Commentary

Commentary on the chastity of amoebae: re-evaluating evidence for sex in amoeboid organisms

A student in one of my mycology classes, after she had been exposed to numerous life cycles, commented, ‘All you mycologists ever think about is sex.’ In a way, it is too bad that biologists, in general, do not spend enough time thinking critically about sex as a biological phenomenon. Lahr *et al.* [1], in their review of sex in amoeboid eukaryotes, make a good start at calling attention to this problem.

It is amazing how little we teach young, potential biologists about the true generalities of biology. If one examines any basic biology text, one comes away with the impression that animals, particularly vertebrates, are the exemplars for all living things. Thus, too many examples are drawn from animals and too few are drawn from the range of variations that are present among the eukaryotes as a whole. That is, students are poorly introduced to the comparative method in biology, and when they become practising biologists, they often cannot put important biological processes in a proper context. Sex is one area where biologists are not well trained.

Many biologists have probably never been asked to state succinctly what is universal about sex, so they have a hard time recognizing its universal features. It is a phenomenon that is exclusive to eukaryotes. Lahr *et al.* [1] elegantly define the essential components of sex; they are ‘... the presence of a meiotic reduction of the genome complement followed eventually by karyogamy ... in an organism’s life cycle.’ Thus, we see that sex is, at its heart, a nuclear phenomenon where there is a stereotypical mechanism for alternating between diploidy and haploidy.

Sex is *not reproductive*, though it is often linked with reproduction as it is in most animals. Therefore, animals are poor models for understanding the universal aspects of sex. The definition of reproduction should be limited to the production of a greater number of individuals from a smaller number of individuals. Fertilization, at least when gametic cells are involved, results in a *reduction* in the number of individuals from two cells to one, a zygote. I will grant that meiosis can potentially be reproductive if all four potential nuclei become housed in individual cells, but that is hardly the rule. At best, one could make a case for sexual reproduction only if one found a hypothetical (and never reported) sexual life cycle where mitosis and somatic growth do not occur and the meiotic nuclei were housed in four cells. In such a case, there would be a net gain of two haploid cells per life cycle (2 cells → 1 cell → 4 cells → 2 cells → 8 cells...). Without such an organism, there is no point in using the term sexual reproduction.

Though there are lots of ways cells and, ultimately, their nuclei can fuse, meiosis is so complex that it could have evolved only once. Thus, meiosis, and therefore sex, must be a shared, derived character, a synapomorphy (*sensu* [2]), of all organisms that share it. When we map sex on the eukaryote tree of life, as shown by Lahr *et al.* [3] and many others, we can only conclude that sex had to have been present in the *last common ancestor* of all extant eukaryotes. Thus, in spite of its perceived complexity, sex is one of the most primitive characters of living eukaryotes.

If present phylogenetic hypotheses are correct, then there is no extant lineage of eukaryotes that diverged from the rest of eukaryotes prior to the origin of sex. That is, there are no longer any presexual eukaryotes. Without such a lineage for comparison, it seems almost pointless to argue about the origins of sex. Whatever its perceived benefits or costs, sex is part of the baggage of all the lineages of living eukaryotes. We should all be willing to consider the possibility that the reasons why the last common ancestor of extant eukaryotes survived and gave rise to our present diversity might have had nothing at all to do with the fact that it was sexual. We should at least attempt to carry out the mental exercise to envision other traits of eukaryotes that could possibly have been more important than sex for survival of the last common ancestor.

If there are any truly asexual lineages of eukaryotes, they must be derived. Therefore, if we can understand the origins of asexual lineages, it may tell us something about whether alternatives to sex are necessary to ‘protect’ long-lived asexual lineages from such perceived risks as Muller’s Ratchet (see [1]).

As Lahr *et al.* [1] point out the absence of the observation of sex is not the same as absence of sex. If one learns to ‘think about sex all the time,’ one may be more likely to find it. When one looks at how different groups of amoebae were divided up among the disciplines of biology, one sees that with amoebae which were claimed as ‘botanical property’, e.g. the fruiting amoebae or slime ‘moulds,’ every effort was made to study their whole life cycle [3,4], and sex was found. It also meant that when new encysted states were found in the dictyostelid ‘social amoebae’ (see [5]) and the sorocarpic *Copromyxa* [6], and multiple trophic states were recognized in protosteloid amoebae [7], hypotheses of sexuality were quickly developed. On the zoological side of the spectrum, there appears to have been less-concerted effort to look for sex. For instance, see how little discussion of the possibility of sex there is in such classic amoeba monographs as Page [8].

Nonetheless, given how often they have been observed, many of the simplest, most reduced amoebae may be truly asexual (see [1]). Even some lineages of more complex amoebae, such as some of the protosteloid amoebae that have been observed intensively [9], may lack sex. Thus, amoeboid eukaryotes may be good organisms in which to find good examples of true asexuals. If so, they can be evaluated to determine whether the different asexual lineages have needed to cope with the theoretical disadvantages of asexuality.

There also exists at least one major group of amoebae, the Myxogastria, or plasmodial slime moulds, in which there are both obligately outcrossing, i.e. heterothallic, sexual strains and apomictic strains in the same morpho-species [10]. In order to go from spore to spore, both types of myxogastriids have to produce the same set of morphological stages in the same sequence, yet one set does it with sex and the other without. Detailed studies of closely related pairs of sexual and apomictic myxogastriids may be extremely useful for studying the sexual to asexual transition.

In summary, if we really want to think critically about sex in the most general sense, amoebae, *s.l.*, can tell us a lot that we can use to develop those generalizations. They can relieve us of the animal-based biases about sex. Perhaps Lahr *et al.* [1] will be a seminal event that will wake the biological community up from its complacent use of 'Just-So Stories' and stimulate a new birth in the development of new, testable hypotheses about what is truly universal about sex and about whether there are truly any costs associated with turning sex off for good.

Is it even possible for an amoeba to be 'chaste'? If so, we will have to develop testable hypotheses to recognize the characters that tell us that a taxon of amoebae is truly asexual. What types of observations would lead us to reject the null hypothesis that a given taxon is sexual? One strong candidate to refute the null hypothesis would be clear evidence that there are no functional meiotic genes. If asexuality can be firmly established in a lineage, then knowing its phylogenetic position with great accuracy would allow us to make careful comparisons with its closest sexual relatives. Only if we can do that will it even be possible to test whether there is general applicability to the concept that being completely asexual

is detrimental. Perhaps, however, it is premature to speculate about the effects of asexuality. First, we must learn to recognize it. That seems to be the most important way to 'think about sex all the time'.

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