Life without sex

There are many reasons why sexual reproduction is beneficial. Indeed, in the long term it is thought that asexuals will simply go extinct, either because they accumulate too many deleterious mutations or parasites will get the better of them (cf. the devastating effects of parasites on monocultures). This, we think, is why asexuality is phylogenetically very spotty. As an asexual lineage goes extinct before it can diversify, we find that a species here or a species there may be asexual, but never a whole group of related species. Well, not quite. In the 360 species of Bdelloid a male has never been observed and reproduction is always asexual. For this reason the group has been dubbed an evolutionary scandal. However, it has never been clear that the group really is anciently asexual and many have suspected that these tiny invertebrates must be having covert sex. Recent analysis of the evolution of their genes by Welch and Meselson[1], strongly suggests, however, that they are as scandalous as once presumed.

Welch and Meselson used the following logic. If we take the two copies of a gene found in a sexual diploid and compare the sequences of the maternally and paternally derived alleles, then because the alleles are in competition at the locus, they should be very similar as they will have a recent age of common ancestry. Compare the same gene between species and we shall see more divergence, the extent of which is dependent upon the time since speciation. But if we have an asexual organism the pattern will be different. The two copies of the gene will no longer be in competition. It would be as though the diploid genome got frozen into one which is effectively haploid and what were two alleles at a locus become two new loci. Therefore, compare the sequences from the two loci within a species and these will now be very different. The amount of difference indicates the time the genome got frozen. By contrast, compare one of these loci with the orthologous one from a related species and the time of common ancestry should be the time of the speciation event. If the speciation event was recent, the extent of divergence between the genes should be lower in the between-species comparison than in the within-species comparison: a prediction opposite to that which we expect in a sexual species.

The authors sequenced four genes that are typically single copy in most species (hsp82, tpb, rpol3l and tpi) in seven sexual (non-bdelloid) rotifers and four bdelloids, representing the three major families. They found the patterns predicted were the sexuals sexual and the asexuals anciently asexual. The time of divergence of homologous genes in the same genome suggests that the two loci stopped being alleles possibly 80 million years previously. Adding this evidence to the fact that in Bdelloids the chromosomes cannot be split into two neat groups (implying they are not functionally diploid) and Southern blots that indicate that all the pertinent genes have been sequenced, and we have evidence that strongly supports the view that these really are ancient asexuals. Theories of sex must explain not only why most groups have sex, but why Bdelloids survive without.

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1 Welch, D.M. and Meselson, M. (2000) Evidence for the evolution of Bdelloid rotifers without sexual reproduction or genetic exchange. *Science* 288, 1211–1215

Transgenic frogs are useful

Availability and ease of manipulation of embryos makes the frog *Xenopus laevis* a popular model organism for the study of tissue-specific gene expression, but its usefulness for studying transcriptional regulation was limited by poor and variable expression from DNA promoter constructs injected into the embryo. The recent development of transgenic *Xenopus* technology, in which exogenous DNA is integrated into the genome, has overcome this problem, and now Lerchner *et al.*[1] demonstrate the potential of this approach in an investigation of the regulation of the gene *Xbra* (*Xenopus Brachury*). *Xbra* encodes a T-box transcription factor that is expressed as an early response to the induction of the mesoderm, and understanding how its expression is regulated will tell us more about the initial mesoderm induction as well as further mesoderm patterning.

Lerchner *et al.* created transgenic frog embryos carrying the *Xbra* promoter linked to a reporter gene. After it was established that a 381 basepair portion of the *Xbra* promoter was sufficient to drive the expression of the reporter gene in the gastrula marginal zone (the site of endogenous *Xbra* expression), a series of deletions and point mutations narrowed down the promoter sequences responsible for establishing this pattern. A surprising result was that transcriptional repression, rather than activation, seems to restrict *Xbra* expression to the developing mesoderm. Thus, disruption of a binding site for SIP1, a member of the δ EF1 family of transcriptional repressors, caused expression of the reporter outside the mesoderm, while disruption of a pair of homeodomain-binding sites caused ectopic expression in dorsal mesoderm (where *Xbra* is usually downregulated), and dorsal ectoderm. The authors speculate that widespread initial expression, followed by specific repression, might be a general mechanism for establishing spatial regulation of early embryonic genes. In support of this, they observe a transient wave of reporter, as well as endogenous *Xbra* expression, throughout the embryo just before gastrulation.

This study leads to several further questions. (1) Which homeodomain proteins are involved in dorsal *Xbra* repression? (2) The role of SIP1 in confining *Xbra* to the mesoderm needs clarifying: it is intriguing that SIP1 interacts with Smad proteins, members of the TGFβ-signalling cascade, as it is known that *Xbra* expression is both positively and negatively regulated by activin, a TGFβ mesoderm inducing factor. (3) 'Missing' promoter elements that maintain *Xbra* expression in the notochord after it is downregulated in other dorsal mesoderm remain to be found, and appear to be located several kb away from the elements defined here. (4) The generality of this model for regulating early embryonic gene expression, of activation followed by repression, must be explored.

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1 Lerchner, W. *et al.* (2000) Region-specific activation of the *Xenopus Brachury* promoter involves active repression in ectoderm and mesoderm: a study using transgenic frog embryos. *Development* 127, 2729–2739