next stage in the advancement of this technology will be to access even shorter wavelengths at which the residues and backbones of proteins and the bases of DNA have their electronic transitions. ■

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Evolutionary biology

Why sex is good

Rolf F. Hoekstra

According to a proposal put forward many years ago, sexual reproduction makes natural selection more effective because it increases genetic variation. Experiments now verify that idea — at least in yeast.

Most animals and plants are sexual, and in organisms that normally multiply asexually, such as microbes and some groups of fungi, sexual processes are rarely completely absent. Such a widespread process must have an essential function. To their embarrassment, however, evolutionary biologists have had great difficulties in finding a simple and general explanation. As they describe elsewhere in this issue, Goddard and colleagues (page 636)[1] have used twenty-first-century techniques to provide confirmation of an idea, first mooted in the nineteenth century, as to why sex is good.

Sexual reproduction involves the marriage of genetic material from two parents to form progeny that transmit new combinations of paternal and maternal genes to their offspring. It has spectacular consequences for the biology of organisms that extend beyond its evolutionary essence — the generation of new genetic combinations. In a world without sex there would be no males and females, no flowers, no insects specialized in pollinating them, no extravagant colour and form like the peacock's tail; and much animal behaviour aimed at finding and selecting mates would not exist.

A large body of theory proposes a variety of hypothetical evolutionary advantages of sexuality and the genetic shuffling (recombination) that it involves[2,3]. Discriminating between these theories empirically has proved very hard. But Goddard *et al.*[1] present the results of an elegant and rigorous experiment with yeast, showing that a sexual population evolves faster than an asexual population when challenged by a novel environment.

When supplied with sufficient nutrients, yeast cells reproduce vegetatively (asexually), but if starved they undergo the process of meiosis, producing four spores that are functionally equivalent to the gametes involved in sexual reproduction. These spores then fuse in pairs to produce the next generation of vegetative cells (Fig. 1). Goddard *et al.* constructed an asexual yeast strain from a normal strain by deleting two genes (*SPO11* and *SPO13*) that are required for normal recombination and meiosis. This asexual strain differs from the sexual strain only in its ability to undergo meiotic recombination. When starved, the asexual strain forms two diploid spores, which are genetically identical to the parental cell, instead of the four recombinant haploid spores produced by the sexual strain.

The authors set out to test an idea, which traces back to August Weismann[4,5] in the late nineteenth century, that sex increases genetic variation and thereby promotes evolutionary adaptation. Subjecting many generations of both the sexual strain and the engineered asexual strain to two novel environments, harsh and benign, they measured adaptation as increased 'fitness' (in this case, growth rate) relative to the non-evolved ancestral strain. In the benign environment, in which growth is limited by glucose concentration and where there is little selection, Goddard *et al.* observed no fitness increase in either the sexual or the asexual strains. However, in the harsh environment — having the same glucose concentration but at a higher temperature and with more demanding osmotic conditions — the sexual strain reached an increase in growth rate of 94% but the

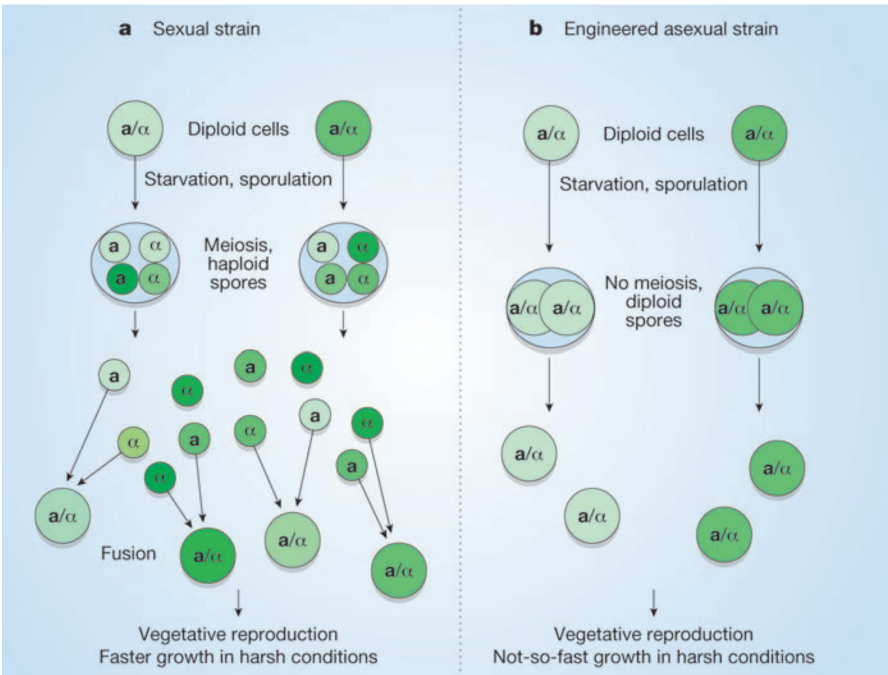

Figure 1 **Yeast reproduction, and Goddard and colleagues' experiments[1]. Vegetative (diploid) cells proliferate asexually when food is available, but starvation induces sporulation; these diploid cells have both forms** (a, α) **of the 'mating type' gene.** a, **In the sexual strain sporulation involves meiosis, and so genetic recombination, and results in haploid spores that differ in genetic composition in mating type and elsewhere in the genome (indicated by the different colours). Pairs of spores with opposite mating type then fuse to produce a new generation of diploid vegetative cells.** b, **In the asexual strain, engineered to form unrecombined diploid spores but otherwise identical to the sexual strain, sporulation does not increase genetic variability. Here the diploid spores develop directly into the new vegetative cells. When both strains are grown in a harsh environment, the sexual strain shows faster evolutionary adaptation than the asexual strain, seen in terms of growth rate, owing to its greater genetic variability.**

asexual strain reached only 80%. These results clearly support Weismann's hypothesis.

The history of ideas about the functional significance of sexual reproduction is remarkable. For a long time Weismann's theory was widely accepted. But in the 1970s several difficulties with his explanation were identified[6,7]. First, genetic recombination will tend to break up favourable combinations of genes that have accumulated by selection, which may slow down adaptive evolution rather than speed it up. Second, in organisms with male–female differentiation, there is a so-called twofold cost of sex. If males do not contribute resources to offspring, a mutation to asexuality, causing females to produce only daughters, will — other things being equal — quickly increase in frequency. This is because sexual females produce only half the number of daughters compared to the asexual mutants, 'wasting' half their reproductive output on sons.

Decades of intense theoretical exploration ensued, aimed at discovering potential benefits of sex that are large enough to overcome these and other disadvantages. Many different hypotheses were advanced, most of them not mutually exclusive. The result was confusion and frustration rather than illumination. By 1993, hypotheses had become so numerous and diverse that a classification of them became necessary[8]. Since then, theoretical analysis has progressed further and has resulted in several plausible and general explanations, again not mutually exclusive, and roughly belonging to two categories: either sex increases the rate of adaptive evolution, or it is more efficient in eliminating deleterious mutations[2,3].

The solution to the evolutionary riddle of sex has to come from empirical tests of the various theories, and experimental studies have been increasingly devoted to the problem[9]. However, clearcut comparisons between sexual and asexual reproduction are hampered by confounding factors. The paper by Goddard and colleagues[1] is exemplary in this respect, owing to the excellent possibilities offered by their yeast system.

Nonetheless, we are still far from a definitive answer to the question of why sexual reproduction is so common. For one thing, yeast has no male–female distinction, so the twofold cost of sex does not apply, which prevents a straightforward generalization of the conclusions to most animals and plants. Moreover, the experiment provides no information as to why the sexual population is more efficient in adapting to the harsh conditions than the asexual population. Is it because sex has brought together different beneficial mutations that have arisen in separate lineages, or because sex has liberated beneficial mutations from unfavourable genetic interactions with other genes? Further genetic characterization of the mutations responsible for the adaptation to the harsh environment would be a first step to distinguishing between these possibilities. ■

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Aceh–Andaman earthquake

What happened and what's next?

Kerry Sieh

The huge earthquake of 26 December 2004 and ensuing tsunami were caused by a submarine rupture running from offshore Aceh, Indonesia, to the Andaman Islands. A clearer picture of events is starting to emerge.

As the human drama of the Aceh–Andaman earthquake and tsunami unfolded in the last days of 2004, laymen and scientists began scrambling to understand what had caused these gigantic disturbances of Earth's crust and seas. One of the earliest clues was the delineation, within just hours of the mainshock, of a band of large aftershocks arcing 1,300 km from northern Sumatra almost as far as Myanmar (Burma)[1]. This seemed to signal that about 25% of the Sunda megathrust, the great tectonic boundary along which the Australian and Indian plates begin their descent beneath Southeast Asia, had ruptured. In less than a day, however, analyses of seismic 'body' waves[2] were indicating that the length of the rupture was only about 400 km.

This early controversy about the length of the megathrust rupture created a gnawing ambiguity about future dangers to populations around the Bay of Bengal. If only 400 km of the great fault had ruptured, large unfailed sections might be poised to deliver another tsunami. If, on the other hand, most of the submarine fault had broken,

100 YEARS AGO

***Philosophy as Scientia Scientiarum and a History of Classifications of the Sciences*.**
The relation of science to philosophy is, in theory, filial. It is, perhaps, no contradiction of the filial relationship that in practice it has an unfortunate tendency to run to mutual recrimination. The man of science too often ignores the philosopher, or despises him as an obscurantist who habitually confounds abstraction with generalisation. To the metaphysical philosopher, on the other hand, the typical specialist in science is a variety of day-labourer, dulled by the drudgery of occupational routine… Prof. Flint's new book should serve as a mediating influence between philosophical and scientific interests. It brings together into one convenient source the leading attempts made, from Plato to Karl Pearson, towards a classification of the sciences… How invaluable a service Prof. Flint has thus rendered to future investigators, can be appreciated only by those who have tediously toiled at the scattered literature of this subject. Its bibliography appears hitherto to have been left unorganised — having escaped even the ubiquitous zeal of German scholarship.
From *Nature* 30 March 1905.

50 YEARS AGO

The Piltdown saga has now been concluded. The British Museum (Natural History) has brought together under the title "Further Contributions to the Solution of the Piltdown Problem"… the views of a large number of specialists who have described their work on the specimens — work which has resulted in demonstrating without any doubt that the whole thing was a hoax… Dr J. S. Weiner's book, "The Piltdown Forgery", deals rather with the many personalities in the case… The story unfolds with the discovery of Piltdown I, and we find not a few of the local amateurs a little suspicious that all is not as presented. We now have evidence for staining of specimens; we have the 'happy' find of Piltdown II which was to clinch the matter… It all reads like a novel, and I have no intention of spoiling it for others by saying more. It is a book to be read with interest and profit. Such a hoax nowadays is impossible; but it was one actually perpetrated and it was a great success.
From *Nature* 2 April 1955.