Sex is not a solution for reproduction: The libertine bubble theory

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Introduction

Although sexual species appeared about 1.2 billion years ago [1], asexual 'species', such as parthenogenetic populations, have been clearly shown to produce more progeny. Because sexual reproduction limits the overall number of offspring, sex is known to have an evolutionary price to pay, the 'twofold cost' of sex [2]. While an asexual parthenogenetic population doubles with each generation, a sexual population has to bear the cost of males. Ultimately, with female-only offspring, the asexual lineage can grow exponentially through the generations, showing greater fitness. Thus, the maintenance of sexual reproduction continues to be an essential evolutionary issue [3]. Consequently, numerous competing theories have attempted to identify the advantages of sexual reproduction.

DNA repair hypothesis

Meiosis was first considered basically to be a 'DNA repair process' [4]. In fact, in its primitive forms, sex could favour the survival of organisms whereby 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 the 'repair and complementation hypothesis' [5, 6], genetic recombination is regarded as a response to the 'noise' that occurs when genetic information is transmitted. One chromosome can duplicate information from another, and use it to recover lost genetic information. Nonetheless, this mechanism requires that recombination leads to a repair process that should be faster than the rate of natural damage. Recombination repair systems exist in both prokaryotes and eukaryotes, but meiosis is limited to eukaryotes, suggesting that the DNA repair hypothesis is not sufficient to explain the advantage of sexual reproduction. Likewise, the ability of meiosis to faithfully transfer information from one generation to the next is affected both by low numbers of sexual partners and by a relatively high rate of unfavourable mutations.

The addition of bad transcripts tends to weaken organisms, and non-neutral mutations can reduce fitness. Based on a 'Muller's ratchet-like' mechanism, Kondrashov [7] in his mutation deterministic hypothesis alleged that sexual reproduction is a process to remove deleterious recessive mutations. As a result, by generating numerous new genotypes with a lower genetic load, sexual reproduction could be a significant advantage when there is a high rate of deleterious mutations. Nonetheless, the movement of Muller's ratchet can be associated with a substantial reduction in genetic diversity that is below the classical neutral expectation [8] and the mechanism is often considered as functioning too slowly to provide short-term benefits [9].

That said, some computer models [10] have shown the impact of Muller's ratchet to be much greater than expected, even in large populations. With recombination, the selective advantage of beneficial mutations is disconnected from neighbouring detrimental ones, thereby allowing additive effects of beneficial mutations to coalesce for their next generations.

In summary, these hypotheses have emphasised that the recombination process is very conservative, preventing gross detrimental changes in phenotype in the offspring.

Promoting variations

By contrast, another research framework emphasised the importance of generated variation to explain why sex is so widespread in nature. Sexual reproduction is said to provide a substantial advantage because it produces genetic variations through allelic recombination, whereas reproduction of parthenogenetic species is expected to result in similar genomes among descendants.

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Fisher [11] argued that the advantage of sex is the formation of variations among siblings, with new combinations of genes being beneficial in a changing environment. Ghiselin [12], with the tangled bank hypothesis, reasoned that sex benefits various siblings because diverse individuals may survive better than clones, using slightly dissimilar resources. Thus, sex proceeds in a raffle-like manner with competition among siblings, and natural selection promotes parents that can produce a wide variety of offspring. Based on the Red Queen hypothesis [13], Hamilton and Zuk [14] hypothesised that sex evolved as an adaptation to resist parasites. In fluctuating environments, previously neutral or weakly disadvantageous alleles can become favourable when faced with pathogens and parasites, increasing the intrinsic resistance of sexual species to diseases and parasites.

This obstacle, however, is not insurmountable. Aphids, for example, are capable of alternating sexual and asexual reproduction [15]. In the spring, aphids proliferate through intense parthenogenetic reproduction, producing 150 larvae in each generation. In early fall, winged sexual individuals appear and lay eggs that are able to survive through the winter. Therefore, reproductive advantages could be doubled by this cyclical parthenogenesis.

One of the limitations of the Red Queen hypothesis is linkage disequilibrium [16]. The consequences of parasite infestation have to be severe and rapid and Otto [17] argued that most parasites do not exert such a burden on their hosts. There is also a poor correlation between the conditions that favour sexual reproduction and those that favour recombination, which implies that most Red Queen models cannot be used to infer the advantage of sex over the long term [18, 19].

Overall, it seems that a sexual population would hardly be able to compete with a parthenogenetic species. First, asexual reproduction avoids wasting energy and any risk of infection and disease related to sexual interactions. Second, sexual recombination also disrupts favourable gene combinations more often than it generates them [20]. If such a pattern of diversification was observed among both sexual and asexual species, the usual theory that sex favours evolutionary diversification should be questioned. Unexpectedly, Fontaneto et al. [21] showed that asexual bdelloid rotifers have diversified into distinct evolutionary species that follow a diversification pattern similar to the one observed in sexual rotifer species.

The libertine bubbles

Although the alleged benefit of sex remains a major unsolved puzzle in evolution [17], the issue may not be solved in the current evolutionary framework where it is expected that 'sex is subservient to reproduction', and in which sex is considered more efficient than asexual reproduction. Reproduction can often occur without sex and numerous polychaeta worms reproduce using different forms of scissiparity, such as paratomy or schizogony [22].

If the concept of sex is uncoupled from reproduction, then sex could be regarded as a general process of genetic exchange between two organisms through a haplo-diploid mechanism, the meiotic phases. Reproduction subsequently begins with mitotic division during embryogenesis. Here, I propose that sex originated from an archaic gene transfer process among prebiotic bubbles. My libertine bubble theory suggests that sex results from three important primitive conditions:

(1) Bubbles form spontaneously and constitute a favourable environment for genetic material.
(2) The promiscuity of bubbles allows the transfer of genetic material among 'libertine' bubbles, gradually leading to a certain membrane selectivity.
(3) Overcrowding promotes primitive features of meiotic recombination.

Rather than a self-replication of a 'naked-gene', numerous models postulate that primitive metabolisms provided a favourable environment for prebiotic components and the emergence of genetic replication. Microspheres are bubbles that form spontaneously under primitive conditions [23]. A macromolecular polymer replication system could be encapsulated within a lipid membrane-bounded bubble and, while DNA transfer by conjugation is known as a common mechanism, naked gene transfers seem to occur very rarely under natural conditions [24–26].

According to aggregation logic, these primitive bubbles gathered and started exchanging materials. Like numerous molecules, DNA could be taken as a cell nutrient [27] so that simple trophic signals could induce gene transfer. Interactions that support the exchange of genetic material may be a mechanism through which a self-promoting element spreads genetic information per se. Bubbles that practise gene exchange would hence be advantaged because the genetic renewal favours adaptive variation.

Genetic drift means that bubbles become progressively different. The selective porosity of proto-cell membranes in contact with other proto-cell bubbles would be selected as long as the process allows the exchange and possible replication of compatible genetic material [26]. These exchanges presumably result in an increasing imbalance in the genetic content among bubbles, with some bubbles losing many genes while others develop an excess. Once inside the bubble recipient, transferred DNA fragments could avoid degradation by recombining with the genetic material and eukaryotes may have solved the problem by coating their chromosomes with histones in a nucleosome.

Meiosis and haplo-diploid cycles are fundamental sex processes that appeared very early in evolution [1]. Meiosis in protists is very similar to that of metazoans [28], suggesting that crucial features of meiosis were already present in their primitive ancestors. The primitive nucleus should have a crucial role both in replication and recombination by controlling cytoplasm reactions. Unlike the eukaryotes, bacterial recombinants are indeed non-reciprocal and fragmentary, which supports the theory that the cellular nucleus should possess a significant function in eukaryotes.

Finally, meiotic recombination in eukaryotic micro-organisms is induced by density-dependent stressful conditions, such as overcrowding [9, 29]. Thus, the genetic exchanges among bubbles that lead to meiosis could be

regarded as an adaptation for dealing with such environmental stress. In adverse environmental conditions, genetic exchanges could then renew the set of proteins, especially those implied in metabolic reactions, so that interactions among 'libertine' bubbles would be mutually beneficial.

Hence, genetic exchanges could appear as an unselected side effect of nutritional interactions [30]. However, a basic law in ecology is that organisms interact with their abiotic and biotic environments, which means that ecosystems are structured through the selection of stable interactions. The fact that interactions between two organisms are stable appears to be a sufficient condition to make these interactions evolutionarily efficient, i.e. to select bubbles that tolerate these promiscuous interactions ('libertine' bubbles) through a blind evolutionary process of self-reinforcing gene correlations and compatibility. The asymmetric nature of female meiosis selects one of the four haploid genetic elements for its own benefit, while the other three degenerate, resulting in a runaway process. Similarly, ciliates generate four haploid micronuclei, three of which also decay. By promoting unequal replication, these genes augment their own evolutionary success.

Although biochemical reactions seem to be evolutionarily conserved throughout phyla [31], greater knowledge about fertilisation molecules will be needed to understand the role of the primitive membrane and the nucleus in gene transfer. Fertilisation might derive from a 'horizontal'-like transfer of transposable elements that involves specialised cells. Meiosis, gametogenesis and fertilisation may have co-evolved from linked equivalent functions to present selective advantages at each evolutionary stage. Finally, natural selection resulted in the differentiation of two gametes, which led to anisogamy.

Anisogamy is related to the diverging interests of males and females, thus introducing sexual conflict as an inevitable consequence [32]. Therefore, while most sexual species develop some stability in their exchanges, others initiate significant antagonistic relationships, which lead to the abandonment of sexual reproduction [33, 34]. The fact that parthenogenetic species often originated from sexual species [35] and that numerous studies appear to be in favour of epigamy as being the ancestral reproductive state of polychaetes [22] supports the hypothesis that asexual reproduction in eukaryotes did not precede sex, but resulted from sexual conflict or hybridisation.

Conclusion

A negative interaction can easily act as an evolutionary dead-end as it affects the survival of one individual. By contrast, in a self-reinforcing cycle, a positive exchange can be beneficial to all the individuals involved, which emphasises the structuring force of interactions, a well-known process in ecology. In a community of proto-cell bubbles, species differences do not exist because there are no barriers to exchanges, hence rather than competition between bubbles, one might expect self-stabilising exchanges of genetic material that would – via primitive metabolism – increase in number at each exchange.

The libertine bubble theory remains very parsimonious, as it only requires that genetic material be carried from one primitive bubble to another. Bubbles that possess membrane proteins or mechanisms for exchanging genes, i.e. libertine bubbles, will tend to interact with each other more frequently than other bubbles that are less prone to such interaction, providing the former with the potential to evolve. In this context, sex should not be regarded as a solution for reproduction but as a primitive interaction.

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