the synapomorphy of an independent sporophyte generation. This hypothesis gains additional corroboration when we observe that liverworts (another outgroup, but not part of the sister group) also have saprophytes that are dependent on the gametophyte.

The final arbitrator of synapomorphy and thus homology is the test of congruence of many independent characters corroborating a particular phylogenetic tree (the congruence test: Patterson, 1988) (see Homology). This is because some identical characters are not homologies, but homoplasies. The assumption inherent in the congruence test is that the most parsimonious explanation of character distribution yields the maximum number of hypotheses of homology and the minimum number of ad hoc hypotheses of homoplasy (Farris, 1980).

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See *also:* Apomorphy; Homology; Phylogeny

Synapsis, Chromosomes

See: Chromosome Pairing, Synapsis

Synapsis in DNA Transactions

M M Cox

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The word synapsis is derived from the Greek word *sunapsis*, meaning point of contact. The term synapse is used to describe a cell–cell junction that allows a nerve impulse to pass from one nerve cell to another. In the study of DNA metabolism, the word synapse is also used to describe the point where two DNA molecules come together during recombination. Genetic recombination is any process that brings about an exchange of genetic information between two DNA molecules, and it can take several forms. Homologous genetic recombination, transposition, and site-specific recombination are the most common, and each of these is described in more detail elsewhere in this encyclopedia. In each case, at least two DNA molecules or two different segments of the same DNA molecule must be brought together at the point where the genetic exchange is to take place. This key step, which may precede any covalent chemistry, is referred to as synapsis. The synapsis may be either DNA-mediated or protein-mediated.

DNA-Mediated Synapsis

Homologous genetic recombination is a genetic exchange between any two DNA molecules (or segments of the same molecule) with a similar sequence. In principle, it can occur at any site on any DNA molecule. Thus, proteins that bind to a particular sequence on the DNA play no role in the synapsis step in this process. Instead, synapsis involves the alignment of similar sequences in the two DNA molecules, a process that requires direct DNA–DNA interaction. Proteins participate in this process as catalysts. Proteins that facilitate DNA–DNA alignment include the RecA protein in bacteria and its homologs: the Rad51 or Dmc1 proteins in eukaryotes, the Rad1 protein of Archaea, and related proteins produced by some viruses. These proteins (with the possible exception of Dmc1) form helical filaments on single-stranded DNA, with the bases of the DNA displayed in the major groove of the filament. The DNA is then aligned with homologous sequences in a second, duplex DNA, in a process sometimes called the search for homology. Recent studies indicate that the homology search involves base flipping, in which Watson–Crick interactions in the duplex are weakened and individual bases in the duplex are flipped out so that they can pair with the bases in the originally bound single strand. The homology search leading to synapsis is thus mediated by standard Watson–Crick base pairing (**Figure 1**). The sampling is very rapid. Once the correct alignment is found, there is an extensive transfer of one strand of the duplex to its new pairing partner.

Protein-Mediated Synapsis

Site-specific recombination and transposition both generally require the activity of at least one protein that binds to specific DNA sequences. This protein also plays a key role in bringing DNA molecules together in the right orientation for the genetic exchanges catalyzed in these reactions. Synapsis is mediated largely by protein–protein interactions. In

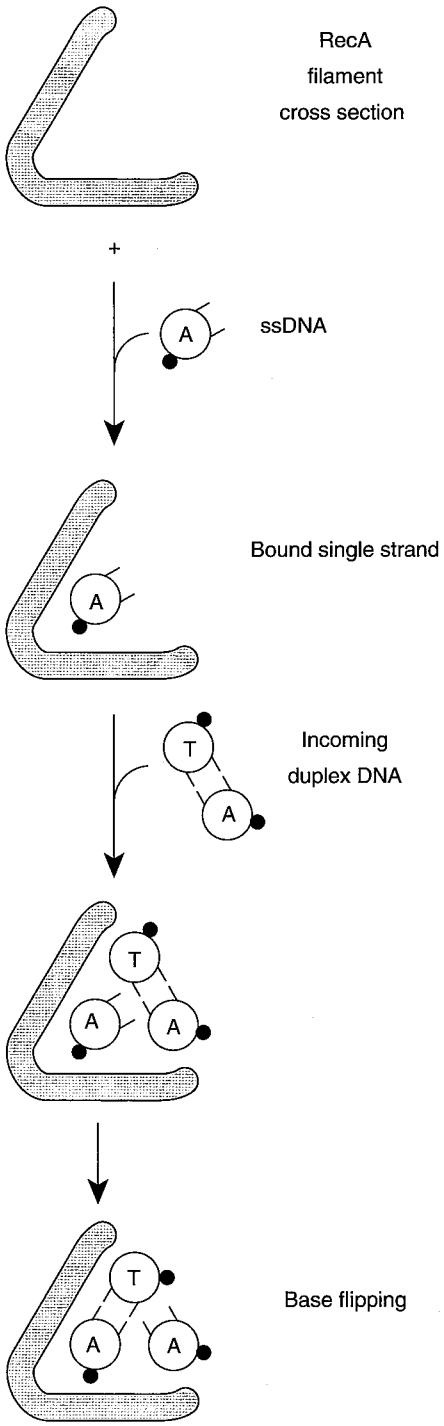

Figure 1 (left) DNA-mediated synapsis in homologous genetic recombination. The reaction is shown in cross section, with a RecA-bound single strand interacting with an incoming duplex DNA. Only one base (A) or base pair (A:T) from each DNA is shown. Base-flipping occurs within the duplex to allow synapsis mediated by a Watson–Crick interaction between the bound single strand and the base flipped out of the duplex. The small filled circles attached to each base are meant to represent the DNA backbone, and the duplex is thus shown approaching the single strand via its major groove. Several recent studies have provided strong evidence for a minor groove approach prior to base flipping, and this aspect of the DNA pairing mechanism is still considered controversial.

many of these systems, very elaborate protein–DNA complexes are formed with the DNA wrapped into the complex in a precise geometry. The architecture of the synaptic complex not only brings two DNA sites together for reaction, but can also determine the outcome of the reaction. In addition, formation of the synaptic complex is often a prerequisite for any covalent chemistry, preventing the occurrence of incomplete DNA cleavage or strand transfer reactions, which could be deleterious to chromosomal DNA.

Site-Specific Recombination

In conservative site-specific recombination, the genetic exchange occurs at specified sequences in the DNA which are recognized and bound by the recombinase enzyme and/or auxiliary proteins. There are two large classes of site-specific recombinases, the integrase class and the resolvase/invertase class.

In the integrase class, the simplest forms of the recombination sites consist of two protein-binding sites flanking a short sequence where the actual DNA recombination occurs. The recombinase proteins bind to a recombination site, then bring two bound recombination sites together in a synapse via protein–protein interactions (**Figure 2**). Recombination is then catalyzed by the recombinase and occurs within the complex.

For the resolvase/invertase class, synapsis not only brings two recombination sites together, but also determines the outcome of the reaction. Synapsis in these systems involves an elaborate complex with multiple proteins, with the DNA wrapped within and around the complex in a precise topology. In addition, the synaptic complex forms efficiently only when the DNA is negatively supercoiled. The synaptic complex acts as a topological filter. In the case of invertases, the architecture of the complex can form only with two recombination sites that are both on the same DNA molecule and inverted in orientation (**Figure 3A**). The result is that the reaction always leads to an inversion of DNA sequences between the recombination sites. Similarly, the architecture of the synaptic complex formed by resolvases allows them to catalyze recombination only between two recombination sites on the same DNA molecule that are in the same orientation, leading to a deletion of the intervening sequences (**Figure 3B**). Each of these systems is thus able to 'sense' the relative orientation of two recombination sites in a DNA molecule even though the sites may be separated by thousands of base pairs.

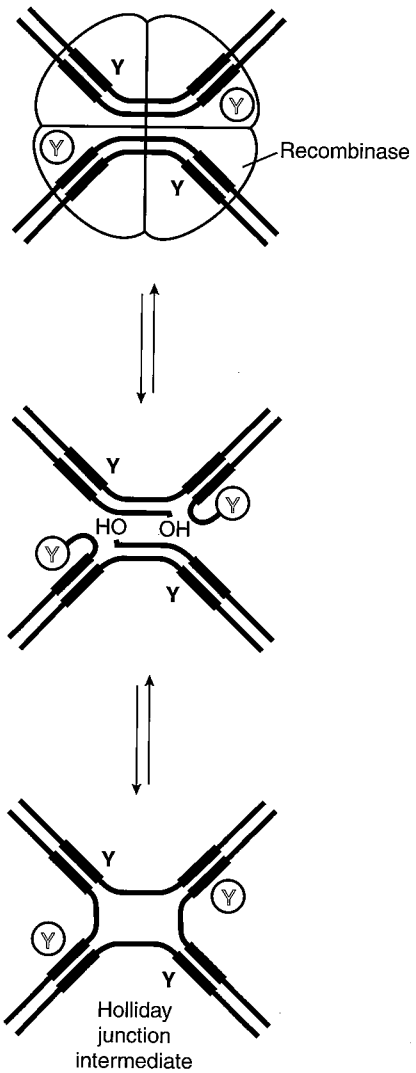

Figure 2 Protein-mediated synapsis in site-specific recombination by integrase class recombinases. Synaptic complexes generally include four recombinase proteins (as shown in the first panel only), but can be considerably more complex (e.g., the complexes formed by the bacteriophage λ integrase). The DNA-binding sites containing the base pairs specifically recognized by the recombinase proteins are indicated with thickened lines. Only the first few steps of the recombination reaction are shown, with the Holliday junction illustrated being a common intermediate in the reactions catalyzed by these enzymes. Integrase class recombinases have an active site tyrosine that forms a covalent intermediate with the DNA. These tyrosine residues are indicated by Y symbols. Only two of the four subunits promote formation and resolution of the covalent intermediates at any given time, and the active ones are circled. Resolution of the Holliday junction into recombinant DNA molecules involves the noncircled Y residues.

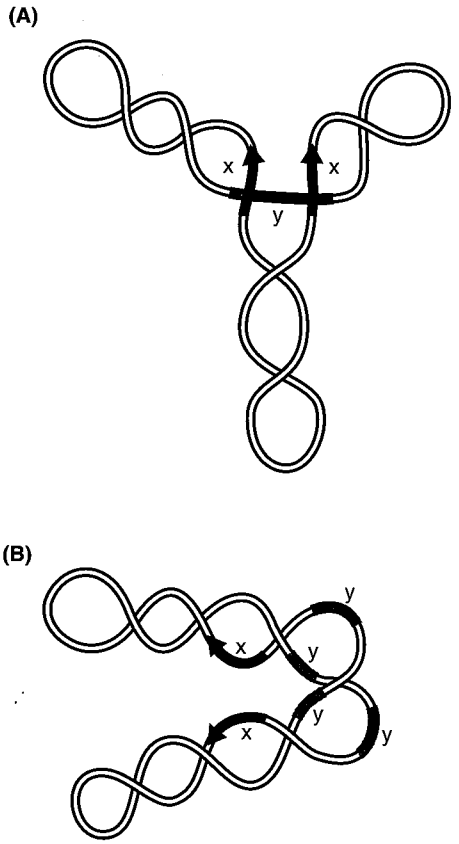

Figure 3 Synaptic complexes as topological filters: The invertase/resolvase class of site-specific recombination systems. Proteins are not shown to keep the figure uncluttered, although multiple recombinase and auxiliary proteins generally bind to the indicated sites and are essential to form and maintain the DNA architecture shown. (A) The likely architecture of the synaptic complex formed by an invertase system. This complex can readily form between two DNA sites only if the sites are in the opposite orientation and the DNA molecule is negatively supercoiled. (B) The likely architecture of a synaptic complex formed by a resolvase system. This complex restricts reaction to recombination sites that have the same orientation within a negatively supercoiled DNA molecule. The structures effectively filter out sites in the incorrect orientation even if they are thousands of base pairs apart. In each complex, the sites labeled x are those where the DNA rearrangement takes place, and these sites are positioned and held together by protein–protein interactions. The orientations of the x sites are indicated with arrows in both panels. The sites labeled y are places where additional recombinase proteins (which do not take place in the chemical steps) or other auxiliary proteins bind to maintain the overall DNA architecture. In the DNA beyond the protein-binding sites, the right-handed twisting represents the natural supertwisting of negatively supercoiled DNA.

Transposition

Transposons are discrete DNA segments that have the capacity to move between different chromosomal locations that may share no homology. Elaborate protein complexes are also used to bring about synapsis between a migrating transposon and a new target site in a host chromosome. The synaptic complex generally includes the target DNA as well as both ends of the transposon, or three sites altogether. The transposase enzyme that catalyzes the DNA splicing steps of the reaction is always a critical, and sometimes the only, protein component in the complex. There are many types of transposons. Transposition can involve a simple cut-and-paste movement from one site to another, or replication of the transposon so that a copy is left behind in the original location. Some transposons can migrate in either a replicative or nonreplicative mode, and the architecture of the synaptic complex can play a role in defining the mode employed. In some complex transposons, the architecture of the synaptic complex also helps ensure that the two transposon ends in the reaction are inverted relative to each other and thus are likely to have come from the same transposon. An example is the synaptic complex formed by the transposing bacteriophage Mu (**Figure 4**). The principle is the same as that employed in the invertase/resolvase systems described above, in which the complex architecture serves as a topological filter preventing the juxtaposition of sites that are not properly oriented on the chromosome.

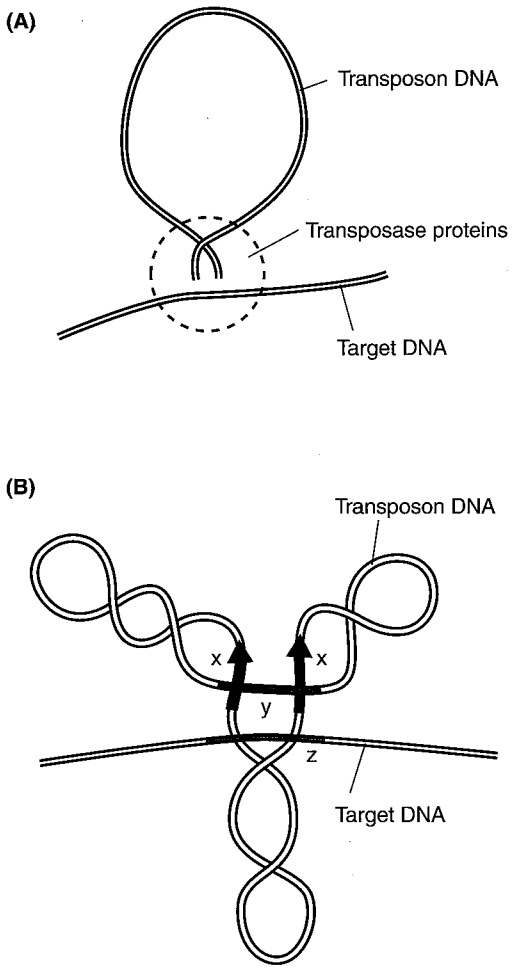

Figure 4 Transposon synaptic complexes. (A) A generic synaptic complex with the two transposon ends juxtaposed over a chromosomal DNA target site. (B) The synaptic complex formed by the transposing bacteriophage Mu. This structure is closely related to the complex formed by the invertase class of site-specific recombinases. There are inverted DNA-binding sites at the ends of the Mu transposon, and the complex helps ensure that the two ends brought together are from the same transposon. The sites labeled x are the sites where the Mu DNA is cleaved. The sites labeled y are places where additional proteins bind to help define the complex architecture. The site labeled z is the target site on a different DNA segment where the Mu transposon will be inserted. As in **Figure 3**, the proteins needed to form and maintain this architecture are not shown.

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See also: **Genetic Recombination; Holliday Junction; Transposable Elements**