Scientific Report of the ESF Exploratory Workshop on

PARTNER - PARThenogenesis NEtwoRk

A future network on the ecology and evolution of asexual reproduction.

held at Wageningen, The Netherlands, 5-8 October 2001

Organisers:

Peter van Dijk & Koen Martens

7-12-2001

Contents:

Executive Summary

Why sexual reproduction is so common in plants and animals remains one of the grand mysteries in biology. Sexual reproduction is a costly and inefficient process. Although sexual reproduction may have long-term advantages (e.g. faster adaptation), there are important short-term disadvantages, such as the cost of producing males, the breakdown of co-adaptive gene complexes and the costs and risks connected with finding mates. Consequently, an asexual mutant arising in a sexual population should rapidly take over a sexual population, leading to a world without sex. However, in reality sexual reproduction is very common and asexual reproduction (parthenogenesis), is relatively rare. This contrast between theory and practice is known as the Paradox of Sex.

Some 30 years ago, biologists became very much aware of this paradox. This has led to a bloom of theoretical models, looking for short- and long term benefits of sexual reproduction that could balance its costs. Such theories, explaining the advantages of sexual reproduction, focus on, for example, arms races between host and parasites (Red Queen hypothesis) or on the accumulation of deleterious mutations in asexual organisms (e.g. Muller's Ratchet). Nevertheless, to date the Paradox of Sex remains largely unexplained. This may be may be due to: (i) lack of biological realism of the models (ii) insufficient empirical work (iii) relative neglect of asexual organisms.

A relatively small number of plants and animals reproduces obligatory or facultatively asexually. When such asexual organisms seemingly do not experience the disadvantages mentioned above, such theories can be rejected. On the other hand when asexual organisms have developed special adaptations to avoid or counter such negative effects, the importance of these factors for the maintenance of sex will be corroborated .

Research on asexual organisms thus provides alternative opportunities to solve 'the queen of problems in evolutionary biology'. The availability of molecular techniques makes it now possible to explore questions that could not be explored before. With DNA fingerprinting, clonal diversity can be assessed with high accuracy. This makes it possible to study the dynamics of clonal diversity. Very long periods of asexual reproduction will be reflected in elevated levels of allele sequence divergence, which therefore becomes a tool to detect ancient asexuals. Accumulation of deleterious mutations, as predicted by some hypotheses, can now be investigated directly at the DNA level. In addition, the relevance of asexual reproduction for society increases with every plan to engineer new apomictic crops and every step closer to commencing artificial cloning of animals.

A considerable number of European research groups study the evolution and ecology of asexual organisms. However, traditionally this field is strongly divided into taxonomic, habitat- and technique-oriented sub-fields. This isolation has, for instance, led to the development of different terms for the same processes in plants and animals. This non-standardised and unnecessarily complex terminology has created barriers for communication, not only between empiricists, but also between empiricists and theoreticians. Consequently, theories often lack sufficient biological reality to be rigidly testable. If parthenogenesis researchers in Europe want to benefit fully from the new molecular analytical tools that now become available and if they want to fulfil their role in guiding new bio-technological developments in the field of asexual reproduction, they will have to leave their traditional sub-fields behind and unite in a scientific network.

In order to stimulate communication and collaboration between the various sub-fields in parthenogenesis research, an exploratory workshop under the auspices of the European Science Foundation, was held from 5-8 October 2001 in Wageningen, the Netherlands. This workshop brought together zoologists, botanists, microbiologists, mathematicians, paleontologists and agronomists, representing nine different ESF member states. The aim of this workshop was to explore the possibility to establish an ESF network on parthenogenesis.

The workshop started on Saturday morning. After a welcome and short introduction by the two organisers, Dr. Peter van Dijk and Dr. Koen Martens, the senior scientific secretary of LESC, Dr. Martina Hildebrandt, gave an overview of the ESF organisation and its scientific activities. Next, all participants gave a short presentation of their research. The diverse presentations reflected that Europe significantly contributes to the research in this field. It also was very clear that botanists and zoologists are often interested in similar phenomena (e.g. geographic parthenogenesis, ancient asexuality). The second part of the Saturday afternoon was used for discussions. It was unanimously agreed that a European network would be very important for the advance of the research field. The following objectives of such a network were formulated:

- To promote effective cooperation between European scientists working on asexual reproduction, bridging the gaps between theoreticians, field biologists and experimental researchers in different taxa.
- To strengthen critical scientific mass in Europe, thus bringing Europe to the forefront of the global scientific community and strengthening Europe's position as a competitor on the international forum
- To contribute to a synthesis of our scientific knowledge on the evolutionary biology of asexual organisms, by combining theoretical and empirical knowledge, and new information coming from other disciplines, such as molecular, cell and developmental biology.
- To train young scientists in the interdisciplinary approaches, specifically in those required in the field.
- To unify the terminology of asexual reproduction, incorporating new information on mechanisms and effects, in order to improve the scientific communication of concepts and ideas.
- To detect the applied and social implications of the past and expected developments in the field, and to disseminate these implications in documents accessible to a wide range of social actors and policy makers.

To meet these objectives, a number of different activities were suggested. The organisation of four interdisciplinary workshops dedicated to pressing questions of asexual reproduction was deemed most relevant. Such workshops would offer ideal forums for the exchange of facts, ideas and opinions on an international, European scale between scientists from different disciplines. The following themes for the workshops were chosen:

(i) Diversity in Asexuals: Patterns and Processes,
(ii) Asexuality and Time-scales,
(iii) Origins, Spread and Extinction of Asexuals and
(iv) The Paradox of Sex: an Evaluation.

These general themes were further subdivided into specific key topics. The workshops were planned to be held in Montpellier (France), London (Great Britain), Valencia (Spain) and Budapest (Hungary). Participants from these countries at the Wageningen meeting agreed to organise these workshops.

It became clear from the discussions that there is an urgent need for an updated comprehensive book on the biology of asexual organisms (plants, animals and micro-organisms), supplemented with the relevant theory. The editing and publishing of such a work would be a second activity of the network.

Several researchers expressed their concern about the environmental consequences of asexual reproduction through seeds (apomixis) in crops. Apomixis is one of the most desired traits in agriculture and therefore several laboratories work on its realisation. It was also pointed out that conservation of natural asexual organisms lacks a firm scientific basis at the moment and that asexual organisms could be very valuable as bio-indicators. Therefore, as a third activity, the preparation of a science policy document on the environmental consequences of natural and applied asexual reproduction, was suggested.

As a fourth network activity, small meetings and exchanges were proposed. For example, experts on the terminology in plants, animals and micro-organisms could meet and produce a document to standardise the terminology. Such a document would then be discussed at the next workshop and could result in a chapter of the book (activity 2). Occasionally, exchanges of scientists should also be supported. For example, a theoretician would visit an empiricists' laboratory, and visa versa. This would lead to more realistic models and to better parameter estimations for the rigid testing of theories.

The discussions continued on Sunday morning. After lunch, most participants left, but a core group of six participants stayed until Monday morning to generate draft texts for the network proposal. This proposal (PARTNER -PARthenogenesis NEtwoRk) was then further edited after the workshop by the two organisers, Dr. Peter van Dijk and Dr. Koen Martens, and was submitted at the beginning of December 2001.

Scientific content of the workshop

On Saturday, all participants gave an introduction to their research. Below follows a short summary of these talks.

Prof. Bengt Olle Bengtsson (Lund, Sweden) argued that the question why partial asexual reproduction through seeds (apomixis) in plants is rare, whereas partial asexual reproduction through other structures (e.g. bulbills) is common, can be answered by the different ecological functions of these propagules. He then stressed that the key reason for the association between asexual reproduction and polyploidy remains unknown. Another issue raised by Prof. Bengtsson was that of the consequences of asexual reproduction at the DNA sequence level. At the simplest level, it can be said that allele sequences at a locus will diverge when there is less than one sexual event every three generations. Otherwise, no difference between sexual and asexual reproduction will be detectable. One important area was that of rare sexual reproduction in a metapopulation context. Until now, not much work has been done here. Finally, Bengtsson argued that it could be possible that apomixis could invade natural systems from agriculture, but that details were important here.

The next speaker was Dr. Joel Peck, a theoretician from the University of Brighton (UK). He talked about Wright's shifting balance theory in an asexual context. In sexual organisms, hybrid zones are kept in place as "tension zones" due to the balance between dispersal and frequency dependent selection cause by low hybrid fitness. This may prevent sexual organisms from reaching the highest fitness peaks in a partially structured environment. Asexuals are "immune" to gene flow and hybridisation and should therefore be able to better adapt to heterogeneous environments.

Prof. Eörs Szathmáry (Budapest, Hungary) talked about transitions that make separate elements to form new cooperative units (e.g prokaryotic cells, eukaryotic cells, chromosomes). Using stochastic corrector models it can be shown that there are optimal compartments and that therefore replication will be followed by division. Strong selection for the reduction of internal competition has lead to the evolution of chromosomes. Sexual reproduction is an absolute necessity as a force for group selection.

Dr. Manuel Serra (Valencia, Spain) gave an overview of his work on monogonont rotifers, which live in ponds and have cyclic parthenogenesis. In these species, sexual reproduction can be triggered environmentally. Some of the questions that his group is working on are: Is sex maintained through a long-term advantage? Do mutation rates differ between sexual and asexual organisms? What is the relationship between obligate vs facultative asexual reproduction and genetic diversity? and: What is the relationship between sexual reproduction and environmental change?

Dr. Arjan de Visser (Wageningen, The Netherlands) presented some of his studies on the experimental evolution in the bacterium *E.coli*. More specifically he was interested in whether adaptation in *E.coli* is limited by the mutation supply. He concluded that in the case of low mutation supply, the rate of adaptation was limited by the mutation rate. In the case of a high mutation supply, clonal interference will restrict the rate of adaptation in asexual populations.

Prof. Rolf Hoekstra (Wageningen, The Netherlands) talked about experimental evolution in sexual / asexual fungi. In experiments on compensatory evolution for fungicide resistance in sexual / asexual fungi, the importance of epistasis could be assessed. If epistasis is common, then asexuals will do better as they would re-establish initial fitness much faster that sexuals. Other experiments were directed towards aging and senescence in asexual fungal strains and "resetting" in sexual strains. Prof Hoekstra correlated incidences of senescence to mitochondrial meltdown.

Prof. Dr. Pierre-Henri Gouyon (Paris, France) put forward a number of facts that are often forgotten in discussions on the maintenance of sex. A very important function of sexual reproduction is that it produces a clean egg, because viruses are not transmitted via the egg cell. Second, in many organisms, sex is associated with diapause and with dispersal, whereas asexual reproduction is associated with growth and local reproduction. Another important aspect is that of the time scale. Sexual and asexual reproduction have short-term and long-term effects. Even if there is a short-term advantage to asexual reproduction and an asexual mutant becomes fixed in a species, such an asexual species could go extinct sooner than a sexual species, due to lack of adaptability and accumulation of deleterious mutations. This would represent a long-term advantage to sexual reproduction. The balance between short-term advantages and long-term disadvantages will be important for the spread of apomixis genes from apomixis-crops into the wild.

Dr. Peter van Dijk (Heteren, The Netherlands) reported on the research on sexual and asexual dandelions (*Taraxacum officinale*). Ecological studies focus on the origins and maintenance of clonal diversity and on the dynamics of mixed sexual and asexual populations. Genetical studies have shown that apomixis in *Taraxacum* is under simple genetic control, involving a few unlinked, dominant genes. Evolutionary studies indicate that these apomixis genes are linked with deleterious recessives and that recombination in these chromosomal regions is suppressed. The idea is that the apomixis genes can become inserted into new clones via pollen transmission in back crosses with sexuals. Hence, clones in *Taraxacum* are recent, but the apomixis genes are ancient.

Dr. Isa Schön and Dr. Koen Martens (Brussels, Belgium) discussed asexual reproduction in the non-marine ostracods. In some of these species males, are absent in the fossil record for several dozens of millions of years, indicating that these organisms have abandoned sexual reproduction long ago. This work illustrates the importance of a good fossil record. Studies of allele sequence divergence (the so-called Meselson effect) in *Darwinula stevensoni* attempts to test ancient asexuality. One possible explanation for the ability of these organisms to abandon sex completely could be more efficient DNA repair. Other non-marine ostracods show clear patterns of geographic parthenogenesis: different distributions of sexual and asexual taxa. Furthermore, there is evidence for the occurrence of 'General Purpose Genotypes' in long-term parthenogenetic ostracods. Dr. Martens also raised the question of a species concept for asexual organisms.

Prof. Roger Butlin (Leeds, UK) talked about molecular phylogenies in a sexual-asexual context. More sophisticated phylogenetic trees would allow the detection of multiple origins of asexuality. Although the allele sequence divergence (Meselson-effect) makes it possible to detect absence of sexual reproduction for long periods of time, Butlin stressed the importance of absolute time scales. More fossil data are needed to calibrate of the molecular clock. He also mentioned that in bdelloid rotifers, the best-studied group of ancient asexuals, transposable elements are silenced or lost. Ancient asexuality apparently needs special (pre?) adaptations.

Prof. Leo Beukeboom (Groningen, The Netherlands) gave an overview of his work in Hymenoptera. The haploid/diploid sex determination system in the Hymenoptera makes parthenogenesis to be relatively easily induced in this group (e.g. *Wolbachia*, *Trichrogramma*). In the parasitoid wasp, *Venturia canescens*, both sexual and parthenogenetic strains occur. Gene flow between these entities is studied. Artificial hybrids can be generated in the laboratory, which opens up the possibility to study the genetics underlying parthenogenesis. Autosegregation is expected to cause increased homozygosity at the ends of the chromosome. The rate of homozygosity increase is being investigated with molecular markers.

Prof. Valerio Scali (Bologna, Italy) reported on parthenogenesis in phasmids (stick insects). Three species, one obligatory sexual, one obligatory parthenogenetic and one facultative parthenogenetic, hybridise. There is no clear geographic

parthenogenesis in these species, the distributions are mixed, often patchy at a small geographic scale. Prof. Scali discussed the various cytological mechanisms leading to parthenogenesis in stick insects. He pointed out that the cytology of stick insects suggests that they were pre-adapted to parthenogenesis. Based on mitochondrial DNA sequences, some hybrids could be between 1 and 5 million years old. There is clear reticulate evolution in these groups; different taxa have interacted independently and repeatedly. According to Prof. Scali, the conservation of asexual organisms needed special attention, as all theory for conservation is based on sexual organisms.

Dr. Cino Pertolid (Aarhus, Denmark) highlighted another applied aspect of asexuals: their usefulness to estimate environmental variability. Environmental stress often leads to developmental instability. Fluctuation asymmetry and increased phenotypic variance in asexual lineages could be used as bio-indicators for environmental stress. This approach was illustrated by the work on parthenogenetic stick insects in Sicily.

Results and contribution to the future direction of parthenogenesis research

During this exploratory workshop, European parthenogenesis researchers from various sub-fields could meet at such a scale for the first time. The talks presented by the participants reflected a whole spectrum of parthenogenesis research. Some concentrated on theory (Bengtsson, Peck, Szathmary, Butlin, Gouyon), others on experimental evolution (De Visser, Hoekstra), and again others on natural parthenogenesis (Scali, Serra, Schoen, Martens, Van Dijk, Pertolid, Beukeboom). Some focused on phylogenies (Butlin, Martens), others on ecology (Peck, Gouyon, Scali, Pertolid, Serra) and others again on the genetical control and mechanisms of parthenogenesis (Van Dijk, Scali, Beukeboom), all irrespective of the taxonomic group or habitat. This clearly illustrates that the parthenogenesis field should not be organised into taxonomic groups or habitats as it is to date, but according to the scientific questions asked. This is a prerequisite for the accelerated advancement of parthenogenesis research in Europe.

The submission of the PARTNER proposal was the direct result of the Wageningen exploratory workshop. Besides this, plans were discussed for an ESF Program as a follow-up of PARTNER. Also the possibilities for an EUROCORES application and an EU framework proposal were discussed. The new mix of disciplines at the Wageningen workshop was felt to be highly stimulating and many new contacts were established. The workshop thus expressed the enthusiastic spirit that will be typical for the proposed PARTNER-network.

Statistical information

There were 15 participants to the workshop, excluding the senior secretary of LESC. Seven participants were full professors, the others assistant professors or senior researchers. There were two female participants. Participants came from 10 different European countries: The Netherlands (5x), United Kingdom (2x), Belgium (1x), Denmark (1x), France (1x), Germany (1x), Hungary (1x), Italy (1x), Spain (1x) and Sweden (1x). Other participants from Norway, Italy and Spain unfortunately had to chancel shortly before for the workshop, due to unforeseen other obligations and private reasons.

Final Programme:

Friday, October 5th:

Arrival at WICC

19.30 Diner

informal, get together, Wageningen pubs

Saturday, October 6th:

breakfast

9.00 Welcome and introduction to the workshop history by Peter van Dijk and Koen Martens

9.15 Dr. Martina Hildebrandt, LESC Senior Scientific Secretary (Life and Environmental Sciences)

9.30 Introduction of the participants, each 15-20' (10.30 coffee break)

12.30 Lunch

14.00 Discussion of the draft proposal
e.g. scope
benefits to the field
scientific objectives
specific topics

15.30 Coffee break

16.00 Discussion of the draft proposal

18.00 Diner

20.00 Evening at Rolf Hoekstra's place (Taxi-bus leaves at 19.45 and 20.00)

Sunday, October 7th:

breakfast

8.30 Discussions
e.g. principle activities
organizational structure
administrative structure
responsibilities
communication strategy
key targets and milestones
asked budget
preliminary list of participants
preliminary list of Steering Committee members
lobbying strategies

12.30 Lunch (first departure of participants)

14.00 Walk to the river Rhine (remaining participants = core group)

16.00 Writing draft texts for the Program proposal

18.30 Diner

20.00 Writing and Wageningen's night life

Monday, October 8th:

Breakfast

8.30 Writing continued

12.30 Lunch

Departure last participants.

Participant list
Unfortunately four participants (Boero, Breeuwer, Gabriel, and Kirkendall) who initially had agreed to come, were not able to participate do to unexpected private reasons or unforeseen important other obligations.

Bengt O. (Olle) Bengtsson, Professor
Dept. of Genetics
Lund University
Sölvegatan 29
S-22362 Lund,
SWEDEN
Bengt_Olle.Bengtsson@gen.lu.se
Tel.: +46-46-2229890
Fax.: +46-46-147874
PLANTS, THEORY

Dr. Leo Beukeboom, Professor
Dept. of Genetics, University of Groningen
University of Leiden (old address)
P.O. Box 9516
NL-2300 RA Leiden
THE NETHERLANDS
beukeboom@rulsfb.leidenuniv.nl
HYMENOPTERA, FLATWORMS

Dr. Ferdinando Boero, Professor
Dipartimento di Scienze e Tecnologie Biologiche e Ambientali
Università di Lecce
73100 Lecce
ITALY
boero@ilenic.unile.it
tel: +39 0832 320619
fax: + 39 0832 320 702
HYDRAZOA, LIFE CYCLES, BENTHOS, PLANKTON, EVOLUTIONARY ECOLOGY

Dr Hans Breeuwer, Assistent professor
Institute for Biodiversity and Ecosystem Dynamics,
University of Amsterdam
P.O.Box 94062, 1090 GB, Amsterdam,
THE NETHERLANDS
email: breeuwer@science.uva.nl
Tel: 31 20 5257745
Fax: 31 20 5257754
ACARI, ENDOSYMBIONTS, EVOLUTIONARY GENETICS, SPECIATION

Dr. Roger Butlin, Professor
School of Biology
The University of Leeds
Leeds LS2 9JT
UK
r.k.butlin@leeds.ac.uk
tel.: +44 113 233 3090
fax: - +44 113 233 2835
EVOLUTIONARY GENETICS, SPECIATION

Dr. Arjan de Visser
Laboratory of Genetics
University of Wageningen
Dreijenlaan 2
6703 HA Wageningen
THE NETHERLANDS
Phone +31 317 483144
Fax +31 317 483146
email: Arjan.deVisser@genetics.dpw.wau.nl
EXPERIMENTAL EVOLUTION OF MICROORGANISMS

Dr. Wilfried Gabriel, Professor
Zoologisches Institut der Ludwig-Maximilians-Universität
Lehrstuhl Ökologie
Karlstrasse 23-25
D - 80333 München
GERMANY
email wilfried.gabriel@lrz.uni-muenchen.de
Tel: +49 89 5902 393
fax +49 89 5902 461
GENERAL THEORY, MODELLING, DAPHNIA

Dr. Pierre Henri Gouyon, Professor
Universitee Paris 11
Batiment 362
F-91405 ORSAY
FRANCE
Pierre-Henri.Gouyon@esv.u-psud.fr
PLANTS, THEORY

Dr. Rolf Hoekstra, Professor
Dept. of Genetics
University of Wageningen
Dreijenlaan 2
6703 HA Wageningen
THE NETHERLANDS
rolf.hoekstra@genetics.dpw.wau.nl
tel.: +31 317 484619
fax: +31 317 483146
THEORY, FUNGI, EXPERIMENTAL EVOLUTION

Dr. Lawrence Kirkendall, Associate Professor
Department of Zoology
University of Bergen
Allegaten 41
N-5007 Bergen
NORWAY
lawrence.kirkendall@zoo.uib.no
tel: (+47) 55 58 23 42
fax (+47) 55 58 96 75
PSEUDOGAMY, EXTREME INBREEDING, BARK BEETLES

Dr. Volker Loeschcke, Professor
(WILL SENDA REPRESENTATIVE:
Cino Pertolid, PhD, Danish National Environmental Research Institute,
Roende, DK-8410 Roende, tel.: +45-89201700
fax: +45-89201515
email: cpb@dmu.dk Denmark)
Dept of Ecology and Genetics
University of Aarhus
Ny Munkegade
DK-8000 Aarhus
DENMARK
Volker.Loeschcke@biology.aau.dk
GENERAL THEORY, MODELLING

Dr. Koen Martens
Freshwater Biology
Royal Belgian Institute
of Natural Sciences
Vautierstraat 29
1000 Brussels
BELGIUM
koen.martens@naturalsciences.be
tel: + 32-2-62 74 315
fax: +32-2-64 64 433
OSTRACODA

Dr. Joel Peck, Reader
Centre for the Study of Evolution
University of Sussex
Brighton BN1 9QG
UK
j.r.peck@sussex.ac.uk
tel: 441273724228
EVOLUTIONARY THEORY, SEX, SOCIAL BEHAVIOUR

Dr. Valerio Scali, Professor
Dipartimento di Biologia Evoluzionistica
Sperimentale
Università di Bologna
Via Selmi 3
I-40126 Bologna
ITALY
scali_v@biblio.cib.unibo.it
tel: 0039 051 2094173
fax: 0039 051 251208
CENTROSOME INHERITANCE, CYTOLOGY OF PARTHENOGENESIS, HYBRID PARTHENOGENS, MOLECULAR EVOLUTION, PHASMATODEA

Dr. Manuel Serra, Professor
Institut Cavanilles de Biodiversitat i Biologia Evolutiva;
Universitat de València;
A.O. 2085
E46071 València
SPAIN
manuel.serra@uv.es
tel: (+34) 96 398 3661
fax: (+34) 96 398 3670
LIFE-HISTORY EVOLUTION, POPULATION DIFFERENTIATION AND STRUCTURE, COMPETITION, CYCLICAL PARTHENOGENESIS, ROTIFERS

Dr. Eörs Szathmáry, Professor
Collegium Budapest (Institute for Advanced Study)
2 Szentháromság u.
H-1014 Budapest
HUNGARY
szathmary@zeus.colbud.hu
T: +36 1 224 8300
F: +36 1 224 8310
MAJOR EVOLUTIONARY TRANSITIONS, SEGMENTED GENOMES, ERROR THRESHOLD, SYNERGY

Dr. Peter van Dijk **(Convenor)**
Dept. of Plant Population Biology
Netherlands Institute of Ecology
P.O. Box 40
6666 ZG Heteren
THE NETHERLANDS
pjvandijk@cto.nioo.knaw.nl
tel: +31.26.47.91208
fax: +31.26.47.23227
APOMIXIS, PLANTS

Dr. Kitty Vijverberg
Dept. of Plant Population Biology
Netherlands Institute of Ecology
P.O. Box 40
6666 ZG Heteren
THE NETHERLANDS
vijverberg@cto.nioo.knaw.nl
tel: +31.26.47.91208
fax: +31.26.47.23227
APOMIXIS, PLANTS