CRISPR (/ˈkrɪspər/) (an acronym for **c**lustered **r**egularly **i**nterspaced **s**hort **p**alindromic **r**epeats) is a family of DNA sequences found in the genomes of prokaryotic organisms such as bacteria and archaea.[2] Each sequence within an individual prokaryotic CRISPR is derived from a DNA fragment of a bacteriophage that had previously infected the prokaryote or one of its ancestors.[3][4] These sequences are used to detect and destroy DNA from similar bacteriophages during subsequent infections. Hence these sequences play a key role in the antiviral (i.e. anti-phage) defense system of prokaryotes and provide a form of heritable,[3] acquired immunity.[2][5][6][7] CRISPR is found in approximately 50% of sequenced bacterial genomes and nearly 90% of sequenced archaea.[3]

Cas9 (or "CRISPR-associated protein 9") is an enzyme that uses CRISPR sequences as a guide to recognize and open up specific strands of DNA that are complementary to the CRISPR sequence. Cas9 enzymes together with CRISPR sequences form the basis of a technology known as CRISPR-Cas9 that can be used to edit genes within living organisms.[9][10] This editing process has a wide variety of applications including basic biological research, development of biotechnological products, and treatment of diseases.[11][12] The development of the CRISPR-Cas9 genome editing technique was recognized by the Nobel Prize in Chemistry in 2020 awarded to Emmanuelle Charpentier and Jennifer Doudna.[13][14]

Evolution

The cas genes in the adaptor and effector modules of the CRISPR-Cas system are believed to have evolved from two different ancestral modules. A transposon-like element called casposon encoding the Cas1-like integrase and potentially other components of the adaptation module was inserted next to the ancestral effector module, which likely functioned as an independent innate immune system.[130] The highly conserved cas1 and cas2 genes of the adaptor module evolved from the ancestral module while a variety of class 1 effector cas genes evolved from the ancestral effector module.[131] The evolution of these various class 1 effector module cas genes was guided by various mechanisms, such as duplication events.[132] On the other hand, each type of class 2 effector module arose from subsequent independent insertions of mobile genetic elements.[133] These mobile genetic elements took the place of the multiple gene effector modules to create single gene effector modules that produce large proteins which perform all the necessary tasks of the effector module.[133] The spacer regions of CRISPR-Cas systems are taken directly from foreign mobile genetic elements and thus their long-term evolution is hard to trace.[134] The non-random evolution of these spacer regions has been found to be highly dependent on the environment and the particular foreign mobile genetic elements it contains.[135]

CRISPR-Cas can immunize bacteria against certain phages and thus halt transmission. For this reason, Koonin described CRISPR-Cas as a Lamarckian inheritance mechanism.[136] However, this was disputed by a critic who noted, "We should remember [Lamarck] for the good he contributed to science, not for things that resemble his theory only superficially. Indeed, thinking of CRISPR and other phenomena as Lamarckian only obscures the simple and elegant way evolution really works".[137] But as more recent studies have been conducted, it has become apparent that the acquired spacer regions of CRISPR-Cas systems are indeed a form of Lamarckian evolution because they are genetic mutations that are acquired and then passed on.[138] On the other hand, the evolution of the Cas gene machinery that facilitates the system evolves through classic Darwinian evolution.[138]

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