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Book Review

The Origin of Sex: Three Billion Years of Genetic Recombination. Lynn Margulis and Dorion Sagan. 1986. Yale University Press, New Haven and London. 250 pp.

Margulis and Sagan explore the relationship between sex and the other developmental processes with which it is so often confused, i.e. autopoiesis, replication, reproduction, gender, etc. and compare and contrast the reasons and pathways for the evolutionary development of each. By combining data from a wide variety of sources (geology, paleobiology, microbiology, molecular biology, endocytobiology, comparative protistology, etc.) they take us through the last four billion years of the earth's history, examining the evolution of sex in the context of the environment within which it first evolved and the factors that led to its evolution. Information is drawn from all five kingdoms of organisms in an attempt to produce a truly integrated approach to this question.

The theory underlying their proposal is that eukaryotes evolved as a result of establishment of permanent relationships between endosymbiotic prokaryotes, the endosymbiotic theory. As a natural progression from this outlook, by examining the origin of sex within the context of the endosymbiotic theory, they suggest a radically new way of viewing the existence of sex. As a vertebrate biologist, it is this novel outlook and its implications that I consider to be the most exciting aspect of this work. Margulis and Sagan remind us that sex evolved over three billion years ago, and that we have often been guilty of trying to interpret the evolution of sex in terms of our current perceptions of what it now achieves.

Margulis and Sagan clearly distinguish between the concepts of autopoiesis (the self-generation, or self-maintenance of an organism throughout its life), reproduction (an increase in the number of individuals of a certain species), replication (the copying of genetic material), fertilization (fusion of gamonts, gametes or gametic nuclei), meiosis (the reciprocal of the process of fertilization in which a reduction from the diploid to haploid condition occurs) and sex (the production of a genetically new individual containing genes from more than a single source, where at least one source is an autopoietic entity). The independence of these conditions and the need to distinguish between them is clearly illustrated with examples of organism's life histories illustrating the various combinations of these conditions. Autopoiesis, for example, need not necessarily depend on reproduction; reproduction can occur without sex and a sexual event does not necessarily lead to reproduction. Furthermore, while sex in animals and plants also requires meiosis to occur, the reverse is not always true.

The authors make a fundamental distinction between the evolution of sex in the prokaryotes and the eukaryotes. Sex (the production of a genetically new individual) first evolved in the prokaryotes. It involves a different mechanism than it does in the eukaryotes, and evolved under different conditions and for different reasons than it did in the eukaryotes. This is consistent with their view that a fundamental dichotomy exists between these two groups of organisms.

The authors note the "number, complexity, and diversity of mechanisms that cells possess to repair injuries to their DNA", and from this develop their ideas concerning the evolution of sex in prokaryotes. The ability of prokaryotes to maintain and replicate accurate copies of their genetic material is considered to have evolved as part of a 'repair system'. Early in their evolutionary history these organisms would have been exposed to high levels of ultraviolet light, which is known to be strongly absorbed by and have mutagenic effects on DNA, RNA and proteins. Margulis and Sagan consider that the ability of a cell to repair its damaged genetic material would be under intense selection pressure. Damaged cells could have potentially made new copies of genetic material from undamaged material within their own cells or from an external "replicon" such as a bacteriophage. Later in the geological time period when oxygen levels increased, thereby reducing incident levels of ultraviolet light on the earth's surface, "ultraviolet repair systems were still retained in many organisms because they had become part of sexual and other systems...". Ultraviolet repair is therefore considered to have preadapted bacteria to sexuality. That the minimal source of undamaged genetic material could be a plasmid or bacteriophage explains why they define sex as only needing to involve at least one autopoeitic entity.

While sex in bacteria operates essentially at the molecular level, sex in eukaryotes required the prior evolution of structures such as nuclei and chromosomes; and the development of the processes of nuclear fusion and subsequent meiotic reduction. Mixis (the production of a single individual from two parents by way of fertilization occurring at the level of fused cells or individuals) was a further development, though not a necessary consequence of these steps.

In a stepwise function, the authors utilize the endosymbiotic theory to explain the evolution of protists, the origins of chromosomes, their deployment in mitosis and eventually in meiosis following the establishment of nuclear fusion ('fertilization'). In brief, the formation of chromosomes and their condensation during mitosis preceeded their subsequent separation along with cytokinesis (division of the cytoplasm). The fusion of nuclei is considered to have preceeded the process of meiosis, the necessary reduction division following fertilization. Fertilization itself is considered to have evolved as a result of cannibalism that resulted in nuclear incorporation rather than digestion. Examples of cannibalism in some hypermastigotes, leading to fusion between the nucleus of the ingested protist with that of the nucleus of the organism that ingested it are cited as evidence for the viability of this step having occurred in the evolution of sex.

Chromosome separation is itself linked to the presence of microtubular organising centers (MTOC's) in the cell and throughout this book the authors stress the importance of these centers and their significance to the theories

developed here. MTOC's are the organising centers or genetic basis for centrioles, kinetosomes, kinetochores and the asters in eggs. These centers are thought to be the remnants of spirochete genomes. Kinetosomes and centrioles for example are interchangeable within the cell and are thought to have had the same evolutionary origin. The subsequent influence of MTOC's on the development of eukaryotes, by allowing mitosis and meiosis to occur, has obviously been profound.

Meiosis is considered to have evolved from the mitotic process, as a result of a delay in the replication of the microtubule organising centre along with the segregation of homologous chromosomes. The synaptonemal complex is thought to have evolved to ensure the segregation of homologous chromosomes, the tendency of homologous proteins to pair being itself a remnant of the repair mechanisms of their prokaryote ancestors. The authors then develop the theory that the chromosome pairing aspects of Prophase I are a necessary step to achieve tissue differentiation in plants and animals. This claim, while one of the most exciting concepts in this book, is unfortunately one of the least convincing. This is due in part to the authors continually using the general term meiosis in reference to tissue differentiation, when it only becomes obvious by the end of this section that it is the more specific chromosome pairing aspects of Prophase I to which they refer. The authors note that 'meiosis' is thought to occur in all organisms with complex tissue differentiation (plants and animals) even though sex itself may be lacking. The chromosome pairing aspects of meiosis are seen as a necessary step to achieve tissue differentiation. Hence the concept that meiosis and tissue differentiation cannot be separated in these eukaryotic groups, and Margulis and Sagan predict that the events of Prophase I of meiosis should be found to occur in all plants and animals if their theory is correct. Biparental sex (mixis) therefore did not arise because of any immediate evolutionary advantages it conferred, but rather arose as a consequence of selection for organisms whose existence is owed to meiosis/tissue differentiation. Sex is not a necessary part of tissue differentiation and was never selected for directly.

Although a plant or an animal can secondarily lose its sexual ability, by hypotheses it can never forego the chromosome pairing aspects (meiotic Prophase I) of meiosis. While the reduction division of meiosis is a necessary correlate of a life cycle that alternates its ploidy, this reduction aspect should be considered independently from the earlier chromosome pairing stage of Prophase I. Pairing of homologous chromosomes is known to occur independently of the reduction phase of meiosis in both plants and animals (Stack and Brown, 1969).

Although the theoretical evidence seems plausible, specific data referring directly to answering this question are unfortunately limited. Even absolute proof that the chromosome pairing aspects of meiosis were universal in plants and animals would only be consistent with, not confirmation of, their theory. The existence of ameiotic animals do not therefore refute this proposal, if chromosome pairing processes were found to be occurring at some stage in their development. However, as noted earlier, the distinction between these two stages of meiosis, and the importance of this distinction is not clearly presented in the text; and the authors must take some of the blame for why critics are presenting the existence of ameiotic animals as evidence refuting

their theories of tissue differentiation (i.e. Maynard-Smith, 1987).

In an attempt to illustrate the interactions between the original symbionts making up the eukaryotic cell, and their influence on tissue differentiation, the authors are forced to resort to the use of what they consider to be an analogous system, a forest community. Unfortunately I do not feel that this analogy achieves what they are attempting and does little to clarify their arguments. It is not necessary, and I feel it detracts from the argument as a whole. Noting that only a small amount of data is presented to support the link between meiosis and tissue differentiation, however, is not a direct criticism of this work as such, but rather serves to illustrate the limitations under which they are acting. In view of the implications of this proposal, especially in discussions concerning the evolution of sex in vertebrates, it would seem an urgent area for research.

Further, they cite evidence suggesting that sex through meiosis is not the great source of genetic variation as was originally thought. The basic problem faced by organisms here is considered not to be the generation of such variation, but rather controlling such variation. They note that the predicted correlations between the occurrence of sexual reproduction and environmental variability have not been substantiated. They consider sex "to be as much a sink of variety as it is a source." The need to distinguish clearly between the evolution of and the maintenance of sex is well illustrated here.

One minor concern is the contents of the chapter entitled "Big Eggs and Small Sperm. Origin of Anisogamy and Gender". The fascinating possibility that asymmetrical cell morphogenesis is associated with the acquisition of movement is mentioned, but unfortunately is not developed further as a possible solution with regards to the question of the evolution of anisogamous gamestes. Although this chapter is headed "Big Eggs and Small Sperm" and discusses the isogamous and anisogamous conditions, as well as commenting on why the motile gamete may be smaller (which is not always the case; either in volumetric or liner dimensions) it does not really address the question of why anisogamy should have evolved at all.

One of the earliest consequences of the linking between meiosis and tissue differentiation in multicellular organisms is claimed to be the independent origins of gamonts (an organism capable of entering a sexual encounter) and anisogamous gametes. The trend from isogamy to anisogamy supposedly happened many times, and determination of gender (sex determination) appears to be polyphletic, repeated over and over many times. An interesting aspect of this is the consequences of what exactly determines a 'male' or a 'female' and how comparable the two are. What is obvious is that the terms male and female are probably only functional definitions, based on relative gamete size and locomotory ability. I might even go so far as to question the theoretical basis underlying comparisons between males or females of different species, especially in situations where the male can either be the heterogamous or the homogamous sex (i.e. birds). If, for example, maleness is defined as the heterogamous sex, then in birds it is the male that lays the eggs and the female that produces the sperm. As mentioned by these authors, the fact that several mating types are present in populations of the ciliate *Paramecium multimicronucleatum*, which can change mating types through-

out the day, further serves to illustrate the variability that can exist around the concept of gender differentiation. I consider this important discussion on the concept of gender to be one of the most significant parts of this chapter; however, the relevance of the section on gamete size I do not see as essential to, or as having been clarified by this book.

This book is aimed at "everyone interested in evolution", and succeeds in organising a large amount of information from a variety of sources into a form that we can assimilate. Throughout the book the authors continually suggest critical areas of examination that could lead to the clarification, rejection and/or acceptance of their ideas, and they are to be commended for this. The book is well-indexed and most importantly, contains a substantial and up-to-date reference list. The glossary aids interpretation of the terminology used, but the authors will probably be disturbed to find that the term 'flagella' is not included here. This is unfortunate considering the importance of maintaining the distinction between the prokaryotic flagella and the eukaryotic undulipodia.

In summary, by looking at the emergence of sex in terms of its components and the steps leading to its development over the entire evolutionary history of those organisms that utilize it, and by relating it to the environments experienced by the organisms at the time they developed it, these authors have not only given us a new and exciting scenario for the evolution of sex, but have also provided us with critical ways in which we can test their hypotheses. It would seem that too often we have been guilty of looking at the sexual process in vertebrates alone, and on the basis of what we perceive it to be achieving now (whether our perceptions are correct or not), infer that this was the reason for its evolution. Further, it would seem that from a vertebrate viewpoint, with regards to the question of the origin of sex, we have been looking at a data set that is three billions years out of date.

Irrespective of whether we are immediately convinced by Margulis and Sagan's arguments, the ramifications of their theories, if correct, are so widespread that we must take account of what they are proposing and explore their suggested tests to validate or refute them. As to the much asked question by vertebrate biologists "Why is meiotic sex so prevalent?", the answer from Margulis and Sagan is simple. Meiosis is an integral part of tissue differentiation in plants and animals and cannot be separated from it, although "uniparental" versus "biparental" sex can be dissociated. The question as worded is therefore intrinsically contradictory. As a result of ideas presented here it would appear that we must modify even our most basic approach to the evolution of sex. This is a stimulating book that is sure to invoke criticism and discussion; I strongly recommend it.

REFERENCES

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