

questions were sharp. The course was held at an institute that was run by a person with a mission to develop a passion for science among the young. For me, the visit showed the power of science in developing society, not at the technological but at a human level. It also showed how science can be a tool in diplomacy, as it provides a common interest that is a starting point for dialogue.

How do you find working in Singapore? When I first came to Singapore in 1999, there were only a handful of labs here. I came for several reasons: it was close to Malaysia and I wanted to be back in South East Asia; there were some excellent group leaders at the institute; and the funding was good. At that time, however, most people in the West had not heard of science in Singapore, and thought this was a strange place to move to. The attitude of strangers at conferences was amusing. They would see the word 'Singapore' on your badge, give you a funny look, and quickly look around for someone with the word 'Boston' or 'London' on their nametag.

Things are quite different now. When strangers see 'Singapore', they are full of questions about what science is like there, and even ask how they can get a job. This shift reflects not only a change in general perception, but a revolution in the scientific landscape here. Singapore now has many more institutes and labs. In my own field, neuroscience, there was a perceptible change when Dale Purves moved here to run the Neuroscience program at the Duke-NUS graduate medical school.

What has been informative is the way in which science was rapidly built here. I hope that the experience can be applied to other countries in the region.

What are your ambitions? I would like to help in the further development of science in this region. Science wise, it would be great to be able to say why the sense of control over a situation is so satisfying and provides such a driving force for many different aspects of life. In this respect, I think whole brain imaging in the zebrafish, combined with behavior, holds a lot of promise.

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Quick guides

Sex

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Isn't it obvious what sex is? Not really. True, everyone seems to think they have a fairly good idea of what sex is — but perhaps for this reason it is often not given a specific definition in the scientific literature. And when a definition is given, it often deviates from others. There are so many ways of making offspring and combining the genetic material of different individuals that it may be futile to hope for a single definitive definition.

Does sex equal reproduction? No! And not only because there are asexual ways to procreate. Even in species that are said to reproduce sexually, sex and reproduction are not always tightly linked. In mushroom-producing fungi, dispersing spores are produced (i.e. reproduction) long after exchange of genetic material (in this case the nuclei) takes place in underground mycelia. Similarly, ciliates can exchange haploid genetic material, but reproduction in these microbial eukaryotes takes place completely separately by cell division.

So sex is synonymous with genetic recombination? No, there is a subtle difference. Definitions of recombination, just like definitions of sex, vary greatly. On a general level, recombination is a process resulting in a new combination of genes. This can take place between different individuals, as in bacterial conjugation, but it can also be based on the genetic material of a single individual. For example, some types of asexual reproduction (more specifically, certain forms of automixis) involve meiosis and crossover, leading to a genetically unique individual; this is often considered recombination in the absence of sex.

OK, so even bacteria and other prokaryotes can recombine their genomes. Do they have sex? That depends on how one chooses to define sex.

So what definitions do we have out there? There are many. Perhaps the broadest definition of sex is

the coming together of genes from different individuals. By this definition, both eukaryotes and prokaryotes do have sex, the latter in the form of conjugation (DNA transferred by direct contact between cells), transformation (direct uptake of exogenous DNA from the surroundings of the cell) and transduction (transfer of DNA via a virus from a bacterium to another). There are also more specific definitions of sex, such as meiosis followed by the fusion of meiotic products from different individuals. This narrower statement avoids one clear disadvantage of the broadest definitions: if any form of uptake of DNA is sex, it becomes hard to draw the line and explain why we do not consider that humans have sex with the HI virus if it inserts its genome to take advantage of our cells. Alternatively, sex can be contrasted with known features of asexual reproduction: when asexual organisms are said to not regularly go through a sexual cycle that involves meiosis and changes in ploidy levels, it is implied that sex involves those things. All definitions of sex that include meiosis, however, imply that prokaryotes do not have sex.

Does sex imply the existence of separate sexes? Or the existence of gametes for that matter? No, neither separate sexes nor gametes are required for sex. The male and female sexes are defined based on their relative gamete sizes: males produce smaller gametes (e.g. sperm) than females (e.g. ova); this size dimorphism, where it exists, is called 'anisogamy'. It can occur in species where male and female gametes are produced by different individuals (called gonochorism in animals, dioecy in plants) or those in which the same individuals can produce both (hermaphroditism in animals, monoecy in plants), or in diverse combinations of the above options (e.g. androdioecy, where a population consists of males and hermaphrodites; there are also sex changers).

Thus, maleness and femaleness require that gametes exist, and that they differ in size. In heterothallic fungi, however, male and female terminology is sometimes used for cells that 'donate' and 'receive' nuclei without cytoplasm. This asymmetry is only distantly analogous to a situation that involves gametes. A gamete is a

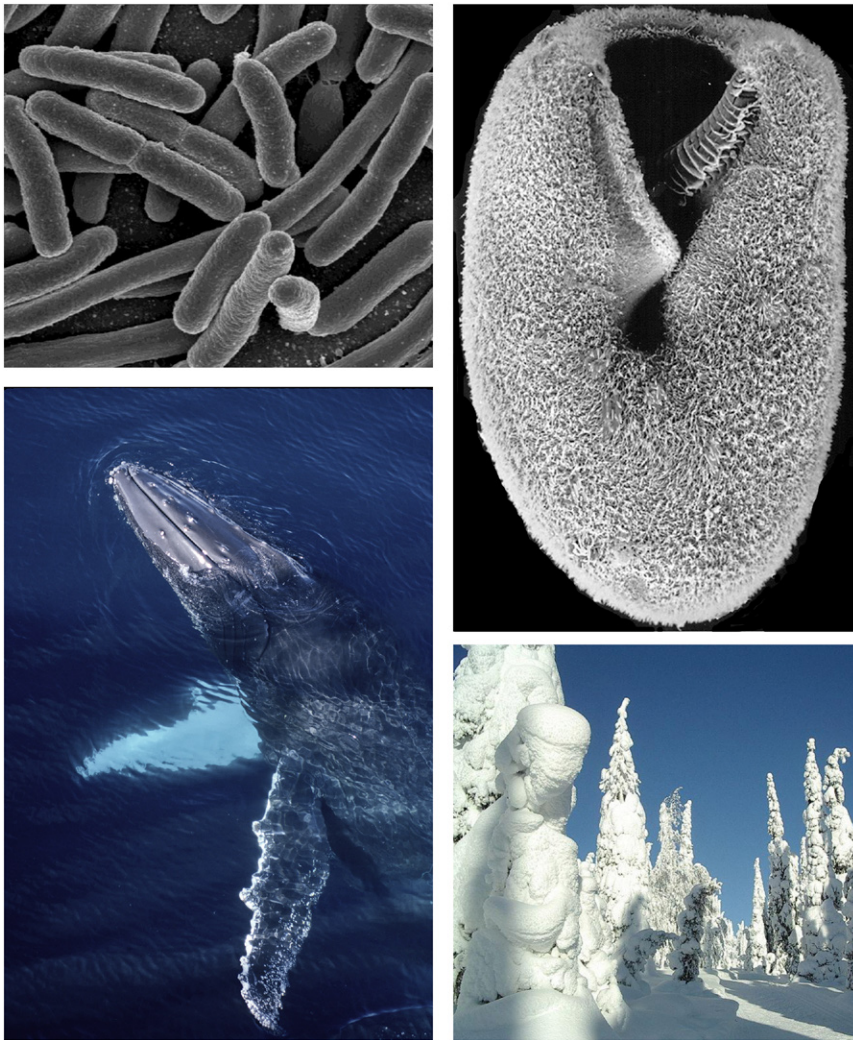


Figure 1. Are these examples of sexuality?

Clockwise from top left: *Escherichia coli* bacteria do not have meiosis, but individuals can exchange genetic material (image: National Institute of Allergy and Infectious Diseases). The eukaryotic microbe *Bursaria truncatella* does not have male and female sexes, nor does it produce gametes in the usual sense, but individuals can exchange meiotic products (image with permission from Wilhelm Foissner). Each individual of the spruce *Picea abies* produces both male and female gametes, and fertilization takes place without copulation (image: Hilikka Pellikka). The humpback whale *Megaptera novaeangliae* reproduces sexually in a manner familiar to us (Gerald and Buff Corsi/Focus on Nature, Inc.). Some definitions of sex include all these cases, while others require a clear sexual cycle to be present.

cell that fuses with another during fertilization (syngamy) — although asexually produced eggs of parthenogenetic females are also, somewhat confusingly, included in the definition of a gamete. Gametes are also absent in prokaryotes, which may or may not have sex depending on one's definition, and unambiguous sex without gamete production also occurs in some microbial eukaryotes. In ciliates, haploid products of micronuclei are formed through meiosis and exchanged mutually between individual cells. This form

of eukaryotic sex is very difficult to detect, as the brief cell fusion could be confused with cell division, and may be more common than it seems.

Even when gametes exist, they need not differ in size (in isogamous organisms they don't), thus sex in general does not require males. It is nevertheless often associated with different genetically determined mating types that determine the compatibility of gametes for fusion, and sometimes there are many more than two, even up to hundreds. In practice, of course, males occur in numerous species.

So, why is sex so difficult to explain?

The maintenance of sex remains an unresolved question in biology due to its costs in comparison to asexual reproduction. Costs, as well as benefits depend on how broad one's definition of sex is. In small organisms with otherwise fast reproduction, meiosis involves a significant time cost, which is relevant whenever sexual reproduction is assumed to require meiosis. Recombination breaks up successful gene combinations (though it can also bring together beneficial combinations, at least temporarily). The famous concept of the 'twofold cost of sex' (i.e. the halving of population growth of sexual relative to asexual organisms), in turn, easily leads one into assumptions that are not generally included in definitions of sex: in its pure form twofoldness requires that males exist, and that they do not contribute materially to the next generation (e.g. by providing parental care). Of course, this does not mean that broadening the definition makes the problem disappear: many of the costs apply regardless of whether the organism is isogamous, anisogamous or has sex without gametes. Also, males are, after all, not a rare feature of sexual reproduction. Divergent evolutionary interests of the two sexes can make sexual reproduction even less efficient at converting resources into offspring, via negative effects of sexual conflict on female reproduction.

Where can I find out more?

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