J. Genet., Vol. 67, No. 1, April 1988, pp. 63–66. © Printed in India.

BOOK REVIEW

Origins of Sex

by LYNN MARGULIS and DORIAN SAGAN. Yale University Press, 13 Bedford Square, London WC1B 3JF, UK, 1986. Price: $35.00.

Bacteria are asexual creatures with an undifferentiated cytoplasm which reproduce by simple binary fission after replicating their single naked DNA molecule. Recombination is an infrequent event involving the partial replacement of the DNA in one organism with complementary DNA from another; it probably serves to repair certain sorts of genetic damage, since strains which have lost the capacity to recombine become very sensitive to mutagens such as ultraviolet light. Eukaryotes evolved as communities of prokaryotic cells, with mitochondria and chloroplasts descending from endosymbiotic bacteria and even now retaining a certain measure of autonomy. The origin of the nucleus remains an unsolved problem, but the characteristic mobility of eukaryotic chromosomes in mitosis and meiosis is derived from another category of endosymbionts, descending from spirochaetes. Their contribution is most clearly seen in the structure of the eukaryotic flagellum. However, the Microtubule Organizing Centres, self-replicating bodies responsible for the orderly movement of chromosomes on the spindle, are also remnants of an ancient symbiosis with spirochaetes. Both the cytoplasmic structure and the nuclear behaviour of eukaryotic cells can therefore be seen as the outcome of the dynamics of a community of prokaryotes, in the light of an expanded theory of serial endosymbiosis.

This is the hypothesis developed in the first half of the book by Margulis and Sagan. It is a bold and speculative hypothesis; they certainly do not succeed in establishing it beyond doubt, but it performs the first duty of a good theory in deriving clear and simple relationships between previously unconnected facts from a general principle. It is coupled with an exceptionally lucid sketch of the major groups of protists, showing how a fresh vision can bring order and interest to the senseless smorgasbord served up in most treatments of the group. So far, so good; in fact, exceedingly good – this is a book that kept me up until late, wanting to know what the next chapter would say. But it is at this point that the text begins to slip a little out of focus; and by the end of the book, the argument has dissolved entirely into a hazy sequence of ill-conceived and often erroneous paragraphs on the evolution of sexuality among unicellular and multicellular eukaryotes. This collapse is all the more startling because of the excellence of the preceding discussion; yet it is in a sense inevitable, for both the vigour and clarity of the first part of the book and the muddle of the latter stem from the same source – an emphasis on historicity, and a contempt for functional and adaptive explanation.

Margulis and Sagan argue that the first step in the evolution of sexual processes is indigestion – cannibalism followed by failure to assimilate at least the chromosomes of the victim. This is a familiar idea, and since protists must be resistant to their own digestive systems it is not inherently implausible. Under what circumstances will doubling-up the genome be favoured, and thus likely to become incorporated as a regular event in the life cycle? Although much less attention has been paid to the alternation of generations than to sex or gender, a number of theories have been put forward. There are ecological theories, which argue that haploidy is cheap, and will be favoured when nutrients, especially N and P, are scarce (Lewis 1985); or alternatively that large size and consequently diploidy enable organisms to resist starvation with haploidy being an *r*-selected strategy adopted under favourable conditions (Cavalier-Smith 1978 – loosely speaking, this is the argument favoured by Margulis and Sagan). Some genetic theories refer to the additive genetic variance, and argue that evolution will be faster in diploids because of their greater rate of favourable mutation per genome (Paquin and Adams 1983); or that it will be slower, since diploidy masks unfavourable mutations, at the eventual expense of a higher load (many authors, e.g. Crow and Kimura 1965). Others refer to the dominance variance, and argue that diploidy is favoured because of heterosis (Raper and Flexer 1970); or to the epistatic variance, suggesting that diploidy creates more variation among vegetative individuals (Svedalius 1927) or among gametes (Bell 1982). Finally, there are developmental theories which claim that diploidy is in some unspecified manner required to construct a complex soma (Maynard Smith 1978). Some of these ideas are more plausible than others; some have been investigated by comparative or experimental techniques and others not; some could be satisfied by heterokaryosis or gene duplication rather than diploidy and others not; Margulis and Sagan simply ignore the lot of them, and assert that cannibalism will occur when nutrients are scarce.

Given that doubling-up the genome is advantageous under some circumstance, it will be equally advantageous to halve it again under others. A regular syngamy-meiosis alternation of generations evolves as a way of ensuring the production of balanced genomes in organisms which have previously evolved mitosis. However, Margulis and Sagan proceed to argue that meiosis is further necessary for somatic differentiation. I do not completely understand their argument, but they seem to be saying that morphological complexity requires a complex genome, which will require continual re-checking, which can only be done in the haploid state. This argument does not refer to recombinational repair – recombination is viewed as an interesting but unnecessary elaboration of meiosis – and it is not explained clearly why diploid genomes cannot be proofread. But there are many entirely non-meiotic animals and plants which develop normally. Asexual lineages may often be short-lived in geological time, but there is no reason to believe that this is caused by a failure to develop properly. Indeed, the only consistent type of morphological deterioration reported from asexual animals is the increased variability or gradual disappearance of the sexual system, as one might expect. Moreover, there is at least one major taxon of completely asexual metazoans, the bdelloid rotifers, which, judging from its abundance and diversity, has not arisen recently – and yet which has not only a highly differentiated soma but also strictly determinate development.

The authors now strike out into even deeper water.

> "Mixis was never selected for directly. An inordinate amount of data has been collected in attempts to prove the selective advantage of mixis, especially in animals living in unstable environments (Bell 1982). No such conclusion is available from the evidence: neither in constant nor in varying environments can mixis be shown to confer selective advantage over amictic (nonsexual) life cycles".

There are two major misconceptions here. In the first place, it has been very clearly established that both the incidence of sexual life cycles and the mixis achieved by these cycles vary consistently with ecological correlates such as habitat, latitude, population density and life history. An adaptive theory of sex is therefore required. Secondly, the statement that this information has been collected in an attempt to show that mixis is adaptive in unstable environments is a complete misreading of the modern literature: the major result of recent comparative work is that mixis is associated with *stable* physical environments, characterized by heterogeneity, age, lack of disturbance, high species diversity and intense interaction within and between species.

This confusion is further confounded when they discuss the loss or lack of sex in endosymbionts, in contrast to its persistence in endoparasites. Both I (Bell 1982) and Hutson and Law (1983) have used such patterns as support for the idea that recombination is favoured in negative species interactions because the cyclic selection thought to occur in such systems requires continual shifts in the sign of the correlation between nonallelic genes; in positive species interactions, both partners wish to conserve successful combinations of genes and recombination is deleterious. Margulis and Sagan simply treat this as an instance of the old idea that sex is favoured in changing environments, dismiss the (rather impressive) comparative evidence, and return to their previous notion that parasites need sex because they are morphologically more complex than endosymbionts.

Ironically, Margulis and Sagan do not invoke morphological complexity in the one case where there are strong grounds for believing it to be an important factor. There is quite a large literature, stemming from a paper by Parker *et al* (1972), which interprets gamete dimorphism (anisogamy) as the outcome of disruptive selection arising from the nonlinear response of viability to zygote size; since large zygotes are likely to be more important to large and complex organisms whose early development draws on zygotic reserves, a correlation of anisogamy with large size and vegetative complexity is anticipated. Reducing the locomotory costs of microgametes and increasing the storage lifespan of resistant zygotes may be contributory factors whose inclusion complements and strengthens the elementary model. In the chapter on anisogamy, as in the previous chapters on diploidy and mixis, Margulis and Sagan maintain an unbroken silence on the last quarter century of theoretical, comparative and experimental work on genetic systems.

The really valuable contribution made by Margulis and Sagan is their insistence that underlying the evolution of genetic systems is the evolution of the constituent mechanisms of mitosis and meiosis, and therefore the evolution of the cellular structures which direct them. This is a point well worth making, and is well made. Their account falters and finally fails because they attempt to reconstruct evolution virtually without reference to adaptation. Since about 1965 our understanding of how genetic systems evolve has advanced at an unprecedented pace, and now represents one of the most exciting areas in modern biology. None of this excitement comes through in Margulis and Sagan's book; the ideas are not discussed, and the literature is not cited. I heartily recommend the first eight chapters to anyone interested in evolution. But as for the last five chapters . . . a hundred pages without Darwin is too much.

Department of Biology
McGill University
1205, Docteur Penfield Avenue
Montreal, PQ
Canada H3A 1B1

GRAHAM BELL

References

Bell G 1982 *The masterpiece of nature* (London and Berkeley: Croom Helm and University of California Press)

Cavalier-Smith T 1978 *r*-and *K*-tactics in the evolution of protist developmental systems: cell and genome size, phenotype-diversifying selection, and cell cycle patterns. *Biosystems* 12: 43–59

Crow J F and Kimura M 1965 Evolution in sexual and asexual populations. *Am. Nat.* 99: 439–450

Lewis W M 1985 Nutrient scarcity as an evolutionary cause of haploidy. *Am. Nat.* 125: 692–701

Maynard Smith J 1978 *The evolution of sex* (Cambridge: University Press)

Paquin C and Adams J 1983 Frequency of fixation of adaptive mutations is higher in evolving diploid than haploid yeast populations. *Nature (London)* 302: 495–500

Raper J R and Flexer A S 1970 The road to diploidy with emphasis on a detour. *Symp. Soc. Gen. Microbiol.* 20: 401–432

Svedalius N 1927 Alternation of generations in relation to reduction division. *Bot. Gaz.* 83: 362–384