

Evolution

Contemplating life without sex

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FROM the selfish-genetic point of view, there are obvious advantages to parthenogenesis. A gene that suppressed meiosis in female diploids would be transmitted to all female offspring instead of only to half and thus would, all else being equal, double in frequency in each generation. Why then, does parthenogenesis not replace sex? The answer has to be that all else is not equal. Why not? One good reason for studying parthenogens is for the light they may shed on the evolution of sex, and the problems of parthenogens were the topic of a recent symposium* from which it is clear that for one reason or another it is very difficult to give up sex once you have it.

Most existing parthenogens have evolved from sexual forms and are hampered to varying degrees by the persistence of mechanisms appropriate only to their ancestral lifestyle. As so often, the fruitfly *Drosophila* provides a good example. Females of many species lay an occasional egg that develops without fertilization. But it is a long way from the occasional egg to functional parthenogenesis (A. Templeton, Washington University, St Louis). Parthenogenetic laboratory strains now exist in several species, including *D. melanogaster*, but it took much selection to establish them. Before selection, unmated females lay few eggs, and even fewer start development. Of those that do start, most die because of genetic homozygosity resulting directly from the mechanism of parthenogenesis. The mechanism is known as automixis: the egg undergoes meiosis, and diploidy is restored by the fusion of two of the four products. Because natural populations carry many deleterious recessive genes, automixis results in heavy mortality. The only species which is parthenogenetic in nature, *D. mangabeiri*, has overcome this problem in an ingenious way. First, the two haploid nuclei that fuse are those that are separated at the first meiotic division; second, there is no crossing over. Together these devices ensure that the offspring are genetically identical to the parent: heterozygosity is preserved. Crossing over is prevented by inversions.

The picture that emerges from these studies of *Drosophila* is probably typical. The disadvantages suffered by recently arisen parthenogens are the direct result of their sexual ancestry; but these 'sexual hang-ups' can be overcome by selection. The precise means of overcoming them varies. Some parthenogenetic animals, and many plants, opt for abandoning

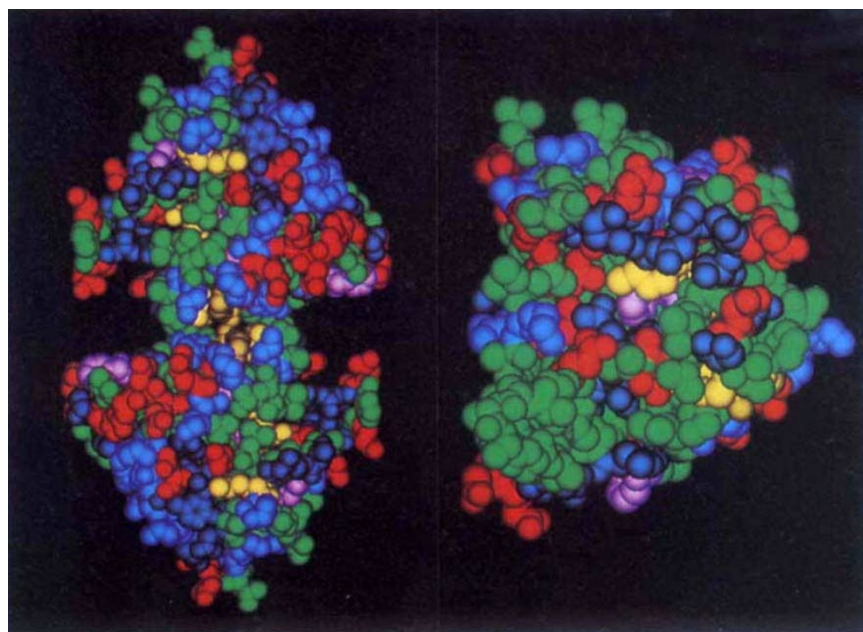
meiosis altogether — apomixis; this is the pattern in the cyclically parthenogenetic aphids and cladocerans. Alternatively, in the parthenogenetic lizards of the genus *Cnemidophorus*, there is a premeiotic doubling of the chromosomes, followed by the pairing of sister chromosomes in the first meiotic division. This has the same genetic consequence as the meiosis of *D. mangabeiri*: offspring are genetically identical to their parents, and do not suffer the enforced genetic homozygosity that is the usual result of automictic parthenogenesis. The parthenogenetic species *C. uniparens*, which is a highly heterozygous species hybrid, consists of a single clone: members of the species accept scale grafts from each other.

Another common type of sexual hang-up in parthenogenesis is the persistence of the need for sperm to trigger development — pseudogamy (that is, the stimulation of egg development by a sperm whose chromosomes do not participate in forming the new individual).

In some lower vertebrates (discussed by H. Hotz and T. Uzell, University of

Illinois and R.C. Vrijenhoek, Rutgers University), the sperm is probably needed to provide a centriole. (No such need, however, exists in lizards.) Pseudogamy is not uncommon in insects. In plants, a nucleus from the pollen tube may be needed to fertilize the endosperm, even if the embryo is parthenogenetic. Some parthenogenetic frogs (*Rana*) and fishes (*Poeciliopsis*) have evolved what is perhaps the strangest mechanism of all for dealing with this requirement. It is known as hybridogenesis. *Rana esculenta*, for example, is a hybrid between two sexual species, *R. ridibunda* and *R. lessonae*. In the germ line, *lessonae* chromosomes are thrown out, so that the egg contains only the *ridibunda* component. If, as is typical, the hybrid female mates with a *lessonae* male, the hybrid *R. esculenta* is reconstituted. Clearly, pseudogamous and hybridogenetic forms cannot wholly replace their sexual ancestors. In some major taxa, for example mammals and gymnosperms, parthenogenesis has not been reliably recorded, but the nature of the hang-up is not known.

Despite the widespread occurrence of sexual hang-ups there are many parthenogens that seem to have escaped the disadvantages derived from their sexual ancestors. The taxonomic distribution of parthenogens, however, suggests that they may be successful in the short run,



THESE three-dimensional views of β -lactoglobulin show two identical monomers tenuously linked. Each monomer is similar to plasma retinol-binding protein and each contains a non-polar pocket similar to that occupied by retinol in retinol-binding protein. The non-polar pocket is in the centre of view in the right-hand figure. The function of β -lactoglobulin, a milk protein, has long been unknown; these new models suggest that it is a transport protein. The structure is described in more detail by M.Z. Papiz and colleagues from the Universities of Leeds, Edinburgh and Uppsala, on pages 383–385 of this issue. The colours represent different types of amino-acid residue: red, acidic; dark blue, basic; light blue, polar; purple, aromatic; yellow, sulphur-containing; green, non-polar. Computer program by Dr H. Nakamura. □

*A meeting on parthenogenesis organized by L. Kirkendall and N.C. Stenseth at Finse, Norway, 17–22 September 1986.