> (2 genomes)	2n=2x=20	745; 738	43912; 44465	Bao et al., 2024
<i>Sorghum bicolor</i>	2n=2x=20	724	32855	Li et al., 2024
<i>Sorghum bicolor</i> (2 genomes)	2n=2x=20	719; 722	35696; 36950	Wei et al., 2024
<i>Theobroma grandiflorum</i>	2n=2x=20	423	31381	Alves et al., 2024
<i>Trifolium alexandrinum</i> (2 genomes)	2n=2x=20	547; 536	48862; 42966	Sato et al., 2024
<i>Triticum monococcum</i>	2n=2x=14	5110	53168	Wang et al., 2024
<i>Vitis vinifera</i>	2n=2x=38	504	32090	Djari et al., 2024
<i>Vitis vinifera</i>	2n=2x=38	504	30397	Wang et al., 2024
<i>Zanthoxylum nitidum</i>	2n=2x=70	2240	32737	Zhu et al., 2025
<i>Zizifus jujuba</i> (2 genomes)	2n=2x=24	383; 373	29950; 28000	Li et al., 2024
<i>Ziziphus mariutiana</i> (2 genomes)	2n=4x=48	425; 410	26000; 26000	Guo et al. 2024
2025				
<i>Arachis hypogaea</i>	2n=4x=40	2600	71099	Wang et al., 2025
<i>Bauhinia × blakeana</i>	2n=2x=28	290	37956	Mu et al., 2025
<i>Brassica juncea</i>	2n=4x=38	981	84664	Qian et al., 2025
<i>Centela asiatica</i>	2n=2x=18	438	25200	Song et al., 2025
<i>Cerasus specioza</i>	2n=2x=16	269	33773	Fujiwara et al., 2025
<i>Fragaria × ananassa</i>	2n=8x=56	783	109000	Zhang et al., 2025
<i>Fragaria iinumae</i>	2n=2x=14	241	28198	Du et al., 2025
<i>Fragaria xananassa</i>	2n=8x=56	782	101000	Han et al., 2025
<i>Gossypium hirsutum</i>	2n=4x=52	2299	78471	Hu et al., 2025
<i>Gossypium hirsutum</i>	2n=4x=52	2299	79642	Yan et al., 2025
<i>Lycium ruthenicum</i>	2n=2x=24	2422	37149	Yisilam et al., 2025
<i>Morus mongolica</i>	2n=2x=28	341	21657	Yang et al., 2025
<i>Oenanthe javanica</i>	2n=2x=42	1012	65763	Feng et al., 2025
<i>Populus trichocarpa</i>	2n=3x=57	394	30150	Gao et al., 2025
<i>Prunus avium</i>	2n=2x=16	342	36150	Zhou et al., 2025
<i>Prunus campanula</i>	2n=2x=16	295	28961	Jiang et al., 2025
<i>Rhododendron liliiflorum</i>	2n=2x=26	793	41406	Wang et al., 2025
<i>Solanum melongena</i>	2n=2x=24	1060	36505	Fang et al., 2025
<i>Sorghum bicolor</i>	2n=2x=20	728	44399	Wang et al., 2025
<i>Triticum aestivum</i>	2n=6x=42	14510	141035	Liu et al., 2025
<i>Vigna radiata</i>	2n=2x=22	500	28740	Jia et al., 2025
<i>Vitis davidii</i>	2n=2x=22	487	27122	Luo et al., 2025
<i>Vitis vinifera</i>	2n=2x=38	502	39000	Guo et al., 2025
<i>Uncaria rhynchophylla</i>	2n=2x=44	634	29049	Hu et al., 2025

Although in 2021 and 2022, information about such plant genomes was scarce (a total of six articles with 10 genomes), in 2023, there were already 34 such articles describing 36 T2T genomes. In 2024, the number of articles on T2T genomes of plants increased substantially, to 58, but at the same time, much more genomes were collected: 98. In the first 4 months of 2025, 22 articles were published mentioning the same number of T2T genomes: one per article. It is likely that by the end of 2025, a similar number of such articles will be published as in 2024; this number will not amount to the same increase that occurred after 2023. Some decline in the sequencing of T2T genomes of plants may be caused by the fact that T2T genomes retain a mosaic consensus assembly, cannot be considered biological genomes<sup>4</sup>, and therefore are not suitable for breeding work. Furthermore, there is no other scientific interest in such genomes except as evidence of certain and even considerable successes in genomic sequencing. Therefore, there is growing attention to pangenomes, including their phased versions, which are much more difficult to sequence and assemble by haplotypes than consensus genomes from telomere to telomere. At the same time, not so many phased genomes in T2T format in 2023–2025 (highlighted in the table with a green background) have already been collected: 38 out of 166, which is less than a quarter of their total number.

As shown in the table, the largest genome in T2T format among such genomes was assembled recently for bread hexaploid wheat *T.aestivum* (14.51 billion bp). It also carries the largest number of predicted genes: almost one and a half hundred thousand, but taking into account subgenomes of genes, each subgenome will have an average of only ~48 thousand, inferior in this parameter to many other plants. More than 100 thousand genes have been predicted for strawberry *Fragaria* × *ananassa*, but this is an octaploid species, which, however, does not have a very large genome: 0.782 million bp. Large T2T genomes have been collected for diploid einkorn wheat *T. monococcum* (5.11 million bp) and for a close relative: *Aegilops umbellulata* (4.28 million bp). Slightly smaller T2T genomes have been found in *Panax ginseng* (3.45 million bp), pepper *Capsicum annuum* (3.103 million bp), and tetraploid peanut *Arachis hypogaea* (2.6 million bp), in two lines of lettuce *Lactuca sativa* (2.59 million bp each), tetraploid cotton *Gossypium hirsutum* (2.299 million bp), and corn *Zea mays* (2.178 million bp). The smallest T2T genomes have been found by sequencing in *Arabidopsis thaliana* (0.133 million bp) and strawberry *Fragaria vesca* (0.22 million bp). In fact, in this table, the

<sup>4</sup> by a biological genome, we mean the one that can actually exist in nature, whereas as a result of consensus mosaic assembly, a genome is reconstructed that may be actually far from the real set of DNA sequences and its owner might not be viable

shown plant genomes assembled at the T2T level differ in size by more than 100-fold. A small number of genes have been found in wild mulberry *Morus mongolica* (21,657), watermelon *Citrullus lanatus* (24,205), and other species of the genus *Citrullus*. Bitter melon *Momordica charantia* has the fewest genes (19,895), and its genome is small, at 0.295 million bp. As for genes in general, different authors present their quantities, taking into account in some articles only the genes encoding proteins, while in some other articles, all the discovered genes are listed. To not complicate the table, we decided not to make such a distinction, because if necessary, this information can be found in the original articles. Meanwhile, it must be recognized that in all these plants, there are no relations between their ploidy, the size of their genomes, and the number of genes in them.

### Conclusion

Representation of genomic information in T2T format, where nucleotide sequences cover each chromosome from telomere to telomere, has become a major milestone in genomic sequencing. This approach has required improved reading with increased coverage, long and ultra-long reads, optical mapping, Hi-C sequencing, specialized software packages for assembling such genomes, and some other approaches. The greatest interest is aroused by the sequencing where genomes from telomere to telomere are assembled for paired chromosomes separately, and approximately 4 dozen similar genomes have already been assembled. Such genomes are the future, which will require DNA sequencing technologies for subsequent generations, because the current ones are still not good enough for such mass assemblies of genomes of especially large sizes and of polyploid species. The usual consensus assembly of T2T genomes—with a mosaic arrangement of fragments of paternal and maternal chromosomes within one of the paired chromosomes and not taking into account *cis* and *trans* positions of individual nucleotide substitutions or their blocks — should be considered only a certain stage of genomic sequencing, which will require novel DNA sequencing technologies for the following generations, since the current ones are still not suitable enough for massive assemblies of genomes of especially large sizes and polyploid species.

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