

# Chapter 4

## Cytology of Asexual Animals

Per Stenberg and Anssi Saura

**Abstract** We review the cytological mechanisms underlying asexual reproduction, i.e. reproduction without fertilization, in animals. Asexuality or parthenogenesis has evolved many times and the cytological mechanisms to restore the parental chromosome number can vary between and even within species. In automictic or meiotic parthenogenesis, meiosis takes place but the chromosomal constitution of the mother is restored through one or several different mechanisms. Some of these mechanisms enforce homozygosity at all loci while some other mechanisms pass the genome of the mother intact to the offspring. In apomictic or mitotic parthenogenesis the eggs are formed through what is essentially a set of mitoses. Polyploidy, is in general incompatible with chromosomal sex determination and is a rare condition in animals. However, many asexual and hermaphroditic forms are polyploid to various degrees. Polyploidy is divided into allo- and autopolyploidy. In the former mode the chromosome sets are derived from two or more different species while in autopolyploidy the multiplication has taken place within one species. We discuss the evolutionary consequences of the different cytological mechanisms involved in asexual reproduction.

### 4.1 The Importance of Cytology

In parthenogenesis or *thelytoky*, a female animal produces female progeny through a process that does not involve fertilization (von Siebold 1856). Fertilization is here defined as involving the fusion of gametes from two different individuals. The definition of parthenogenesis is based on cytological observations. The roles of cells and chromosomes in sexual reproduction and parthenogenesis were worked out in the first half of the 20th century. The growth of animal cytology is covered in “Animal Cytology and Evolution” by White (1973), a *magnum opus* that evidently will be

---

P. Stenberg (✉)

Umeå Center for Molecular Pathogenesis, Umeå University, SE-901 87 Umeå, Sweden  
e-mail: Per.Stenberg@molbiol.umu.se

also the last of its kind since nobody is expected to master the entire field of the role of cytology in animal evolution like its author.

Cytology had, like e.g. *Drosophila* and population genetics, been an important branch of the new science of genetics. It was overtaken by the spectacular rise of molecular genetics, the tools of which were soon used in *Drosophila* and other model organisms. Chromosomes, the objects of cytogenetics, are large and complex, and the application of molecular methods to cytology has been neither easy nor rapid. Chromosomes still represent a challenge that is not solved as easily as the reductionist exploits of molecular biology thus far. We see, however, that progress is being made again by methods such as fluorescent microscopy and image capturing while epigenetic phenomena stress the importance of cytogenetics once more.

## 4.2 Cytological Mechanisms of Animal Parthenogenesis

Mendelian genetics, diploidy, meiosis and fertilization are intertwined phenomena. In normal meiosis, the chromosome pairs, chiasmata, are formed and the resulting gametes are haploid. Diploidy is restored at fertilization. In *automictic* or meiotic parthenogenesis, meiosis is present. Since there is no fertilization, the parental level of ploidy has to be restored in one way or another. This can be accomplished through several different mechanisms, the genetic and evolutionary consequences of which differ extensively.

In *apomictic* or mitotic parthenogenesis, egg cells are produced through mitosis. Only one cell division takes place in the eggs. The number of chromosomes is not reduced. As a consequence, the offspring are true *clones*, genetically identical to their mother, save for mutations (see also Chapter 9).

Parthenogenesis has arisen repeatedly and independently during the evolution of animals. As expected, cytological mechanisms do not show any clear evolutionary patterns. A single species or related species can reproduce through different mechanisms. As an example, lepidopterans make use of several automictic mechanisms (Suomalainen et al. 1987) as do strains and species of the crustacean *Artemia*, while parthenogenetic weevils all reproduce through apomictic parthenogenesis (Saura et al. 1993; Stenberg et al. 2003).

Polyploidy is a rare condition in sexually reproducing animals. In contrast, it is common in parthenogenetic forms (Lewis 1980), even though asexuality and polyploidy need not be directly related to each other (Lundmark and Saura 2006). In the following, we describe the different cytological mechanisms of animal parthenogenesis, assess briefly their evolutionary significance and discuss the role of polyploidy in parthenogenesis.

### 4.2.1 Automictic Parthenogenesis

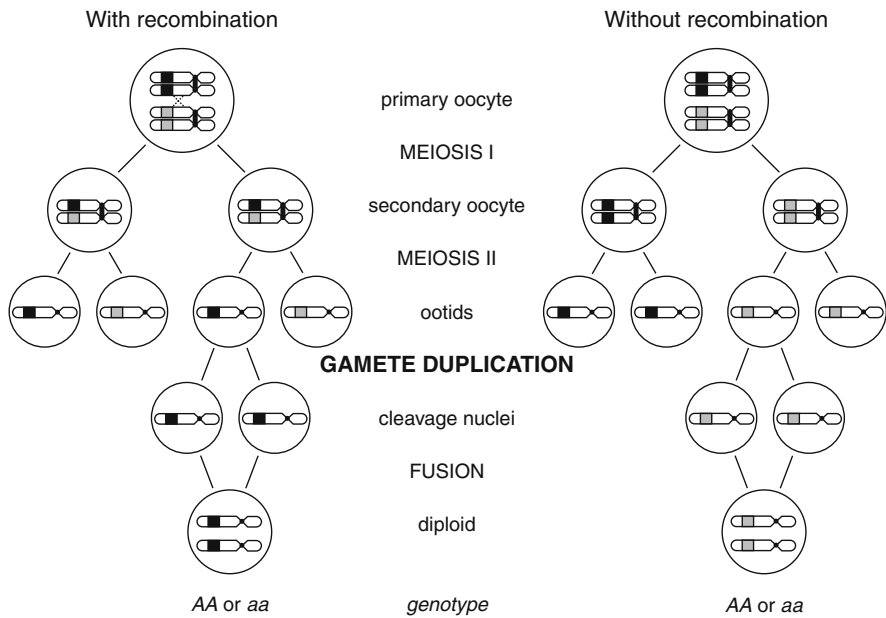
In this mode of parthenogenesis, the early stages of meiosis are in most cases unaffected. The chromosomes pair and crossing-over takes place. The chromosome number is halved during the formation of the egg and polar bodies. The original

diploid chromosome number is restored thereafter through a fusion of the products of meiosis, the details of which are variable. In fact, about all imaginable mechanisms have been described. The main difference to normal fertilization is that the cells involved in fusion are derived from a single individual and a single meiosis.

The evolutionary consequences of automictic parthenogenesis are often poorly understood. It is true that certain modes enforce homozygosity but even in these cases, there may be exceptions. Natural selection can sort out these homozygous lineages and evolution can still take place. Other modes of automixis transfer the genotype of the mother intact to the offspring. The confusion seems to stem mainly from the rather short description of automixis in White (1973, pp. 705–709) and in particular from his essay on heterozygosity (White 1970), where he downplayed the evolutionary potential of parthenogens. In addition, there are cases where members of a single population reproduce simultaneously through several automictic mechanisms (Suomalainen et al. 1987).

**4.2.1.1 Gamete Duplication**

In this mode, the haploid egg cell divides and produces cleavage nuclei. These nuclei fuse with each other producing a diploid nucleus. Alternatively, the divided chromosomes remain in the same nucleus, which becomes diploid (see Fig. 4.1).



**Fig. 4.1** The genetic consequences of gamete duplication (modified after Asher 1970; Suomalainen et al. 1987)

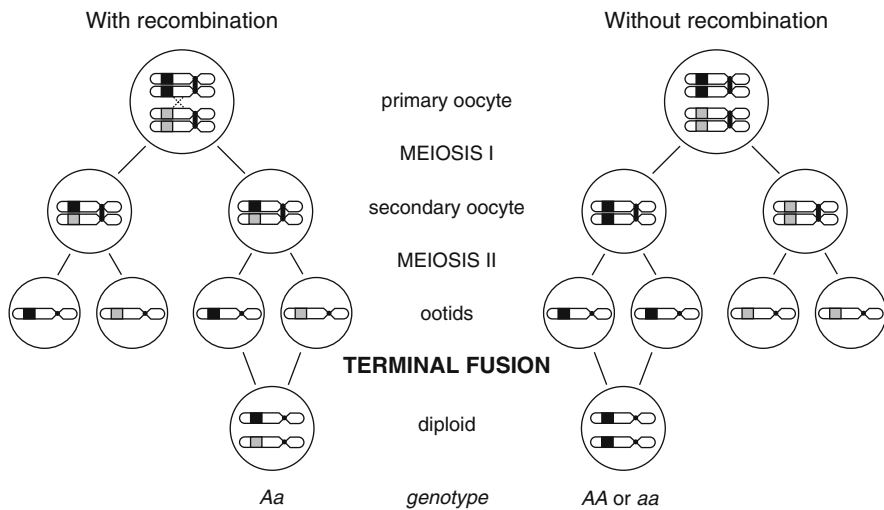
Gamete duplication enforces homozygosity at all loci, irrespective of crossing-over at meiosis. If the founding lineage has been polymorphic, lineages derived from it can differ genetically from each other. They will be subject to evolution being independent from each other. Gamete duplication has been observed in the *Artemia salina* complex (Crustacea), among insects in phasmids, aleyrodids, coccids, lepidopterans, in some parthenogenetic *Drosophila*, cynipids and in certain mites (see Suomalainen et al. 1987 and Norton et al. 1993 for details).

Plantard et al. (1998) demonstrated that *Wolbachia* is responsible for the transition from arrhenotoky (and haplodiploidy) to parthenogenesis through gamete duplication in the cynipid *Diplolepis spinosissima*. It seems that *Wolbachia* invariably gives rise to parthenogenesis through gamete duplication in hymenopterans (Bordenstein and Werren 2007; see also Chapter 17). This topic is reviewed in van Wilgenburg et al. (2006) and it appears that other microbes, e.g. *Cardinium*, (Bacterioidetes) can have effects.

### 4.2.1.2 Terminal Fusion

In this mode, the second polar nucleus fuses with the egg nucleus. The genetic consequences of terminal fusion are shown in Fig. 4.2.

Given that the mother is heterozygous for two alleles but there is no crossing-over, terminal fusion enforces homozygosity. If, on the other hand, there is crossing-over between the locus and the centromere, heterozygosity can be maintained (Asher 1970; Suomalainen et al. 1987). A population reproducing through terminal fusion can, at least to a certain extent, maintain polymorphism and selection can operate on the different genotypes.



**Fig. 4.2** The genetic consequences of terminal fusion (modified after Asher 1970; Suomalainen et al. 1987)

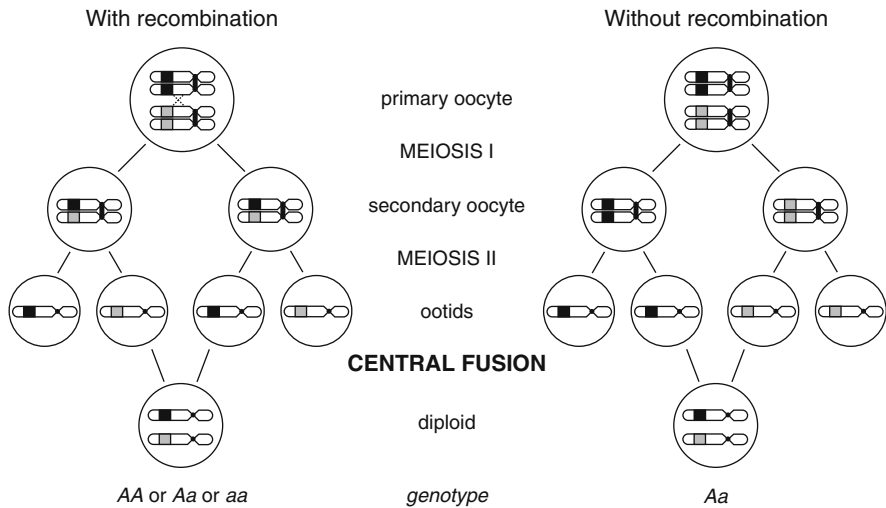
Nematodes, enchytraeids, some *Artemia*, isopods, among insects: acridids, coccids, thrips, certain *Drosophila* and other dipterans, some hymenopterans, some mites and tardigrades reproduce through terminal fusion (see Suomalainen et al. 1987 and Norton et al. 1993 for details; see also Chapter 12).

### 4.2.1.3 Central Fusion

Here, the two central polar nuclei fuse and give rise to the embryo. If the mother is heterozygous, all her offspring will be heterozygous, given that there is no crossing-over. If there is crossing-over between a locus and the centromere, there will be segregation among the offspring so that a heterozygote *Aa* will produce 1/4 *AA* individuals, 1/2 *Aa* individuals and 1/4 *aa* individuals (see Fig. 4.3). In cases where heterozygosity is advantageous, selection will favour loci that are tightly linked to the centromere. This is evidently the case in lepidopterans and in *Drosophila mangabeirai*, which reproduce through central fusion. Lepidopteran females have achiasmatic oogenesis that guarantees the maintenance of heterozygosity; *D. mangabeirai* is heterozygous for three inversions that inhibit crossing over (see Suomalainen et al. 1987 for details).

Many hymenopterans combine persistent heterozygosity under single locus complementary sex determination with thelytoky, which implies that the sex locus must be located in a region without recombination (e.g. a centromere) (Beukeboom and Pijnacker 2000; see also Chapter 17).

Animals that reproduce through central fusion include the psychid moth *Dahlica* (*Solenobia triquetrella*), the obligately parthenogenetic *Drosophila mangabeirai*



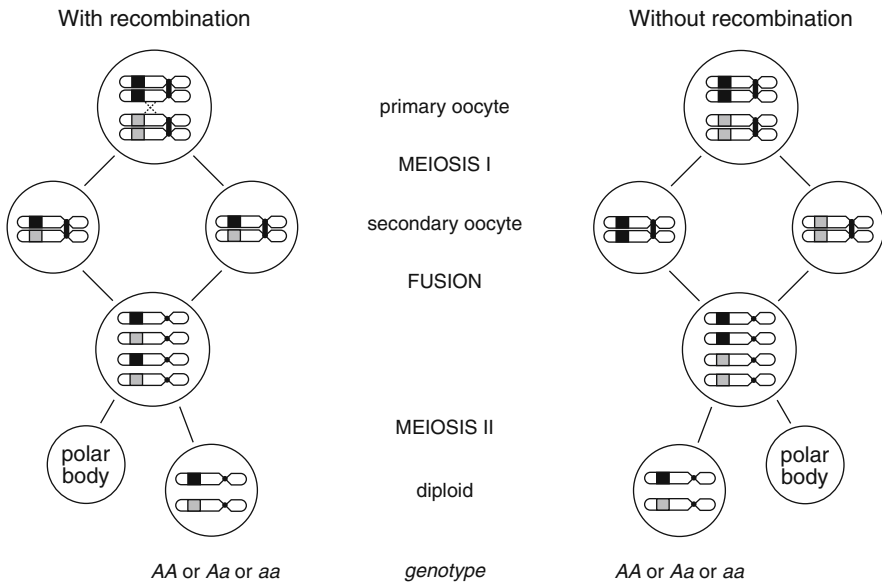
**Fig. 4.3** The genetic consequences of central fusion (modified after Asher 1970; Suomalainen et al. 1987)

and strains of other accidentally parthenogenetic *Drosophila* (among other automictic mechanisms), the fly *Lonchoptera dubia*, the parthenogenetic strains of the honey bee (see Seiler 1963 and Suomalainen et al. 1987 for details) and also some other hymenopterans (Beukeboom and Pijnacker 2000).

#### 4.2.1.4 The First Polar Nucleus Fuses with the Nucleus of the Secondary Oocyte

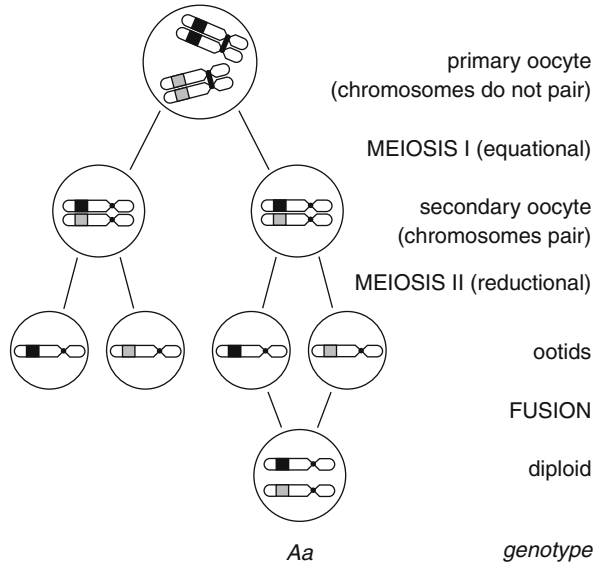
This can either happen directly after the first meiotic division or alternatively, the nuclei derived from the above nuclei fuse (see Fig. 4.4).

A heterozygous mother *Aa* will produce  $1/6$  *AA* homozygotes,  $4/6$  *Aa* heterozygotes and  $1/6$  *aa* homozygotes. Linkage will not affect this erosion of heterozygosity. Narbel-Hofstetter (1964) has shown that several psychid moths reproducing through this mechanism keep the meiotic metaphase plates together. There is one mode, in which the two halves of the first anaphase spindle collapse on one another and form the spindle of the second division. In another mode, second meiotic spindles come together side by side and fuse (White 1973, p. 722). This ensures that the genotype of the mother is kept intact without any segregation of alleles (Narbel-Hofstetter 1964). In addition to the psychids, the liver fluke *Fasciola hepatica* and some strains of the crustacean *Artemia* reproduce through this mechanism (see Suomalainen et al. 1987 for details). The collembolan *Folsomia candida*



**Fig. 4.4** The genetic consequences of a case where the first polar nucleus fuses with the secondary oocyte

**Fig. 4.5** The genetic consequences of gonoid thelytoky (modified after Nur 1979; Suomalainen et al. 1987)



seems, at least in part, to also use this mechanism; Fountain and Hopkin (2005) put evidence forward that *Wolbachia* is responsible for parthenogenesis in *Folsomia*.

**4.2.1.5 Gonoid Thelytoky**

In this mode, the parthenogenetic egg undergoes two meiotic divisions; the chromosomes pair at the second meiotic metaphase (see Fig. 4.5). Certain scale insects (coccids) reproduce this way (Nur 1979).

The genotype of the mother is passed on unchanged to the offspring (Nur 1979, Suomalainen et al. 1987). Spitzer (2006) has studied the evolutionary potential of different strains of the pest *Saissetia coffeae* that differ extensively in adaptability.

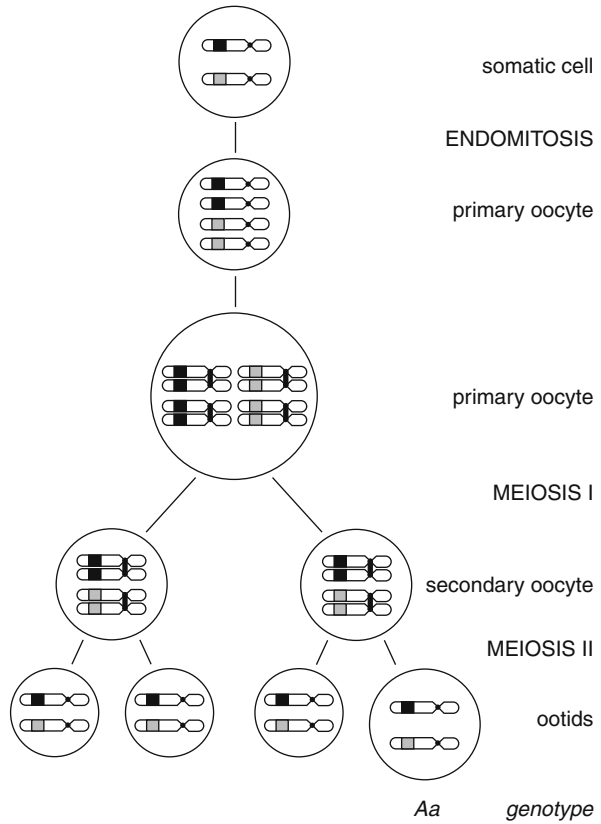
**4.2.1.6 Premeiotic Doubling**

This mode of automictic parthenogenesis involves an endomitotic process: a premeiotic doubling of chromosome numbers is reduced through meiosis. The resulting daughter chromosomes pair in the first meiotic prophase. All chromosomes pair with their genetically identical counterpart, and the original even number of chromosomes is maintained (see Fig. 4.6).

As a result, the genotype of the mother is passed on to the offspring unchanged.

Premeiotic doubling is a common mechanism used by turbellarians, most parthenogenetic earthworms, several insects, mites, tardigrades and parthenogenetic fishes, amphibians and reptiles (Suomalainen et al. 1987; Cuellar 2005).

**Fig. 4.6** The genetic consequences of premeiotic doubling



### 4.2.2 Apomictic Parthenogenesis

In apomictic parthenogenesis, the essential features of meiosis are lacking. The chromosomes do not pair and the oocyte undergoes a single maturation division, which is in most cases indistinguishable from mitosis. Consequently, the genotype of the mother is passed on to the offspring without changes. Apomictic parthenogenesis is the most common cytological mode of parthenogenesis and it is found in many animal groups (see Suomalainen et al. 1987 for details).

The parthenogenetic phase of animals with cyclical parthenogenesis is apomictic. Such groups include cladocerans (see Chapter 15), monogonont rotifers (see Chapter 14), aphids, the beetle *Micromalthus*, cecidomyid midges and cynipid wasps. Note that hymenopterans produce males parthenogenetically from haploid unfertilized eggs but these males participate in normal sexual reproduction. Other animals with verified apomictic parthenogenesis (following Suomalainen et al. 1987) include coelenterates, certain tubellarians, trematodes, nematodes, gastrotrichs, bdelloid rotifers (they have two equational maturation divisions in the oogenesis; Hsu 1956; Pagani et al 1993; see also Mark Welch et al. 2004 and



Chapter 13), parthenogenetic gastropods and the earthworm *Dendrobaena octaedra*. The latter record needs to be rechecked, since the distribution of genotypes does not support apomixis and rearing experiments show a segregation of alleles (Terhivuo and Saura 2006; Simonsen and Holmstrup 2008). This variation can be explained either through occasional sex or gene conversion. Also the enchytraeid *Lumbricillus lineatus* and amongst crustaceans, some members of the *Artemia salina* complex, parthenogenetic ostracods (see also Chapter 11) and certain isopods reproduce apomictically. Among the insects, blattids, phasmids, tettigonids, psocids, certain coccids, dipterans, chrysomelids (including *Calligrapha*), the large group of parthenogenetic weevils and certain hymenopterans are apomictic, as are, mites, tardigrades and the fish *Poecilia formosa* (Monaco et al. 1984; Balsano et al. 1989; see also Chapter 19). Finally, Weeks and Braeuwer (2001) have shown that *Wolbachia* gives rise to apomictic parthenogenesis in a mite.

### 4.3 Evolutionary Consequences

Even though the evolution of asexual animals is discussed in depth elsewhere in this book, we wish to stress the importance of knowing the cytological mechanism of parthenogenesis. Many modes of automixis result in offspring being genetically identical to their mother, and can not be distinguished from offspring being produced through apomictic parthenogenesis. A single morphological species can have several modes of automixis, and a population may be composed of females using different mechanisms in the oogenesis. Finally, a single female can give rise to offspring through different automictic mechanisms. Obviously, the evolutionary consequences will be radically different in such cases.

Most of the experimental cytology on parthenogenesis is old. When molecular results contradict the predictions of cytology, the latter has to be rechecked. This requires learning the techniques described in handbooks and consulting practising cytologists doing routine work, e.g., in hospitals. There is no other way.

### 4.4 Polyploidy in Association with Parthenogenesis

Polyploidy characterizes angiosperm plants, to the extent that the proportion of polyploidy is estimated to range from 43 to about 58% among angiosperm species, but the proportion of species that are polyploid in some sense, so that there are traces of paleopolyploidy, may be as high as 70–80% (Lewis 1980). Virtually all apomictic angiosperms are polyploid (Asker and Jerling 1992; see also Chapters 3 and 8). In contrast, animals are seldom polyploid. Chromosomal sex determination is apparently the main reason for the absence of polyploidy in animals (White 1946). This argument still stands, even though there is evidence for rounds of polyploidization in the history of vertebrates (Carroll et al. 2005). In addition, there are several sexually reproducing frogs and fishes that are polyploid (e.g. Ma and Gustafson 2005; Zhu et al. 2006; Holloway et al. 2006; see also Chapters 19 and 20).

Polyploid formation often involves hybridization between two species (allopolyploidy). The alternative, autopolyploidy (where the multiple chromosomes come essentially from the same genome), has been relegated to the background but has experienced a revival among botanists (e.g. Soltis and Soltis 2000). This distinction needs, however, not be sharp since it depends on the definition of species. There may well be genetic and chromosomal differences that do not allow for a normal segregation of homologous chromosomes in crosses involving forms that belong to what is called a species.

Parthenogenetic animals and the ones with apomictic parthenogenesis in particular, lack the obstacles to polyploidy, i.e. chromosomal sex determination. Polyploidy is indeed very common among parthenogenetic animals (Suomalainen et al. 1987). To give an example, among the 52 morphological species of parthenogenetic weevils that have been cytologically studied, only four cytological races are diploid, while 43 are triploid, 18 tetraploid, 6 pentaploid, three are hexaploid and one is decaploid (Saura et al. 1993). In addition, the polyploid races have a much wider distribution in comparison with diploid sexuals or parthenogens, a pattern called *geographical polyploidy* by Stenberg et al. (2003). Lundmark and Saura (2006) provide a list of insect taxa with geographical polyploidy (see also 8 on geographic parthenogenesis in general).

White (1970, 1973) had a rather negative view on the evolutionary potential of polyploid parthenogens. Even though they can be highly heterozygous, they can not respond to challenges from the environment and are, accordingly, blind alleys of evolution. The merger of different genomes in allopolyploids leads to differently adapted offspring that will have difficulties to reproduce sexually due to improper pairing of chromosomes. It will suffice that at least one asexual lineage out of many will be well adapted for the benefits of asexual reproduction to become manifested (Lundmark and Saura 2006). The tetraploid race of *Dahlia triquetrella* has been shown to be autopolyploid (Seiler 1961). The fecundity of diploid sexual females exceeds that of diploid parthenogens, but the tetraploid females produce more offspring than either diploid race (Seiler 1961). Since the genome of an autopolyploid is duplicated without addition of any new genes, a superior fitness of a polyploid female should then in that case show a positive effect of polyploidy per se.

Earthworms are another interesting example. Up to 40% of the cytologically examined species among Palaearctic earthworms are polyploid. In the fashion of plants, many are hermaphrodites, which shows that animals can attain high proportions of polyploids once they rid themselves of chromosomal sex determination (Lundmark and Saura 2006). Interestingly, there are both sexually reproducing and asexual forms among the polyploids, and both sexuals and asexuals show geographical polyploidy. Lundmark and Saura (2006) argue that geographical polyploidy may be attributable to the adaptive effects of polyploidy rather than asexuality. If so, the two are separate phenomena that need to be studied individually.

D'Souza and Michiels (Chapter 18) show that parthenogenesis is often linked to hermaphroditism in flatworms and their polyploidy is not due to hybridization between species. Flatworm parthenogens can also have occasional sex. We note that the earthworm *Dendrobaena octaedra* mentioned above may be a similar case.

## 4.5 Conclusions

The evolutionary potential of an asexual lineage depends on the cytological mechanism underlying asexuality. Cytological data are therefore needed in order to understand the evolutionary potential of an asexual animal. As molecular methods have reached the level of sophistication that allows studying chromosome structures, we expect a revival of the interest in cytology of asexual animals. Studying the role of polyploidy in asexual reproduction may be methodologically even more demanding, but it is, nevertheless, important for its own sake. Many asexual animals are polyploid while about all sexuals are diploid.

## References

- Asher J Jr (1970) Parthenogenesis and genetic variability. PhD thesis. University of Michigan, Ann Arbor
- Asker SE, Jerling L (1992) Apomixis in plants. CRC Press, Boca Raton
- Balsano JS, Rasch EM, Monaco PJ (1989) The evolutionary ecology of *Poecilia formosa* and its triploid associate. In: Meffe GK, Snelson FF (eds) Ecology and evolution of livebearing fishes (Poeciliidae). Prentice Hall, Englewood Cliffs, pp. 277–297
- Beukeboom LW, Pijnacker LP (2000) Automictic parthenogenesis in the parasitoid *Venturia canescens* (Hymenoptera: Ichneumonidae) revisited. *Genome* 43: 939–944
- Bordenstein SR, Werren JH (2007) Bidirectional incompatibility among divergent *Wolbachia* and incompatibility level differences among closely related *Wolbachia* in *Nasonia*. *Heredity* 99: 278–287
- Carroll SB, Grenier JK, Weatherbee SD (2005). From DNA to diversity: molecular genetics and the evolution of animal design. Blackwell, Oxford
- Cuellar O (2005) Reproduction and the mechanism of meiotic restitution in the parthenogenetic lizard *Cnemidophorus uniparens*. *J Morphol* 133: 139–165
- Fountain MT, Hopkin SP (2005) *Folsomia candida* (Collembola): a “standard” soil arthropod. *Annu Rev Ent* 50: 201–222
- Holloway AK, Cannatella DC, Gerhart HC, Hillis DM (2006) Polyploids with different origins and ancestors from a single sexual polyploid species. *Am Nat* 167: E88–E101
- Hsu WS (1956) Oogenesis in *Habrotricha tridens* (Milne). *Biol Bull* 111: 364–374
- Lewis WH (ed.) (1980) Polyploidy/biological relevance. Plenum, New York
- Lundmark M, Saura A (2006) Asexuality does not explain the success of clonal forms in insects with geographical parthenogenesis. *Hereditas* 143: 24–33
- Ma XF, Gustafson JP (2005) Genome evolution in allopolyploids: a process of cytological and genetic diploidization. *Cytogenet Genome Res* 109: 236–249
- Mark Welch JL, Mark Welch DB, Meselson M (2004) Cytogenetic evidence for asexual evolution of bdelloid rotifers. *Proc Natl Acad Sci* 101: 1618–1621
- Monaco PJ, Rasch EM, Balsano JS (1984) Apomictic reproduction in the Amazon molly, *Poecilia formosa*, and its triploid hybrids. In: Turner BJ (ed.) Evolutionary genetics of fishes. Plenum Press, New York, pp. 311–328
- Narbel-Hofstetter M (1964) Les altérations de la meiose chez les animaux parthénogénétiques. *Protoplasmatologia* VI. F2. Springer-Verlag, Wien
- Norton RA, Kethley JB, Johnston DE, O'Connor BM (1993). Phylogenetic perspectives on genetic systems and reproductive modes of mites. In: Wrensch DL, Ebbert MA (eds) Evolution and diversity of sex ratio in insects and mites. Chapman and Hall, New York, pp. 8–99
- Nur U (1979) Gonoid thelytoky in soft scale insects (Coccoidea: Homoptera). *Chromosoma* 72: 89–104

- Pagani M, Ricci R, Redi CA (1993) Oogenesis in *Macrotrachela quadricornifera* (Rotifera, Bdelloidea). *Hydrobiologia* 255–256: 225–230
- Plantard O, Rasplus J-Y, Mondor G, Le Clainche I, Solignac M (1998) *Wolbachia*-induced thelytoky in the rose gallwasp *Diplolepis spinosissima* (Giraud) (Hymenoptera: Cynipidae), and its consequences on the genetic structure of its host. *Proc R Soc Lond B* 265: 1075–1090
- Saura A, Lokki J, Suomalainen E (1993) Origin of polyploidy in parthenogenetic weevils. *J Theor Biol* 163: 449–456
- Seiler J (1961) Untersuchungen über die Entstehung der Parthenogenese bei *Solenobia triquetrella* F.R. (Lepidoptera, Psychidae) III. Die geographische Verbreitung der drei Rassen von *Solenobia triquetrella* (bisexuell, diploid und tetraploid parthenogenetisch) in der Schweiz und in angrenzenden Ländern und die Beziehungen zur Eiszeit. Bemerkungen über die Entstehung der Parthenogenese. *Z Vererbungsl* 92: 261–316
- Seiler J (1963) Untersuchungen über die Entstehung der Parthenogenese bei *Solenobia triquetrella* F.R. (Lepidoptera, Psychidae). IV. Wie besamen begattete diploid und tetraploid parthenogenetische Weibchen von *S. triquetrella* ihre Eier? Schicksal der Richtungskörper im unbesamten und besamten Ei. Vergleich der Ergebnisse mit F1-Aufzuchten und Beziehungen zur Genese der Parthenogenese. *Z Vererbungsl* 94: 29–66
- Simonsen V, Holmstrup M (2008). Deviation from apomictic reproduction in *Dendrobaena octaedra*? *Hereditas* 145: 212–214
- Soltis PS, Soltis DE (2000) The role of genetic and genomic attributes in the success of polyploids. *Proc Natl Acad Sci USA* 97: 7051–7057
- Spitzer B (2006) Local maladaptation in the soft scale insect *Saissetia coffeae* Hemiptera: Coccidae. *Evolution* 60: 1859–1867.
- Stenberg P, Lundmark M, Knutelski S, Saura A (2003) Evolution of clonality and polyploidy in a weevil system. *Mol Biol Evol* 20: 1626–1632
- Suomalainen E, Saura A, Lokki J (1987) Cytology and evolution in parthenogenesis. CRC Press, Boca Raton
- Terhivuo J, Saura A (2006) Dispersal and clonal diversity of North-European parthenogenetic earthworms. *Biol Inv* 8: 1205–1218
- Van Wilgenburg E, Driessen G, Beukeboom LW (2006) Single locus complementary sex determination in Hymenoptera: an “unintelligent” design? *Frontiers Zool* 3: 1
- von Siebold C (1856) Wahre Parthenogenese bei Schmetterlingen und Bienen. Engelmann, Leipzig
- Weeks AR, Braeuwer JAJ (2001) *Wolbachia*-induced parthenogenesis in a genus of phytophagous mites. *Proc R Soc Lond B* 268: 2245–2251
- White MJD (1946) The evidence against polyploidy in sexually reproducing animals. *Am Nat* 80: 610–619
- White MJD (1970) Heterozygosity and genetic polymorphism in parthenogenetic animals. In: Hecht MK, Steere WC (eds) *Essays in evolution and genetics in honour of Theodosius Dobzhansky*, suppl. *Evol Biol*. Appleton-Century-Crofts, New York
- White MJD (1973) *Animal cytology and evolution*, 3rd ed. Cambridge University Press, Cambridge, UK
- Zhu HP, Ma DM, Gui JF (2006) Triploid origin of the gibel carp as revealed by 5S rDNA localization and chromosome painting. *Chromosome Res* 14: 767–776