The how and why in the origins of sexual reproduction

Zubair Mohammed
Lake Forest College
Lake Forest, Illinois 60045

Abstract
The origin of sexual reproduction, how it evolved, and its benefits have been topics of active research. Many different theories have been proposed and various models have been made to explain sexual reproduction in species. There is an inherent problem of which proponent of the evolution of sex is correct or whether it is a combination of theories that is correct. Although not exhaustive, the current review aims to synthesize and explore this issue and ideas based on some of its arguments including the generation of sex differences, the molecular basis for sex, and why it may have been selected for and kept in certain species. By providing a baseline for the discussion, further research may be executed in deriving the reasoning behind the evolution of sex and its pros and cons compared to asexual reproduction.

What is obligatory sex and who has it?

The definition of sex has generally been accepted as a means of reproduction that requires the genetic material of two parents combining (via gametes) to form a zygote (Bai 2015). However, this is not the only means of reproduction as organisms can also pass on their genetic material through asexual reproduction where the parent clones its genes for the offspring. It is important to note that about only 0.1% of animal species reproduce asexually (Phillips et al. 1990). An even more curious and interesting note is most asexual lineages have come from sexually reproducing ancestors which may indicate that asexual reproduction is probably a niche tool for evolution in certain evolutionary situations (Geodakyan 1991). Both sexual reproduction and asexual reproduction have a facultative side and an obligate side that can be observed in species. Obligate asexual reproduction has been thought to arise because of inbreeding or mutation in large populations (Scheuerl et al. 2011). Facultative sexual reproduction is relatively rare, being only observed in a few animal species. The reason for this seems to be a response from species for lack of viable mates in certain environments. On the other hand, obligate sexual reproduction is when species reproduce exclusively via sexual reproduction and is the reproductive method most observed in the animal kingdom. It may initially appear evident and obvious as to why and how sexual reproduction is advantageous and thus so prevalent. Unfortunately, this is not the case, as the origin and maintenance of sexual reproduction is still one of the most elusive and hotly debated topics in evolutionary biology. The reasons behind this are because sexual reproduction requires more resources and has more costs associated with it compared to asexual reproduction, and yet it is still prevalent. Therefore, there must be a greater payoff to the risks and costs that keeps sexual reproduction the main mode of propagation in species. In face of this logic, no concrete and agreed upon theory has been presented which explains how sexual reproduction came to be and how it is maintained. In the current review, some major theories and hypotheses will be discussed to provide a foundation for future research.

The sexual cons

One of the most famous costs of sex is known as the “two-fold” cost of sex. The idea is that a female can reproduce asexually and make many clones of herself which can then propagate further unhindered. Compare that to a sexual female who has a 50% chance of producing a male and cannot reproduce by themselves, decreasing the growth rate of the sexual population. Besides that, males and females have to first find each other to mate and produce one male and one female at the very least to keep the population at equilibrium (Gibson et al. 2017). This is significantly more difficult than cloning and duplicating which allows the asexual population to quickly double and outgrow the sexual population. Also, there is the loss of genetic information on both sides, known as the “cost of meiosis”, where each parent is only contributing half of their genetic material (Williams 1975). This is obviously a problem as the genetic traits that helped the parent survive in the environment are not fully transferred from parent to the offspring. There are other problems that contend with the evolution of sexual reproduction. For example, recombination can and does destroy successful gene combinations which reduces individual fitness (Lehtonen et al. 2012). Logically, natural selection should therefore act against recombination. Furthermore, the act of having sex can increase the transmission of sexually transmitted diseases (Otto 2009). These diseases can be crippling to populations of animals if the sexually reproducing members are dying from them. Genetic problems to consider include genetic linkages where certain areas of DNA are inherited together based on proximity and can carry disadvantageous alleles that may cause disease. There is also evidence showing that some genetic sequences can enhance their transmission and decrease other gene transmission regardless of whether they have no effect or are detrimental to organismal fitness (Hickey 1993). A simple way to avoid these problems would be to just not reproduce sexually, so what possible advantages could sex offer that overshadow its cons?

The sexual pros

Many experiments and explanations have been offered to demonstrate why sex may be advantageous. One explanation as to why obligatory sex can evolve over facultative sex is that sexual selection exists in sexually reproducing species (Hadany & Beker 2007). It is usually the case that the sex investing less in the offspring have varied fitness. Via sexual selection, natural selection is sped up in these species, and this presents the long-term benefits of quicker adaptation to the environment. The short-term benefits of sexual reproduction include allowing sexual organisms to compete in the “evolutionary arms race” better than asexual organisms. This is known as the Red Queen hypothesis (Lively 2010). By recombining the genotype, sexual organisms can better adapt to the fluctuating environments that are deterministic. In other words, the back and forth of the arms race may continue without sex, but sex enables the “race” to continue efficiently. Similarly, the haploid-diploid nature of sexual organisms is thought to exploit a very simple form of the Baldwin effect, where changed needs lead to learned behavior and natural selection takes care of the rest (Bull 2017). Simply put, the diploid stage of sexual organisms acts like the learned behavior stage and associated phenomenon, such as recombination or the varied lengths of haploid-diploid stages, can be evolution fine tuning the learning experienced by organisms. In this way, sex would be maintained as it allows for this learning stage to exist. Gandon and Otto (2007) looked at the specifics of the Red Queen hypothesis and argue that there are multiple factors that contribute to the phenomenon, including fluctuating epistasis, drift, and directional selection. They show that fluctuating epistasis is likely the most important factor in the development of sex. Natural selection often leads to certain allelic combinations that work well together, but recombination can break these links. In the short-term, this is reducing fitness for the organism; however, over the long-term, sufficiently high rates of recombination can work to help break those linkages which do not work well together (Otto & Feldman 1997). In this way, recombination and sex would be favored as they increase the ability to correct linkages if the incorrect ones are being broken, thus increasing the fluctuations in epistasis. Some phylogenetic evidence has also been provided showing that obligate sex organisms may have evolved from facultatively reproducing ancestors (Kleiman & Hadany 2015). It begs the question: why is obligate sex so common? One important realization to note is that most facultatively reproducing organisms are unicellular whereas multicellularity has been correlated with the development of sex (Kleiman & Hadany 2015). Unicellular organisms that reproduce asexually would accumulate DNA damage from the environment and pass it on until it becomes debilitating. This answers the question of why organisms may develop recombination, but that fails to account for the development of sex and sexual dimorphism, which allows sex to happen in the first place. It seems that there are many intertwining theories that are filling in different pieces of the puzzle, but there does not seem to be one apparent theory everyone can agree with. For this reason, the field has taken a “pluralist” approach in addressing the origin of sex. As stated before, so many different factors have contributed to the development and maintenance of sex, including the development of meiosis, anisogamy, sexual dimorphism, recombination, environmental constrains and pressures, and many more unlisted contributors, that this view is the best way to approach the problem. In this review, a few early theories will be discussed along with some modern theories. This is not an exhaustive list as many topics are outside the scope of this review, but a foundational understanding of the field will be posed.

Some early theories on why sex evolved

Fisher-Muller hypothesis

In a set number of asexual populations, the efficacy of natural selection is impeded by elements of genetic drift. The linkage of alleles talked about previously cannot happen by any efficient means. Recombination offers selection at individual loci; over time, the mean fitness should increase. It has been shown in the past that recombination in conjunction with sex increases the genetic variability in the genome of the species. Therefore, natural selection will then eliminate the unfavored combinations and have a better chance at bringing together successful allele pairs compared to asexual organisms. This was experimentally formalized by Fischer (1930) and Muller (1932) in a case applied to a set of 2 alleles, which are both beneficial but arise in two different loci that are linked. They both logically conclude that sexual organisms would have an easier time combining the two alleles into a new genome than asexual organisms. Asexual organisms would have to wait for the mutation to be made and to fix it into their sequence in the same generation. This would naturally take a much longer time period, comparatively.

Muller's hypothetical ratchet

Muller (1964) proposed another hypothesis in which recombination and sex could evolve in a set population. Muller argued that most mutations, due to random chance, are deleterious and restoration of the original wildtype allele, even in long periods of time, is rare. So, imagining a scenario where there is an initial population of asexual organisms of which some incur this mutation, there will be a few which do not. However, this initial subset of mutation-free organisms will be lost over time and cannot be recovered evolutionarily. This constitutes as one "crank" of Muller's Ratchet. Allowing for multiple generations to continue as such would result in the least loaded group being weeded out. Eventually, this would result in the irreversible degeneration of the genome to a point of no return as the entire species is driven to extinction. Recombination and sex evolved to combat these deleterious mutations as even a little bit of recombination can stop the cranking of the ratchet.

Geodakyan's evolutionary theory

Geodakyan (1991) suggests another interesting theory involving sexual reproduction and why it has become the most common form of reproduction over the three other ones discussed prior: asexual, hermaphrodite reproduction, and sexual reproduction. The theory is broken down into two components: the principle of conjugated systems and the theory of asynchronous evolution. The first hypothesis involves the variance produced in a sexual population in the males and females and compares the two. It has been shown in subsequent analysis that males have higher variability compared to females in humans and in other plants and animals. (Lehre et al. 2009) Geodakyan proposes then that sexual dimorphism is inherent to the development and maintenance of sex because the male acts as an experimental ground for recombination and variation whereas females function as a conservative subsystem. The second hypothesis takes these subsystems and separates them further by stating that they evolve slightly differently. The trait is first adapted to the males and then in future generations, the females. In this way, they evolve asynchronously. This theory was also described in subsequent studies (Andersson, & Wallander 2004).

Hickey's theory

Hickey (1993) helps establish an even more rudimentary aspect of sex, describing how recombination came to be. Hickey relates that conjugation, or the linking of two unicellular organisms for genetic transfer, had to be a precursor step to recombination. After conjugation, karyogamy would have to develop, and then right before recombination is meiosis. He also suggests that outbreeding is very much in line with what evolution wants and is therefore favored. By having multiple copies of a successful transposon spread within a population, it would be favored, and this ability would be kept in the genome. This somewhat relates back to the selfish gene theories mentioned prior. Sex may have evolved as a byproduct of ensuring rapid transmission of such elements, even if they cause a substantial reduction in the host's fitness (Hickey 1982). Although this explanation is sound for the initial emergence of sex, it cannot similarly explain how sex is maintained. Once selfish genes invade a population and reach a high frequency, asexual individuals should be able to propagate selfish elements just as quickly as sexual individuals. Therefore, multiple theories are needed in order to explain each facet of this paradox.

Current working theories

There is some recently emerging evidence that helps explain and expand on the early working theories. One such study helps us to understand how meiosis may have developed originally as a response to errors in spontaneous auto-ploidy or whole genome reproduction. This would combat problems like aneuploidy, gene-overexpression, or even other negative effects of polyploidy (Niklas et al. 2014). This study also asserts that the reason for the continued maintenance of sexual reproduction has to do with decreased competition between siblings via increasing variability. Although their research is incomplete in addressing everything, they do point out important ideas. A more focused hypothesis looks at the Red Queen hypothesis once again, but this time from a genetic standpoint and as a cancer prevention theory. Aubier (2020) and his colleagues point out that early multicellular organisms may have been afflicted by transmissible cancers. In this scenario, the cell line of the host will continue to generate cancer cells (also known as neoplasia). They propose that although it is difficult to be horizontally transmitted, it is easily transmitted vertically, and this is what promotes the evolution of sex through a mechanism known as similarity selection. To further elaborate, the study asserts that sexual reproduction evolved as a defensive strategy against vertically transmissible cancers, but only in certain circumstances where the host life history is slow, neoplasia is slow, and the transmission rate is high. Once that occurs though, sex can allow faster development of immunity to cancerous cell lines much like the arms race posed by the Red Queen hypothesis. Another recent study confirms the longstanding and previously discussed hypothesis that sex is beneficial and that recombination speeds up adaptation to the environment. McDonald et al. (2016) show the specific mechanisms that allow sex to speed up adaptation. Looking at sexual and asexual Saccharomyces cerevisiae populations, they arrive at the conclusion that sex alters the spectrum of mutations that fix compared to deleterious mutations can easily fix in asexual organisms. Recombination actually prevents this substantially deleterious mutation from fixing in the genome.

Summary

As is evident from the varied fields of research, there are many angles from which to tackle the evolution of sex. This review only covered a select few, including the Red Queen hypothesis, Cancer deletion theory, the Fisher-Muller hypothesis, and more. Although each question comes from and leaves on different roads, the central theme of each theory is that sexual reproduction evolved to reduce the amount of errors in the replicated genome being passed down and to increase variation in the genome to increase the chances of survival of the organism via natural selection.

Discussion

Even after many decades of research, it is still not concrete why obligate sex is so ubiquitous. However, it is clear from the findings how each facet and underlying mechanism works to a certain degree. Theories like the Red Queen hypothesis and selection interference only go so far in providing cases for the maintenance of sex in relation to its costs. They have not yet yielded models in which sex appears in a large range of biological scenarios. It is true that even in the models and papers posed in this review that constraints are put into the models which do not reflect all the possible situations. Also, we need evidence for diploid organisms that addresses both questions of origin and the maintenance of sex in order for them to be robustly answered. One of the most important tasks for evolutionary biologists is to determine all the different situations in which it would be the most conducive in making the maintenance of sex necessary for organisms. Some other direction could possibly be how multiple processes coexist and maybe even balance each other in producing both advantageous and deleterious mutations. An example could be if parasitic infections and cancerous cell lines were both generated and studied in a Red Queen model. Regardless of the direction, it is pertinent to the field that more experimental data must be generated. There are a great number of phenomena and theoretical predictions that need to be tested. The situation has seemingly gotten better over the past few years with many studies showing the advantageous sides of sex, dimorphism, parasitic co-evolution, and breaking selection interference. However, more empirical evidence is needed to showcase the main mechanisms that select for sex in nature. There were a few discussed in this review but there must be verification studies and replications to really establish these leads. It is certainly possible that a combination of theories may be the best bet in understanding the selective pressures for sexual reproduction to evolve, but most of the foundational data has been in the theoretical papers that introduced them. There should be some work done on the theoretical predictions, such as if the evolution of sex and recombination truly do lead to an increase in fitness variance. The outcomes of these studies will no doubt be providing key insights in determining what key factors are the main determinants of the evolution of sex and its maintenance.