What's sex really all about?

Sex is a pretty primitive business – after all, species that used sexual reproduction appeared over a billion years ago. But its success is still a big evolutionary puzzle because it has so many downsides. Time for a rethink, says **Thierry Lodé**

THERE'S no way sex could ever be considered a good solution for reproduction among organisms like us – eukaryotes with complex information contained within membraned cells. After all, the exponential growth of a population reproducing asexually seriously outcompetes any sexual strategy: it doubles with each generation, while a sexual population has to bear the cost of males.

Most of the supposed advantages of sexual strategies stem from the idea that sexual reproduction enlarges the genetic variation in the lineages on which it operates. Mutation-based models argue that sexual reproduction reduces mutations, which suggests the recombination of DNA during the process exists to prevent detrimental changes in offspring. As a result, sexual reproduction could be beneficial by generating offspring with a lower genetic load (a number measuring the extent to which the average individual in a population is inferior to the best possible kind of individual) when there is a high rate of bad mutation.

The special cell division of sexual reproduction – meiosis, which produces gametes with half as many chromosomes – was first seen as a sort of DNA-repair process for eukaryotes. Thus, each strand of the original double-stranded DNA molecule served as a template for the replication of a new, complementary DNA molecule, allowing damaged DNA to be repaired. In this hypothesis, genetic recombination is seen as a response to the "noise" occurring when genetic information is transmitted. One chromosome can duplicate information from another, and use it to recover any lost genetic information. Even so, this mechanism requires that recombination leads to a repair process that should be faster than the rate of natural damage. Further, recombination repair systems exist in both prokaryotes and eukaryotes, but sexual meiosis is limited to eukaryotes, suggesting that the DNA repair hypothesis is not sufficient to explain the advantage of sexual reproduction .

Then there is the Red Queen hypothesis, named after the scene in Lewis Carroll's *Through the Looking-Glass* in which the Red Queen says: "It takes all the running you can do to keep in the same place." This hypothesis aims to explain the advantage of sexual reproduction at the individual level, and the evolutionary arms race between competing species. Sexual reproduction generates a wide diversity of progeny, helping the species survive disease outbreaks, while cloning results in similar genomes between descendants, making the population vulnerable. The diversity resulting from sexual reproduction also allows sexual species to co-evolve with pathogens.

Such hypotheses face major obstacles, however. First, if sex increases the anti-parasite advantage in sexual lineages, sexual species should diversify more often than asexual populations. In fact, asexual groups do not diversify less than sexual species, as shown by rotifers, a diverse group of tiny aquatic organisms.

Then there is the problem of origins. Studies of worm species that reproduce asexually have revealed their hybrid origins, with sexual reproduction as their likely ancestral state.

Another obstacle is that sex is expected to confer selective advantages over generations. But the correlation is poor between the conditions selecting sexual reproduction and viability of future offspring and those favouring recombination - and Red Queen models cannot be used to infer the advantage of sex over the long-term. Plus the results from experiments are by no means straightforward: sexual recombination disrupts favourable gene combinations more often than it generates them – and some clonal species do have great adaptive potential.

So, how should we understand the evolution of sex? Enter my libertine bubble theory, which argues that rather than providing reproductive advantages, it might be better to see sex as a genetic exchange between two

PROFILE
Thierry Lodé is a biologist at the ETHOS unit of the University of Rennes 1, France. This essay is based on his paper "Sex is not a solution for reproduction" (*BioEssays*, vol 33, p 419)

CHRISTIAN STEINHAUSEN/GETTY

Despite its downsides, sexual reproduction is common in complex-celled organisms

organisms, as originating from an archaic horizontal gene transfer process among the prebiotic bubbles on the ocean surface, which are thought to have played a major role in the creation of living cells. My theory suggests sex results from three key primitive conditions: first, bubbles form spontaneously, creating a favourable environment for genetic material; second, the "promiscuous" nature of these bubbles allows transfer of genetic material among the most "libertine" of the bubbles, gradually leading to a certain membrane selectivity; and third, DNA overcrowding encourages primitive meiotic recombination.

These bubbles did indeed form – and start to exchange material. Since interactions involving the exchange of genetic material could be a mechanism through which a self-promoting element spreads genetic information, bubbles practicing gene exchange were advantaged as genetic renewal favours adaptive variation.

Genetic drift meant that the bubbles would have become progressively different. The porosity of proto-cell membranes in contact with other proto-cell membranes would be selected for as long as the process allowed the exchange and possible replication of

"Sex is best seen, not as a solution for reproduction, but a primitive interaction"

compatible genetic material. Presumably these exchanges would result in an increasing imbalance in the genetic content among bubbles, with some bubbles losing many genes while others had too many.

Now, meiosis and haplo-diploid cycles are basic processes that appeared early in evolution. And the fact that such interactions became stable appears to have been enough to make the primitive "sexual" relations efficient at selecting the most "libertine" bubbles. The asymmetric nature of "female" meiosis, selecting one of four haploid genetic elements for its own benefit while the other three degenerate (in the male the four are conserved), resulted in a runaway process.

The last link in the chain is that sex and meiotic recombination in eukaryotes is known to be induced by stressful conditions. In bad conditions, genetic exchanges could renew the proteins in metabolic reactions so interactions among the most "libertine" proto-cells would be mutually advantageous. And genetic exchanges could increase the rate at which proto-eukaryotes segregate new adaptive mutations, promoting sex.

During their evolutionary history, the efficiency of sexual exchanges was enhanced by the formation of haploid gametes, but a dissymmetry between sperm and ova was also the basis for sexual conflict. The ability to produce numerous sperm means males can mate with many partners, passing genes to many offspring. Females, by contrast, cannot obtain more offspring by so doing; instead, exercising a selective preference for a specific male may increase their reproductive success. Sexual conflict is now recognised to drive the attempted manipulation of the sexes. The antagonistic co-evolution generated by sexual conflict may be a reasonable explanation why so many asexual animals originated from sexual species. The genetic divergence of parental genomes could be large enough to drastically lessen fertility in hybrids and to lead to asexual forms of reproduction.

My theory remains parsimonious: DNA should pass through proto-membranes as they touch and fuel an asymmetric exchange between proto-cells. Bubbles with membrane proteins or favourable mechanisms for exchanging genes would tend to interact more than other bubbles, providing the former with the potential to evolve. The most libertine bubbles – those practising genetic exchanges – would be advantaged because genetic renewal promotes adaptive variation. Focusing on primitive interactions, selection pressures may have led to the emergence of a sexual process in the primitive stages of proto-cell evolution. Rather than competition between proto-eukaryotic bubbles, self-stabilising exchanges of genetic material would increase and enhance their efficiency. All of which is why sex is best seen, not as a solution for reproduction, but as a primitive interaction. n