the synapomorphy of an independent sporophyte
generation. This hypothesis gains additional corro-
boration when we observe that liverworts (another
outgroup, but not part of the sister group) also have
saprophyses that are dependent on the gametophyte.
The final arbitrator of synapomorphy and thus
homology is the test of congruence of many independ-
ent characters corroborating a particular phylogenetic-
tree (the congruence test: Patterson, 1988) (see
Homology). This is because some identical characters
are not homologies, but homoplases. The assumption
inherent in the congruence test is that the most parsim-
onious explanation of character distribution yields
the maximum number of hypotheses of homology
and the minimum number of ad hoc hypotheses of
homoplasies (Farris, 1980).

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See also: Apomorphy; Homology; Phylogeny

Synapsis, Chromosomes
See: Chromosome Pairing, Synapsis

Synapsis in DNA
Transactions
M M Cox

The word synapsis is derived from the Greek word
synapsis, 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 mol-
ecules 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
generic 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 mol-
ecules 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 seg-
ments of the same molecule) with a similar sequence. In
principle, it can occur at any site on any DNA mol-
ecule. 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 inter-
actions 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 cor-
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 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.

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 synapsis 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.

Further Reading

See also: Genetic Recombination; Holliday Junction; Transposable Elements