

Isa Schön
Koen Martens
Peter van Dijk
Editors

Lost Sex

The Evolutionary Biology
of Parthenogenesis



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Lost Sex

Foreword

The idea to compile this book was first raised during an Exploratory ESF workshop in Wageningen in 2001. At that meeting, it was thought that it should provide the long-needed update on parthenogenesis and its genetic and ecological consequences, but that it should also look at the paradox of sex from an asexual perspective. Already then, it was decided to only focus on eukaryotes, as this would avoid discussions on whether bacteria have sex or not. . . The book would thus deal with these evolutionary opportunists that had given up or lost sexual reproduction. We also wanted to make sure that both animals and plants were included and to help the zoological and botanical communities in understanding each other. When ESF funded the proposal of PVD and KM for a scientific network on parthenogenesis, (PARTNER) we started hunting for authors and contributions during the four PARTNER workshops in 2003 (Wageningen), 2004 (Valencia and Münster) and 2005 (London). This is why most authors of this book have also been participants of one or several PARTNER workshops, and this book can be seen as an ESF deliverable. However, there are also contributions from authors outside of PARTNER, which have added additional expertise to this book. Their contributions also illustrate that the field of research on parthenogenesis is currently moving very fast.

The book contains five parts. The first one consists of the introduction to the theme (see Chapter 1) to catch the reader's interest and its history by concentrating on four major scientists who have significantly contributed to the field (Chapter 2). The general part also comprises the necessary descriptions of the cytology and the mechanisms related to the different asexual and sexual modes of reproduction in plants (Chapter 3) and animals (Chapter 4). In Chapter 3, great care has been taken to explain the botanical terminology of parthenogenetic reproduction and potential pitfalls are pointed out, which have greatly hampered the discussion between zoologists and botanists on asexual reproduction in the past.

The second part of the book discusses the main hypotheses behind the paradox of sex and how modern science regards them. Although there are more than 25 hypotheses attempting to explain the paradox of sex, we have decided to concentrate on four major ones. Is the accumulation of mutations (Muller's ratchet (Muller 1964) and Kondrashov's hatchet (Kondrashov 1988)) still regarded as one of the major problems of long-term asexuality and if so, under which conditions might it apply to the real biological world (see Chapter 5)? What is the reaction norm of

asexuals? Can the general-purpose genotype and frozen niche hypotheses indeed be found in biological reality (Chapter 6)? Is the Red Queen still in the running as one of the major theories to explain the prevalence of sex (Chapter 7)? And if so, what are the conditions that have to be matched? Chapter 8 deals with the phenomena of geographic parthenogenesis and presents a new theory on how hybridisation could have caused the patterns in both plants and animals.

The third part of the book deals with more philosophical questions, which have nonetheless a practical impact on working with asexuals: how can clones (Chapter 9) and asexual species (Chapter 10) be defined? It is our hope that readers will find workable solutions in both chapters.

The fourth part comprises numerous case studies, illustrating the enormous variety of mechanisms by which asexual plants and animals reproduce in the living world. The first set of case studies includes examples of putative ancient asexual scandals (following the terminology of Judson and Normark 1996) from the animal world, namely darwinulid ostracods (Chapter 11), oribatid mites (Chapter 12) and bdelloid rotifers (Chapter 13). The surprising conclusion seems to be that none of these so-called scandals has followed the same route in avoiding the long-term disadvantages of asexuality, and that each of them might have found a novel way to circumvent the paradox of sex. There appears to be a general consensus that there are no ancient asexual plants (see Chapter 3).

The three scandalous chapters are followed by a number of items on invertebrates with mixed reproduction. These include examples of cyclic parthenogenesis, namely monogont rotifers and cladocerans (Chapters 14 and 15, respectively), which combine the best of both worlds and provide important insights into the factors triggering the switch between sex and asex. Also, stick insects with an amazing variety of reproductive modes (Chapter 16) are described, followed by examples of Hymenoptera, where microbial infections are one of the most common causes of asexuality (Chapter 17). The last invertebrate case study is on hermaphrodite planarians with asexual reproduction, but also with a little bit of sex (Chapter 18). The invertebrates are followed by vertebrate examples of parthenogenesis, covering fish (Chapter 19), waterfrogs (Chapter 20) and reptiles (Chapter 21). All three chapters provide good explanations on the mechanisms of vertebrate parthenogenesis and why it is less common than in invertebrates.

Two case studies on apomictic plants, the common dandelion (Chapter 22) and Böcher's rock cress (Chapter 23) close the section on case studies. Both author teams provide new, unpublished data on the evolutionary age of an apomixis gene (Chapter 22) and the Meselson effect, respectively (Chapter 23).

Last comes a section on applied aspects of parthenogenesis, a novel and important part. The section starts with examples of asexual diseases and why their reproductive mode poses a major threat to humanity (Chapter 24). The next chapter introduces aphids as agricultural pest and links their detrimental effects with their asexual reproduction. Chapter 26 explains why cloning of mammals is still so unsuccessful and how it can be improved. The last Chapter, 27, deals with clonal grape vines and its implication on wine making.

This last chapter provides the perfect excuse to raise the glass to all authors and readers and to wish them a very fruitful and enjoyable reading – may the bouquet be rich, the flavour be crisp and the finish be lasting!

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Chapter 1

Asex and Evolution: A *Very* Large-Scale Overview

Bengt O. Bengtsson

Abstract Asexuals come in all sorts. In this personal overview, I identify asexual organisms with eukaryotes that do not regularly go through the meiotic cycle. Such organisms may be asexual in many different ways and of many different reasons. The spread of asexuality is therefore always a unique process, and any notion of a general evolutionary advantage for asexuality is at best misleading. In discussions on the evolution of asexuality, ideas about genetic conflicts are often more helpful than notions about “costs”. Many asexuals are associated with different fitness problems, and most of them are not particularly good at being asexual either. Their absence of long-term evolutionary success follows from their lack of recombination, leading to complex effects involving drift and selection that we are just beginning to understand. The interest in asexual organisms comes not from what they say about sex, but from what they say about living as a eukaryote.

1.1 Eukaryote Reproduction and the Meiotic Cycle

The asexual organisms that will be discussed in this chapter have one thing in common: they have all dropped out of the regular meiotic (sexual) cycle. In this they differ from the majority of eukaryotes in which meiosis and fertilization occur regularly. Among the large multi-cellular organisms that make up our visual natural environment – plants, animals and fungi with large fruiting bodies – the cycle is often easy to follow and study, with its prominent outer signs of sexual and reproductive activities. But the meiotic cycle predominates also among the small unicellular eukaryotes about whose lives we often know very little.

Regular meiotic sexuality evolved once, a long time ago. According to recent phylogenetic information, there are strong reasons to believe that the meiotic cycle

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developed at the origin of eukaryotes or very soon thereafter (Cavalier-Smith 2002). It cannot, of course, be excluded that one day we will find a eukaryote that departed from the “ur-eukaryote” lineage before meiosis evolved, but no such organism is currently known. Meiosis must have had a complex evolutionary history leading up to it, and some more or less alternative variants for decreases in ploidy-numbers have been characterized and discussed (Pontecorvo 1958; Haig 1993; Hurst and Randerson 2000). However, meiosis constitutes by far the most common mechanism for the separation of homologous genomes, and it functions in basically the same way wherever found, down to its most intricate cellular and molecular details (John 1990; Raikov 1995; Cnudde and Gerats 2005; Ramesh et al. 2005).

If the meiotic cycle is common to almost all eukaryotes, this does not mean that it always looks the same. Its basic structure of fertilization (with cell and nuclear fusions), diploid cellular life, meiosis, haploid cellular life, back to fertilization and a new round of the cycle, has taken on an almost infinite number of forms during eukaryote evolution. Careful investigations are often needed to ascertain exactly when, where and how the key events in the process occur. In humans, the length of the diploid state is measured in decades while the haploid state passes in hours. In mosses, the haploid state dominates and the diploid state is an ephemeral outgrowth extending from the top of a long-lived haploid structure. In aphids, after meiosis and fertilization there are rounds of asexual reproduction before meiosis occurs again. In the unicellular organism *Paramecium*, meiosis/fertilization occurs separately from reproduction/multiplication, which comes about via ordinary mitotic cell division. The last example is rare, however, since in most sexual organisms reproduction and dispersal is closely associated with the events of meiosis, gamete formation and fertilization.

Sometimes, the sexual cycle has become elaborated with new structural elements, as illustrated by the evolution in higher plants of a system for *double* fertilizations, where the sole use of the endosperm is to help regulate and support the development of the embryo.

Another way sexual organisms differ is in the appearance of the haploid cells produced by meiosis and intended for fertilization. In animals and plants, a clear division has evolved between small motile “male” gametic cells and large nutrient “female” gametic cells. This morphological distinction is often extended back to the individuals that produce these cells – thus many animals and some plants are segregated into males or females also during their diploid stage. Among the organisms that produce haploid gametes of both kinds (called hermaphrodites), yet other variants become possible. Fertilizations may occur between gametes produced by the same individual (selfing), or between gametes formed by different individuals. In general it appears as if outbreeding, of one kind or another, is the most common mode of reproduction in eukaryotes, and many mechanisms – ranging from cellular surface markers to the manipulation of pollination vectors – have evolved to promote it.

Thus, the underlying structure of the meiotic cycle seems not to have limited the morphological and behavioural evolution in sexual eukaryotes to any noticeable