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Adenovirus Strand Nomenclature: a Proposal[1, 2]

Thirty-six scientists have agreed to standardize the nomenclature of DNA strands of all adenovirus serotypes according to certain criteria.

The study of the biochemistry and molecular biology of adenoviruses began soon after their identification, but the construction of a genomic map of viral mRNA sequences and proteins awaited the purification of base-sequence specific endonucleases and the separation of the two strands of viral DNA. These endonucleases are in many cases known to be a component of restriction and modification systems of bacteria and are therefore commonly designated restriction endonucleases (11). The sites of cleavage of many restriction endonucleases have been mapped on the genome of adenovirus serotypes 2, 5, and 12 and adenovirus 2-simian virus 40 hybrid viruses (8, 12). Thus, specific fragments of viral DNA can be used to map biochemical products of adenovirus infections to discrete regions of the genome.

In common with the DNA of most bacteriophages, the strands of adenoviruses 2, 5, and 12 DNA can be separated by centrifugation to equilibrium in CsCl gradients after binding of poly(U,G) (7, 9, 10, 14, 16). One strand of the viral DNA binds a greater quantity of the ribopolymer and thus comes to equilibrium at a higher density in the gradient than its complement. The strand banding at higher density has been referred to as the "heavy" strand and denoted as both *h* and H; its complement, the "light" strand, is denoted as either *l* or L. The strands of adenoviruses 2 and 5 DNA have also been separated by equilibrium sedimentation of denatured viral DNA in alkaline CsCl gradients (15). A net bias in the distribution of guanine and thymine between the two strands results in one strand binding more Cs^+ ion and therefore banding at a higher density than its complement (17). Again, the strand sedimenting to the higher density in alkaline CsCl gradients has been called the "heavy" strand and denoted as the H strand; its complement has been called the "light" strand and denoted as the L strand. Unfortunately, the adenovirus DNA strand sedimenting to the higher density in alkaline CsCl gradients bands at the lower density in poly(U,G)-containing CsCl gradients (13, 16). The *h* and *l* designation for the separated strands of adenovirus is therefore ambiguous and depends on the method used for strand separation.

Electrophoresis of denatured DNA in gels has been used to separate the strands of specific restriction endonuclease fragments of adenovirus types 2 and 5 DNA (13). This procedure was originally developed for the separation of the two strands of bacteriophage DNA (5). The strands of all six *Eco*RI cleavage fragments, five of the seven *Hpa*I cleavage fragments, and all four *Bam*HI cleavage fragments of adenovirus 2 DNA migrate, for example, as a faster (F) and slower (S) band during electrophoresis (2). The bias in base sequence between the two strands that causes their different mobility in these gel systems is not known. However, Weingärtner et al. (18) have reported that the strand migrating more slowly during electrophoresis has a lower thymine content than its complement. Viral DNA recovered from the faster and slower migrating bands in agarose gels has been assigned as a component of either total viral strand (2, 13).

Genomic maps are now being constructed from data from many laboratories, and it is therefore necessary to develop conventions for referring to the two strands of adenovirus DNA and the left-to-right orientation of the conventional map. To avoid the cumbersome notation of designating a particular strand after the physical property employed to separate the two complements, we suggest acceptance of the nomenclature developed in bacteriophage systems; that is, on the conventional map, the strand transcribed from left to right should be denoted the *r* strand and its complement, which is transcribed from right to left, the *l* strand. By generally accepted convention, the genetic maps of adenovirus subgroup C serotypes have been drawn with the following asymmetric physical and biological features defining the

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left-to-right orientation: (i) the AT-rich half of the viral DNA is positioned to the right (1, 8); (ii) a non-essential region of the genome deleted in nondefective adenovirus 2-simian virus 40 hybrid viruses is positioned to the right (6); (iii) the only segment of the viral genome necessary for transformation of cells in culture is positioned to the left (3, 4); (iv) the strand of the genome coding for the virion major structural proteins is transcribed from left to right.

When the map has been oriented according to these parameters, we recommend that the positions on the map be defined as the percentage of the total distance of the adenovirus genome.

Maps of other adenovirus serotypes should be oriented in accord with as many of these criteria as possible to facilitate direct comparison between different serotypes.

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