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Research article

Columnar structure of SV40 minichromosome

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Abstract: Like the sequence of the strongest 601 clone nucleosome of Lowary and Widom, the SV40 genome sequence contains tracks of YR dinucleotides separated by small integers of the 10.4n base series (10, 11, 21 and 30 bases). The tracks, however, substantially exceed the nucleosome DNA size and, thus, correspond to more extended structure - columnar chromatin. The micrococcal nuclease digests of the SV40 chromatin do not show uniquely positioned individual nucleosomes. This confirms the columnar structure of the minichromosome, as well as earlier electron microscopy studies.

Keywords: nucleosome; sequence periodicity; YR dinucleotides; YR tracks; stacked nucleosomes; rotational positioning; nucleosome sliding; nucleosome mapping

1. Introduction

SV40 minichromosome is classical object for chromatin structure studies that, in particular, provided convincing EM pictures of the nucleosomes organized in the beads-on-string manner [1,2]. The efforts towards determination of the expected unique positions of the nucleosomes along the 5243 bases long genome of the virus gave inconclusive results, both by computational mapping [3], and by cloning of the micrococcal nuclease (MNase) digest nucleosome DNA size fragments [4]. It was found that 22 of 41 cloned and mapped fragments overlap with other fragments sharing from ~25 to ~125 bases. "Nucleosomes do not occupy unique positions in SV40 minichromosomes" [4]. It appears, thus, that the nucleosomes of SV40 are sliding, so that each individual pattern of the beads is different, and no specific nucleosome repeat length, as in eukaryotes in general, is observed.

There is an alternative view at the chromatin structure—organization of the "nucleosomes" in tight oligonucleosomes [5], also called columnar structures [6–9], or meganucleosomes [10]. In this case, the nucleosomes excised by MNase from the columns in the process of their disintegration

would slide like in SV40 minichromosome, occupying many nearly equivalent alternative positions shifted by 10–11 bases. Such separation (i.e., overlapping) has been first observed by Ponder & Crawford [11].

What we call columnar structures, as referred above, is manifested in the extended ~10 base ladder of nuclease digestion of chromatin [5,10,12], well beyond the nucleosome DNA size. The columns are also seen directly by various versions of electron microscopy of the minimally perturbed samples. They appear as smooth 10 nm fibers [13–15]. Nucleosomes in the fibers seem to be "closely packed forming a continuous 100 Å filament" [13]. The existence of the columns is suggested by observation of long, far exceeding nucleosome size 10–11 base periodic sequence regions in various chromatins [7–9]. Finally, the nucleosome repeat lengths of various eukaryotic organisms, derived by MNase digestion of the chromatins, display discrete values, with increments of ~10 base-pairs [16,17]. The lengths, actually, closely follow 10.4xn series (Trifonov, in press).

The nucleosomes can be mapped on genome sequences by matching to standard periodic consensus pattern $(RRRRRYYYYY)_n$ [18–20]. In case of the columns the mapping reveals RR/YY oscillations significantly beyond the nucleosome DNA size [9]. Apart from the RR/YY oscillation the pattern contains also the periodic YR dinucleotides which appear to make significant contribution, especially due to TA periodicity [21,22]. There is no mapping algorithm available which would take into account the corresponding (unknown) weights of the RR/YY and YR components. One can apply, however, for the nucleosome (column) mapping purposes two separate algorithms based on the above $(RRRRRYYYYY)_n$ consensus (which includes YR as a part of the signal) and on the YR-periodic tracks [23]. The prominent strong nucleosome forming sequence, clone 601 [21], is good example of both components present [22].

In this study we used both algorithms, combining the data in one map, with conclusion that the SV40 minichromosome consists of several connected columnar structures, rather than of solitary beads of the nucleosomes.

2. Materials and Methods

The 5243 base sequence of the SV-40 genome is taken from NCBI Genbank.

The construction of the YR tracks follows the rule suggested by the crystal structure of the 601 clone nucleosome [24]: The sequence bound by histone octamers consists of 10-mers or 11-mers starting with YR dinucleotides, occasionally separated by ordinary sequence 10–11mers (up to three 10–11 base period separations). Such succession of YR 10-11-mers makes a YR track.

The nucleosome mapping by the $(RRRRRYYYYY)_n$ probe is described in [20] and can be implemented via server http://strn-nuc.haifa.ac.il:8080/mapping/home.jsf

3. Results and Discussion

3.1. Sequence evidence in favor of columns in SV40 chromatin

As it follows from crystal data on the 601 clone nucleosomes [24], the YR•YR stacks of the nucleosome DNA are located in positions "minor groove *in*". They interact with arginines of the histones and, thus, serve as "anchors" uniquely determining the inner side of the bound nucleosome

DNA. The special role the YR dinucleotides should play in the nucleosome positioning has been advocated by Zhurkin and his colleagues since 1979 [25–28].

The YR elements of the clone 601form a "track" of CG, 5TA and 3TG separated from one another by integer number of bases corresponding to one to three periods of nucleosome DNA of average value 10.4 bases (10, 11, 21 and 30 bases). Such YR track, if found in DNA sequence, would correspond to region bound to histone octamers. The periodically arranged YR elements would keep DNA in specific rotational setting and provide stability to the nucleosomes and columns, in addition to the contribution of the alternating RRRRRYYYYY pattern.

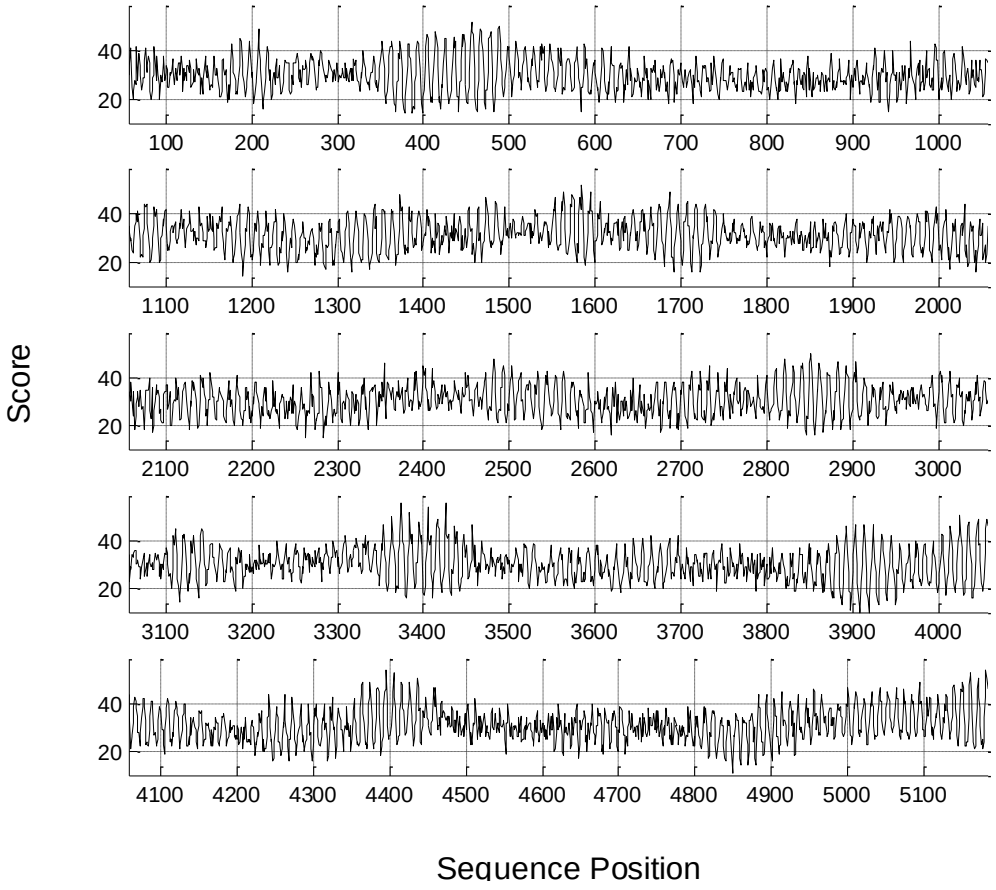

Figure 1. Nucleosome map of SV40 chromosome calculated with the (RRRRRYYYYY)n probe (Tripathi et al., 2015, http://strn-nuc.haifa.ac.il:8080/mapping/home.jsf). The amplitudes correspond to the simple dinucleotide match counts of respective sequence segments to the sequence probe.

In Figure 1 the map of the SV40 chromatin DNA periodicity is shown derived by the application of the $(RRRRRYYYYY)_n$ mapping to the sequence. The regions with 10–11 base oscillations correspond to either nucleosomes or to their tight oligomers, columns. The largest RR/YY periodic region spans ~540 bases (sequence coordinates 4800–5243 and further to ~100, over the circular genome sequence start). Numerous peaks of the map indicate the locations of the pseudodyads, central points of the calculated nucleosome positions, separated one from another by

10–11 bases. These are positions "minor groove *out*" [9]. Respectively, the minima indicate positions "minor groove *in*" where the YR elements would be preferentially located. The sections of the map where the RR/YY periodicity is not obvious, however, still show the periodic distribution of YR dinucleotides following one another at one- to three-period distances, as in the clone 601. Altogether, the periodically distributed RR/YY and YR elements make long regions, which would correspond to the columnar chromatin structures.

In Figure 2 the full map of the YR-tracks identified in the SV40 genome is shown. The tracks are of various sizes, from 31 bases (track 17) to 725 bases (track 9). The tracks longer than tight dinucleosome DNA size, ~250 bases [5], occupy together about half of the SV40 genome (2564 bases). The longest track 9 would correspond to the tight oligonucleosomes involving 5 to 6 units ~125 bases each [5], stacked together in one column.

The construction of the tracks from the sequence positions of YR elements and their match to positions of minima in the RR/YY nucleosome map allowed for the gaps between the YR 10–11-mers of the size two or three periods (20–22 and 30–33 bases) as in the 601 clone nucleosome. The larger gaps between the tracks would mean the discontinuity in the columnar organization. Remarkably, however, there seems to be no discontinuity, since the sizes of the observed gaps are all combinations of the 10-mers and 11-mers (see Table 1). That is, although the 10–11-mers of the gaps are not decorated by the YR elements at their starts, length-wise they can be accommodated to the column, thus, fusing the YR tracks in a single long structure - a continuous genome size column.

Table 1. Gaps of ordinary sequences between the YR tracks in SV40.

Gap size(bases)	Number of cases
40 (4 × 10)	7
41 (3 × 10 + 11)	1
42 (2 × 10 + 2 × 11)	2
43 (10 + 3 × 11)	2
44 (4 × 11)	2
54 (10 + 4 × 11)	1
55 (5 × 11)	3
60 (6 × 10)	3
66 (6 × 11)	2

Perhaps it is not a mere coincidence that the starting 8 bases of the Figure 2 and ending 3 bases together make 11 bases, which means that the whole genome consists of 10-mers and 11-mers, as the continuous columnar structure would suggest. It is quite possible that the long smooth 10 nm filaments observed by electron microscopy in vitrified samples of SV40 chromatin [14], indeed, correspond to the columns as suggested by periodic distribution of the YR elements in the nucleotide sequence (this work). Moreover, as EM of vitrified samples of metaphase arrested eukaryotic cells suggests, chromosomes seem to be "formed by the compact association of 11 nm filaments, or

portions thereof" [29]. In other words, it may well be that the columnar organization of chromatin is common feature of eukaryotic chromosomes in general, not just of the SV40 minichromosomes.

3.2. Relation to experimental nucleosome mapping data

The overlapping nucleosome positions in [4] are all confined to the long YR track regions (Figure 2), though few are located in approximate nucleosome size tracks: track 1 which actually contains 2 overlapping MNase nucleosomes (at positions 221 and 247), track 7 (nucleosome at 1768), track 12 (3762), track 14 (4374 and 4392) and track 16 (4876). The frequent overlapping of the nucleosomes defined by ~145 base fragments resulting from MNase digest suggests that the "nucleosomes" may center at any peak of the RR/YY map with as many alternative positions as number of the peaks. In this sense they may slide, in discrete steps, all along the DNA sequence of the column, making series of overlapping "nucleosomes". The longest YR track 9 harbors at least three pairs of such sliding nucleosomes (2198, 2274; 2495, 2588; and 2734, 2752). The authors of [4] conclude: "nucleosomes do not occupy unique positions in SV40 minichromosomes".

Since practically all sequence territory of the SV40 minichromosome is covered by the periodic YR-tracks (and RR/YY oscillations) it is not surprising that practically all nucleosomes experimentally identified in [4] are located within the periodic regions. The experimental accuracy (± ~5 bases) does not allow to observe all the alternative positions of the nucleosome centers which should be separated by 10–11 bases. More accurate mapping does show the alternatives [11] for the nucleosomes which cover the unique BamHI restriction site. The site is, indeed, located within the periodic YR track 11. The corresponding RR/YY map shows about 10 alternative center positions for the nucleosomes covering the site (coordinates 2450–2600). In view of the above the term "nucleosome", actually, describes any one of the particles, products of MNase digestion of the columnar structure, centered at one of ~400 sequence locations (according to the peaks of the nucleosome map).

4. Conclusion

The RR/YY nucleosome map of the SV40 ninichromosome and the periodic distribution of YR dinucleotides along the SV40 genome, similar to the distribution of these elements in the strongest known 601 clone nucleosome, suggests that the SV40 chromatin consists of long (perhaps, even full-length) continuous columnar structures, rather than of individual beads-on-string nucleosomes.


1-GCCTCGGC
CTCTGCATAAA
Track 18
TAAAAAAAAT
TAGTCAGCCA
TGGGGCGGAGA
ATGGGCGGAAC
62-TGGGCGGAGT
TAGGGGCGGGA
83-TGGGCGGAGT
TAGGGGCGGG
ACTATGGTTG
CTGACTAATT
GAGATGCATG
CTTTGCATAC
TTCTGCCTGC
Track 1
TGGGGAGCCT
GGGGACTTTC
173-CACACCTGGT
183-TGCTGACTAAT
194-TGAGATGCAT
GCTTTGCATA
CTTCTGCCTGC ●
225-TGGGGAGCCT
GGGGACTTTC
CACACCCTAAC ○
TGACACACAT
TCCACAGCTG
GTTCTTTCCG
CCTCAGAAGG ○
TACCTAACCA
AGTTCCTCTT
TCAGAGGTTA
TTTCAGGCCA
Track 2
TGGTGCTGCG
CCGGCTGTCA
356-CGCCAGGCCTC
367-CGTTAAGGTT
CGTAGGTCATG ●
GACTGAAAGTA
AAAAAACAGCT
410-CAACGCCTTTT
421-TGTGTTTGTTT
432-TAGAGCTTTT
GCTGCAATTT
452-TGTGAAGGGG
AAGATACTGT
472-TGACGGGAAA
482-CGCAAAAAAC
CAGAAAGGTT
AACTGAAAAAC
CAGAAAGTTA
ACTGGTAAGT
TTAGTCTTTT
TGTCTTTTAT ○
TTCAGGTCCA
TGGGTGCTGC
TTTAACACTGT
584-TGGGGGACCT
AATTGCTACTG
605-TGTCTGAAGC
615-TGCTGCTGCT
ACTGGATTTT
635-CAGTAGCTGA
AATTGCTGCTG
GAGAGGCCGC ○
666-TGCTGCAATTG
AAGTGCAACT
687-TGCATCTGTT
GCTACTGTTG
AAGGCCTAAC
AACCTCTGAG
GCAATTGCTG
CTATAGGCCT
CACTCCACAGG
CCTATGCTGTG
ATATCTGGGGC
TCCTGCTGCTA
Track 3
TAGCTGGATT ●
TGCAGCTTTAC
812-TGCAAACTGTG
ACTGGTGTGAG
834-CGCTGTTGCT ●
CAAGTGGGGTA
TAGATTTTTTA
GTGACTGGGAT
CACAAAGTTTC
TACTGTTGGTT
899-TATATCAACAA
CCAGGAATGGC
921-TGTAGATTTG
931-TATAGGCCAG
ATGATTACTA
951-TGATATTTTAT
TTCCTGGAGTA
973-CAAACCTTTGT
TCACAGTGTT
CAGTATCTTG
ACCCCAGACAT
1015-TGGGGTCCAA
CACTTTTTAA
TGCCATTTCT
CAAGCTTTTT
GGCGTGTAATA
CAAAATGACA
TTCCTAGGCTC
ACCTCACAGGA ●
GCTTGAAAGAA
GAACCCAAAGA
Track 4
TATTTAAGGGA
CAGTTTGGCA
AGGTTTTTAGA
GGAAACTACT
TGGACAGTAA
TTAATGCTCC
TGTTAATTGG
1192-TATAACTCTT
1202-TACAAGATTAC
TACTCTACTT
1223-TGTCTCCCAT
1233-TAGGCCTACAA
1244-TGGTGAGACA
AGTAGCCAACA
GGGAAGGGTTG ○
CAAATATCATT
1287-TGGGCACACC ○
1297-TATGATAATAT
1308-TGATGAAGCA
GACAGTATTC
AGCAAGTAAC
1338-TGAGAGGTGGG
AAGCTCAAAGC
1360-CAAAGTCCTAA ●
TGTGCAGTCAG
GTGAATTTAT
TGAAAAATTTG
AGGCTCCTGG
TGGTGCAAATC
AAAGAACTGCT
CCTCAGTGGAT
GTTGCCTTTAC
TTCTAGGCCTG
Track 5
1468-TAGTGTCGGAA
TACTTCTGCTC
1490-TAAAAGCTTAT
GAAGATGGCCC
CAACAAAAAGA
AAAGGAAGTTG ○
TCCAGGGGCAG
CTCCCAAAAAA
CCAAAGGAACC
AGTGCAAGTGC
Track 6
1578-CAAAGCTCGT
CATAAAAGGA ○
GGAATAGAAG
TTCTAGGAGT
TAAAACTGGAG ○
TAGACAGCTTC
ACTGAGGTGG
AGTGCTTTTT
AAATCCTCAAA
TGGGCAATCC
Track 7
1681-TGATGAACAT
1691-CAAAAAGGCTT
AAGTAAAAGCT
1713-TAGCAGCTGAA
AAACAGTTTA
1734-CAGATGACTCT
CCAGACAAAG
AACAACTGCCT
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ACTTAACCTG
Track 8
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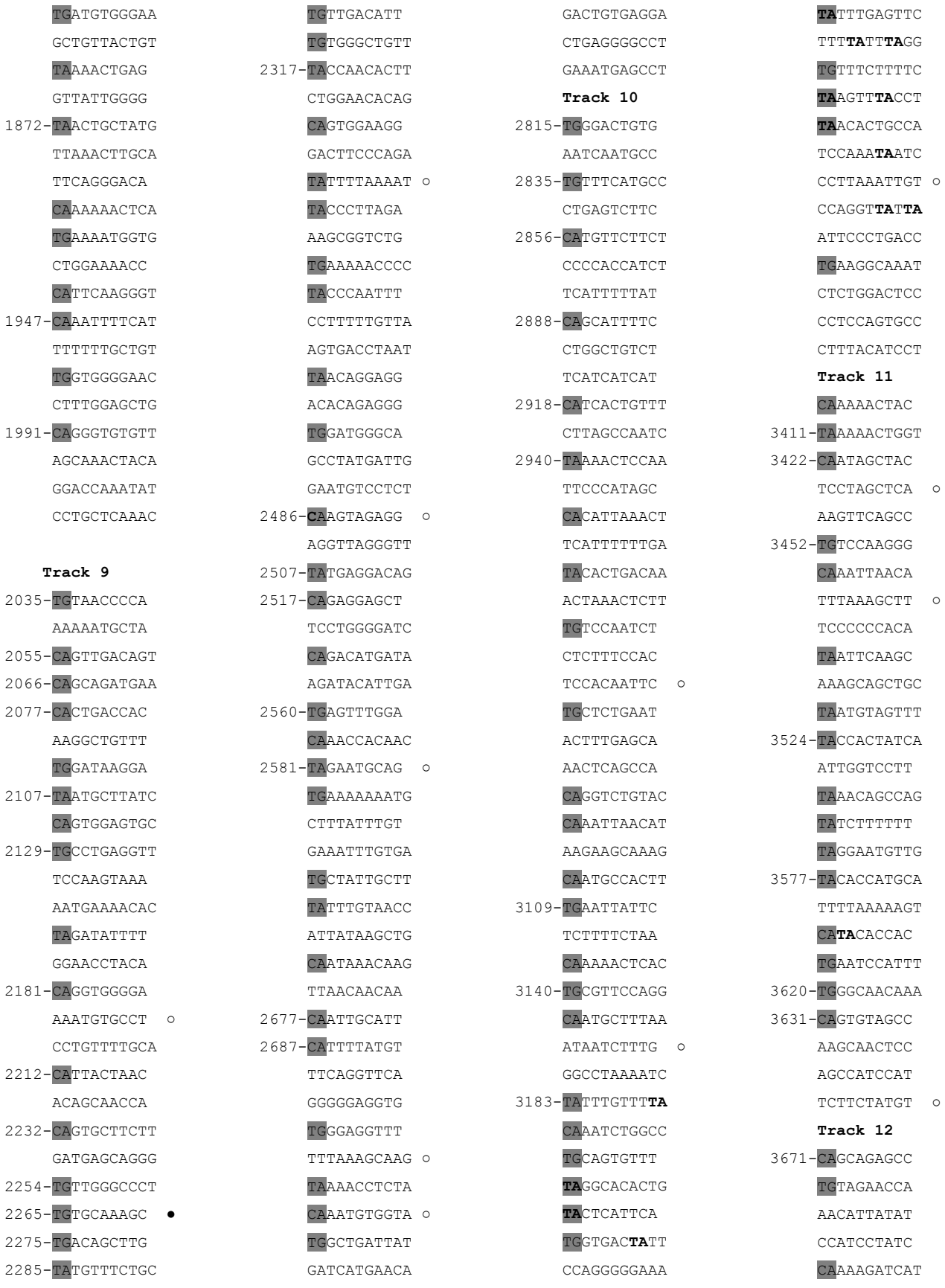
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CATTCAAGGGT
1947-CAAATTTTCAT
TTTTTTGCTGT
TGGTGGGGAAC
CTTTGGAGCTG
1991-CAGGGTGTGTT
AGCAAACTACA
GGACCAAATAT
CCTGCTCAAAC
Track 9
2035-TGTAACCCCA
AAAAATGCTA
2055-CAGTTGACAGT
2066-CAGCAGATGAA
2077-CACTGACCAC
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TGGATAAGGA
2107-TAATGCTTATC
CAGTGGAGTGC
2129-TGCCTGAGGTT
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AATGAAAACAC
TAGATATTTT
GGAACCTACA
2181-CAGGTGGGGA
AAATGTGCCT ○
CCTGTTTTGCA
2212-CATTACTAAC
ACAGCAACCA
2232-CAGTGCTTCTT
GATGAGCAGGG
2254-TGTTGGGCCCT
2265-TGTGCAAAGC ●
2275-TGACAGCTTG
2285-TATGTTTCTGC
TGTTGACATT
TGTGGGCTGTT
2317-TACCAACACTT
CTGGAACACAG
CAGTGGAAGG
GACTTCCCAGA
TATTTTAAAAT ○
TACCCTTAGA
AAGCGGTCTG
TGAAAAACCCC
TACCCAATTT
CCTTTTTGTTA
AGTGACCTAAT
TAACAGGAGG
ACACAGAGGG
TGGATGGGCA
GCCTATGATTG
GAATGTCCTCT
2486-CAAGTAGAGG ○
AGGTTAGGGTT
2507-TATGAGGACAG
2517-CAGAGGAGCT
TCCTGGGGATC
CAGACATGATA
AGATACATTGA
2560-TGAGTTTGGA
CAAACCACAAC
2581-TAGAATGCAG ○
TGAAAAAAATG
CTTTATTTGT
GAAATTTGTGA
TGCTATTGCTT
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ATTATAAGCTG
CAATAAACAAG
TTAACAACAA
2677-CAATTGCATT
2687-CATTTTATGT
TTCAGGTTCA
GGGGGAGGTG
TGGGAGGTTT
TTTAAAGCAAG ○
TAAAACCTCTA
CAAATGTGGTA ○
TGGCTGATTAT
GATCATGAACA
GACTGTGAGGA
CTGAGGGGCCT
GAAATGAGCCT
Track 10
2815-TGGGACTGTG
AATCAATGCC
2835-TGTTTCATGCC
CTGAGTCTTC
2856-CATGTTCTTCT
CCCCACCATCT
TCATTTTTAT
2888-CAGCATTTTC
CTGGCTGTCT
TCATCATCAT
2918-CATCACTGTTT
CTTAGCCAATC
2940-TAAAACTCCAA
TTCCCATAGC
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TCATTTTTTGA
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ACTAAACTCTT
TGTCCAATCT
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TCCACAATTC ○
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ACTTTGAGCA
AACTCAGCCA
CAGGTCTGTAC
CAAATTAACAT
AAGAAGCAAAG
CAATGCCACTT
3109-TGAATTATTC
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3140-TGCGTTCCAGG
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ATAATCTTTG ○
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3183-TATTTGTTTTA
CAAATCTGGCC
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TAGGCACACTG
TACTCATTCA
TGGTGACTATT
CCAGGGGGAAA
TATTTGAGTTC
TTTTATTTAGG
TGTTTCTTTTC
TAAGTTTACCT
TAACACTGCCA
TCCAAATAATC
CCTTAAATTGT ○
CCAGGTTATTA
ATTCCCTGACC
TGAAGGCAAAT
CTCTGGACTCC
CCTCCAGTGCC
CTTTACATCCT
Track 11
CAAAAACTAC
3411-TAAAAACTGGT
3422-CAATAGCTAC
TCCTAGCTCA ○
AAGTTCAGCC
3452-TGTCCAAGGG
CAAATTAACA
TTTAAAGCTT ○
TCCCCCCACA
TAATTCAAGC
AAAGCAGCTGC
TAATGTAGTTT
3524-TACCACTATCA
ATTGGTCCTT
TAAACAGCCAG
TATCTTTTTT
TAGGAATGTTG
3577-TACACCATGCA
TTTTAAAAAGT
CATACACCAC
TGAATCCATTT
3620-TGGGCAACAAA
3631-CAGTGTAGCC
AAGCAACTCC
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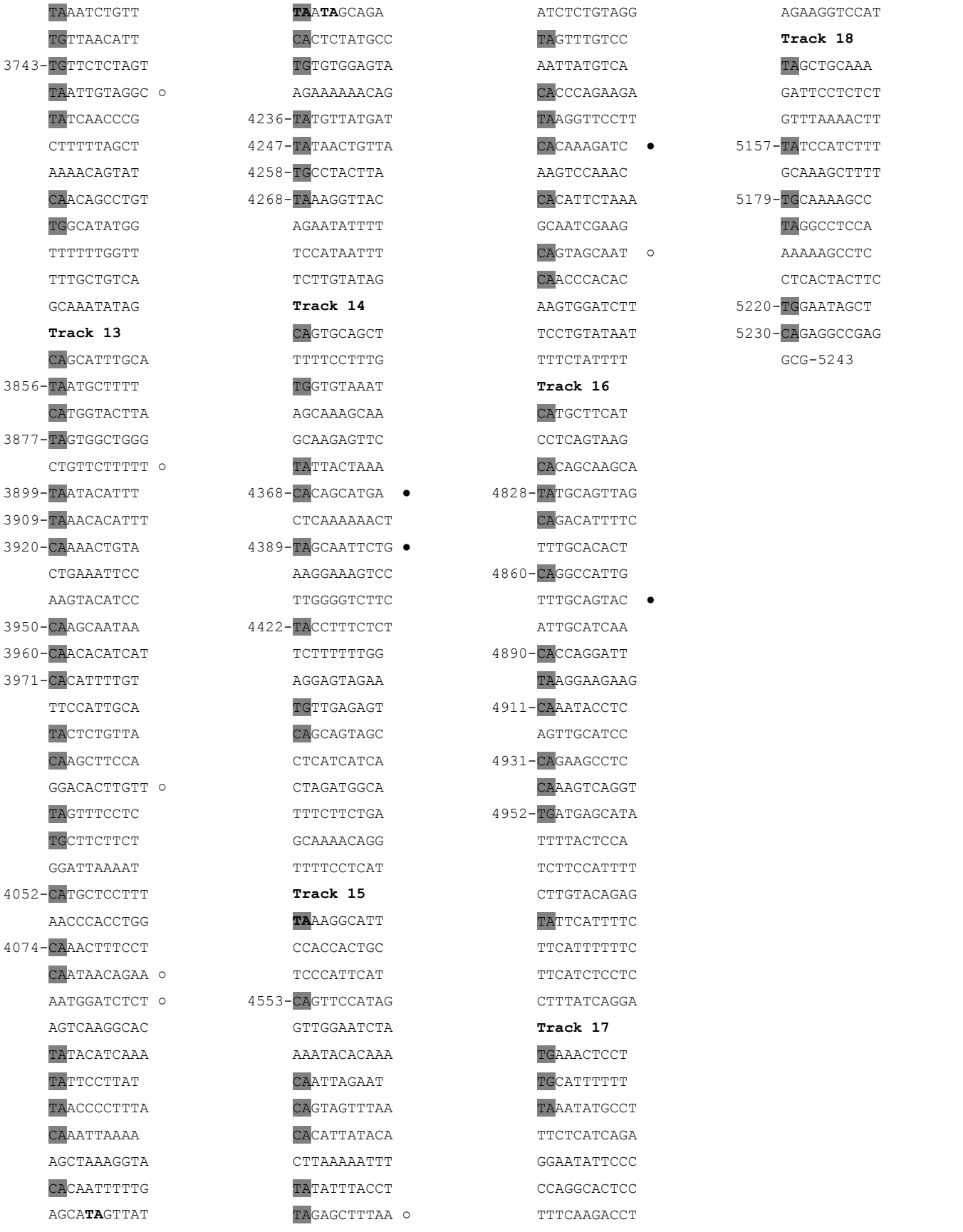
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GCAAATATAG
Track 13
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3899-TAATACATTT
3909-TAAACACATTT
3920-CAAAACTGTA
CTGAAATTCC
AAGTACATCC
3950-CAAGCAATAA
3960-CAACACATCAT
3971-CACATTTTGT
TTCCATTGCA
TACTCTGTTA
CAAGCTTCCA
GGACACTTGTT ○
TAGTTTCCTC
TGCTTCTTCT
GGATTAAAAT
4052-CATGCTCCTTT
AACCCACCTGG
4074-CAAACTTTCCT
CAATAACAGAA ○
AATGGATCTCT ○
AGTCAAGGCAC
TATACATCAAA
TATTCCTTAT
TAACCCCTTTA
CAAATTAAAA
AGCTAAAGGTA
CACAATTTTTG
AGCATAGTTAT
TAATAGCAGA
CACTCTATGCC
TGTGTGGAGTA
AGAAAAAACAG
4236-TATGTTATGAT
4247-TATAACTGTTA
4258-TGCCTACTTA
4268-TAAAGGTTAC
AGAATATTTT
TCCATAATTT
TCTTGTATAG
Track 14
CAGTGCAGCT
TTTTCCTTTG
TGGTGTAAAT
AGCAAAGCAA
GCAAGAGTTC
TATTACTAAA
4368-CACAGCATGA ●
CTCAAAAAACT
4389-TAGCAATTCTG ●
AAGGAAAGTCC
TTGGGGTCTTC
4422-TACCTTTCTCT
TCTTTTTTGG
AGGAGTAGAA
TGTTGAGAGT
CAGCAGTAGC
CTCATCATCA
CTAGATGGCA
TTTCTTCTGA
GCAAAACAGG
TTTTCCTCAT
Track 15
TAAAGGCATT
CCACCACTGC
TCCCATTCAT
4553-CAGTTCCATAG
GTTGGAATCTA
AAATACACAAA
CAATTAGAAT
CAGTAGTTTAA
CACATTATACA
CTTAAAAATTT
TATATTTACCT
TAGAGCTTTAA ○
ATCTCTGTAGG
TAGTTTGTCC
AATTATGTCA
CACCCAGAAGA
TAAGGTTCCTT
CACAAAGATC ●
AAGTCCAAAC
CACATTCTAAA
GCAATCGAAG
CAGTAGCAAT ○
CAACCCACAC
AAGTGGATCTT
TCCTGTATAAT
TTTCTATTTT
Track 16
CATGCTTCAT
CCTCAGTAAG
CACAGCAAGCA
4828-TATGCAGTTAG
CAGACATTTTC
TTTGCACACT
4860-CAGGCCATTG
TTTGCAGTAC ●
ATTGCATCAA
4890-CACCAGGATT
TAAGGAAGAAG
4911-CAAATACCTC
AGTTGCATCC
4931-CAGAAGCCTC
CAAAGTCAGGT
4952-TGATGAGCATA
TTTTACTCCA
TCTTCCATTTT
CTTGTACAGAG
TATTCATTTTC
TTCATTTTTTC
TTCATCTCCTC
CTTTATCAGGA
Track 17
TGAAACTCCT
TGCATTTTTT
TAAATATGCCT
TTCTCATCAGA
GGAATATTCCC
CCAGGCACTCC
TTTCAAGACCT
AGAAGGTCCAT
Track 18
TAGCTGCAAA
GATTCCTCTCT
GTTTAAAACTT
5157-TATCCATCTTT
GCAAAGCTTTT
5179-TGCAAAAGCC
TAGGCCTCCA
AAAAAGCCTC
CTCACTACTTC
5220-TGGAATAGCT
5230-CAGAGGCCGAG
GCG-5243

Figure 2. The YR tracks of the SV40 genome, in format 10 or 11 bases in line. The numbers on the left correspond to the sequence positions of the map minima, i. e., positions "minor groove *in*". Small circles on the right show approximate positions (centers) of strong (●) and moderate (○) nucleosomes experimentally mapped in (Ambrose et al., 1990). Note that some 10-11-mers start with YR, while others are ordinary sequence segments of the same lengths.

Conflict of Interest

All authors declare that there are no conflicts of interest.

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