
Intraclonal genetic variation: ecological and evolutionary aspects.

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Phylogenetic relationships between parthenogens and their sexual relatives: the possible routes to parthenogenesis in animals

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In theory, parthenogenetic lineages have low evolutionary potential because they inexorably accumulate deleterious mutations and do not generate much genotypic diversity. As a result, most parthenogenetic taxa occupy the terminal nodes of phylogenetic trees. The rate and mode of development of parthenogenesis are important factors to consider when assessing its costs and benefits since they determine both the level of genetic diversity and the ecological adaptability of the resulting lineages. The origin of parthenogenesis is polyphyletic in many taxa, suggesting that genetic systems maintaining sexuality are often labile. In addition, the loss of sex may be achieved in several ways, leading to parthenogenetic lineages with distinct genetic profiles. This could then influence not only the fate of such lineages in the long term, but also the outcome of competition with their sexual counterparts in the short term. In this paper, we review the possible evolutionary routes to parthenogenesis based on a survey of the phylogenetic relationships between sexual and parthenogenetic lineages in a broad range of animals. We also examine the different mechanisms by which parthenogenetic lineages could arise, and discuss the influence of these mechanisms on both the genetic properties and the ecological life styles of the resulting lineages. © 2003 The Linnean Society of London. *Biological Journal of the Linnean Society*, 2003, **79**, 151–163.

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INTRODUCTION

Despite the two-fold cost associated with sexual reproduction, this is the mode which largely predominates. While there is consensus concerning the benefits of sex in the long term, there is no general agreement on the explanation for its superiority over asexuality in the short term (Maynard Smith, 1971). Hypothetical short-term advantages fall into two main classes: (1) mutational – the accumulation of deleterious mutations is a major cost for asexual lineages that are incapable of purging them from the genome; (2), ecological

– the higher level of genetic diversity released by sexual reproduction is a major advantage because it facilitates escape from parasites or limits competition with relatives (Hurst & Peck, 1996).

While asexual reproduction encompasses a variety of mechanisms, including fission in unisexual organisms and fragmentation in colonial organisms, we have chosen to focus on parthenogenesis which, in the strict sense, is the development of an egg without fertilization and typically results in the production of female offspring. Resolving the paradox of why parthenogenetic females do not out-compete sexual females has stimulated evolutionary biologists for decades and generated many theories that have yet to be validated. In this context, the question of the origin and diversity of parthenogenetic lineages is an impor-

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tant issue, as these two factors may influence some fundamental assumptions of the models (Dybdaahl & Lively, 1995; Johnson & Leefe, 1999).

To begin with, the 'all else is equal' assumption, which is central to the evolution of sex theories, assumes that parthenogenetic mutants are derived from local sexual populations and have similar life-history traits to their sexual ancestors. It is likely that this assumption is violated if, for example, parthenogens arise via hybridization as they will be far more heterozygous than their sexual congeners and possibly benefit from heterosis. Second, mutational models assume that parthenogenetic lineages inexorably accumulate deleterious mutations with no process to get rid of them. However, some essentially parthenogenetic lineages experience rare sex, which may be sufficient to significantly reduce this cost and allow their persistence in both the short and long term. Third, ecological models make the assumption that sexual populations harbour greater genetic diversity than clonal populations. If parthenogenetic lineages are produced at a high rate and from various sources, their genetic diversity may reach levels comparable to those of sexual populations. Therefore, the rate and mode of development of parthenogenesis are important factors when assessing its costs and benefits since they determine both the level of genetic diversity and the ecological adaptability of the resulting lineages. This could in turn influence not only the fate of such lineages in the long term, but also the outcome of competition with their sexual counterparts in the short term.

In this paper, we review the possible evolutionary routes to parthenogenesis based on a survey of the phylogenetic relationships between sexual and parthenogenetic lineages in a broad range of animals. We also examine the different mechanisms by which parthenogenesis could arise, and discuss the influence of these mechanisms on both the genetic properties and the ecological life styles of the resulting lineages.

DISTRIBUTION OF UNISEXUAL REPRODUCTION IN EUKARYOTES

The vast majority of eukaryotic species reproduce bisexually, yet approximately one out of every 1000 multicellular eukaryotic taxa is unisexual (parthenogenetic) or asexual. Parthenogenetic reproduction occurs in many phyla, especially in plants, rotifers, nematodes and arthropods (Bell, 1982). In the animal kingdom, 19 out of 34 phyla contain unisexual taxa. Approximately 70 unisexual taxa have been identified in vertebrates, although none have been found in birds and mammals (Avisé, Quattro & Vrijenhoek, 1992). The spread of parthenogenetic reproduction throughout the tree of life suggests multiple origins of unisex-

uality. However, it also appears that most unisexual taxa occupy terminal nodes of phylogenetic trees which indicates that, even if initially successful, they are evolutionary dead-ends. There are exceptions to this pattern in that exclusively parthenogenetic species can form higher taxonomic groups, as has occurred in the famous 'unisexual scandals' (Maynard Smith, 1986) including the rotifer class Bdelloidea (360 described species) and the ostracod family Darwinulidae (26 described species) (Judson & Normark, 1996; Mark Welch & Meselson, 2000).

MODES OF PARTHENOGENESIS

There are many modes of parthenogenesis that are associated with a wide variety of cytological mechanisms, which are too numerous to cover here: the main ones are described in Figure 1. Further details can be

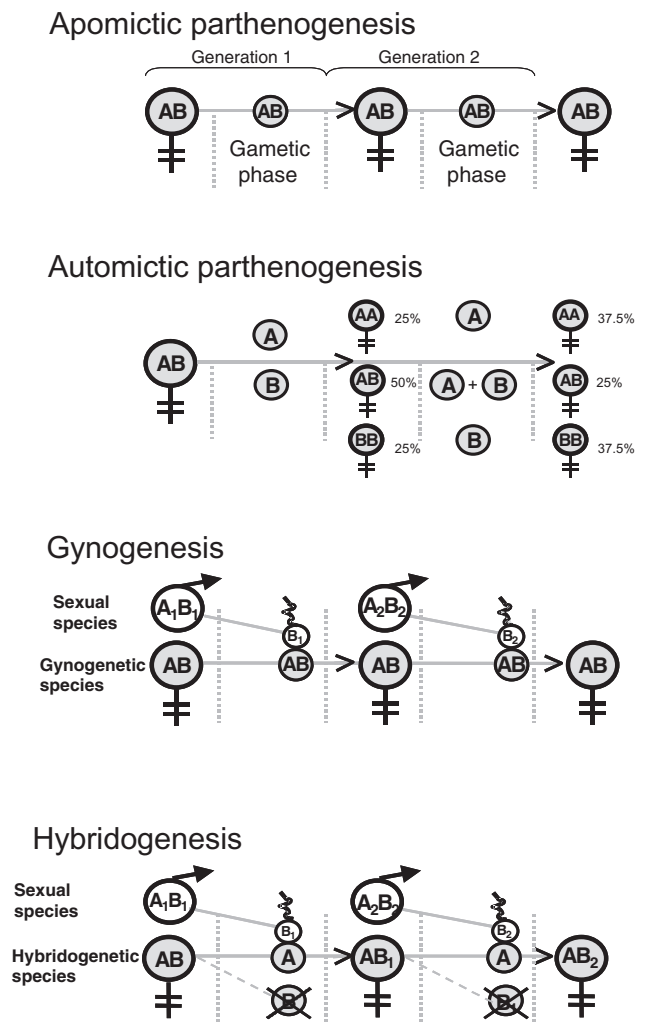


Figure 1. Main parthenogenetic modes of reproduction in animals.

found in White (1973), Parker & Niklasson, 1999), Vrijenhoek (1998) and Beukeboom & Vrijenhoek (1998).

Tychoparthenogenesis (or facultative parthenogenesis) refers to the occasional, spontaneous development of eggs without fertilization in animals. Occasional or facultative parthenogenesis is quite common: for example, it is found in at least ten insect orders and occurs with obligate parthenogenesis in genera within at least six of them. The cytological mechanisms associated with tycho-parthenogenesis are diverse and include both apo- and automixis (see below). It is likely that some obligately parthenogenetic species have evolved from tycho-parthenogenetic ones (Kramer & Templeton, 2001). Although this is an important phenomenon to consider in context, we will concentrate on animal species for which parthenogenesis has been irreversibly established.

Apomictic parthenogenesis (or apomixis) involves the suppression of meiosis so that offspring are produced from unfertilized eggs by a mitosis-like cell division resulting in genetic identity to the mother, barring mutation (but see Lushai & Loxdale, 2002). Apomixis is commonly found in invertebrates such as rotifers and all major groups of arthropods.

Automictic parthenogenesis (or automixis), in contrast to apomixis, retains meiosis with restoration of diploidy by duplication or fusion of the gametes produced by the female parent. Automixis occurs in many parthenogenetic stick insects and some weevils. In general, it rapidly leads to complete homozygosity (Fig. 1). However, one form found in unisexual lizards (Cuellar, 1971) and Australian grasshoppers (White, 1973), known as endomeiotic doubling, involves replication of the chromosomes prior to normal meiosis, which restores diploidy in the resulting egg. Because replicated chromosomes pair prior to meiosis I, the offspring are genetically identical to the mother, and heterozygosity is maintained.

Gynogenesis is a form of parthenogenesis in which sperm from a related bisexual species are required to stimulate egg development without contributing to the genetic composition of the offspring.

Hybridogenesis is a hemiclinal mode of reproduction in that half of the genome is transmitted sexually while the other half is transmitted clonally. Sperm and egg nuclei fuse and paternal genes are expressed in the offspring, but only the maternal genome is transmitted to the next generation. For example, both gynogenesis and hybridogenesis are utilized by unisexual fish species in the genus *Poeciliopsis*.

MOLECULAR TESTS FOR THE EVOLUTION OF PARTHENOGENESIS

In the last decade, patterns of evolution in parthenogens have been resolved through the use of molecular markers and the reconstruction of phylogenetic relationships between bisexual and unisexual taxa above and below the species level. Three molecular approaches, described below, have been commonly used to address questions concerning the evolution of parthenogenesis, in particular: (1) Do parthenogenetic lineages have a single (monophyletic) or multiple (polyphyletic) origin? (2) Which mechanisms are responsible for the loss of sex? (3) How old are the parthenogenetic lineages?

SINGLE MARKER APPROACH

Phylogenetic approaches to study the origin of parthenogenetic lineages originally used a single category of molecular markers, in particular mitochondrial DNA (mtDNA). Work based on restriction enzyme site or sequence analysis was mainly devoted to finding the number of independent events leading to the loss of sex within a particular species, genus or family, and to determine whether unisexual taxa had a monophyletic or a polyphyletic origin (e.g. Avise *et al.*, 1992). Phylogenetic trees were generally rooted with the closest sexual outgroup to reconstruct the history of the loss of sex assuming: (1) that sexual reproduction is the ancestral state (which is generally well supported) and (2) that the loss of sex is irreversible (which is rarely demonstrated but more parsimonious).

COMBINATION OF NUCLEAR AND MATERNALLY INHERITED MARKERS

In strictly unisexual lineages, phylogenies based on maternally inherited (e.g. mtDNA) and nuclear markers should correspond perfectly. Indeed, since recombination does not occur, nuclear and mitochondrial genomes are inherited as one unit. In contrast, if unisexual lineages result from hybridization with conspecific or interspecific sexual relatives, or if rare sex occurs within unisexual lineages, incongruence between nuclear and mitochondrial phylogenies should be found. Using this approach, Crease, Stanton & Hebert (1989) demonstrated the repeated emergence of obligately parthenogenetic *Daphnia* lineages from crosses between cyclic parthenogens and male-producing obligate parthenogens. On the other hand, Belshaw *et al.* (1999) showed rare sex in parthenogenetic species of parasitoid wasps of the genus *Lysiphlebus*.

ALLELE DIVERGENCE TEST

The allele divergence test was proposed independently by Birky (1996) and Mark Welch & Meselson (2000) to show the antiquity of some unisexual taxa. It consists of a comparison of allelic divergence within and among bisexual and unisexual taxa. If unisexual lineages undergo millions of years of mitotic reproduction, nuclear homologous alleles within lineages, if not lost, will be highly divergent. Moreover, if unisexual lineages derive one from another (sexual reproduction being lost once), each of their alleles is expected to be most similar to alleles in another unisexual lineage. This is because divergence time between two homologous alleles within an individual genome is always greater than divergence time between two unisexual lineages. Moreover, alleles and mitochondrial haplotypes in the bisexual lineages from which unisexual lines are derived might also be very divergent from those in the unisexual lineages. In contrast, when hybridization leads to unisexuality, the hybrid parthenogen will inherit half of its nuclear alleles from each of two separate bisexual lineages, but will inherit its maternally transmitted genome from only one parent. This test was applied for the first time to bdelloid rotifers and confirmed that these organisms have evolved without sex for tens millions of years (Mark Welch & Meselson, 2000).

UNIQUE OR MULTIPLE ORIGINS OF PARTHENOGENESIS?

An important step in understanding patterns of evolution in parthenogens is to distinguish the cases of single vs. multiple origins from their bisexual ancestor. A compilation of phylogenetic studies based on one of the three possible molecular approaches described above clearly indicates that parthenogenesis has evolved multiple times in most sexual-parthenogenetic complexes studied so far (Table 1). For example, at least five independent origins of the unisexual fish *Poeciliopsis monacha-lucida* Miller are inferred from mtDNA phylogeny (Avisé *et al.*, 1992). Similarly, combined nuclear and mtDNA phylogenies support at least four independent losses of sex in the ostracod *Eucypris virens* (Jurine) (Schön *et al.*, 2000) and a minimum of three losses in the aphid *Rhopalosiphum padi* (L.) (Fig. 2; Delmotte *et al.*, 2001). There are a few exceptions to this general pattern, such as the bdelloid rotifers, a class that is entirely unisexual suggesting that unisexual reproduction has evolved only once in this group. The polyphyletic origin of parthenogens can be recognized at several taxonomic levels, although it is difficult to define the exact taxonomic level in some sexual-parthenogenetic complexes. Many studies have shown multiple origins of parthe-

nogenetic taxa not only at the genus but also at the species level (Table 1).

There are other ways, in addition to phylogenetic methods, to infer unique vs. multiple origins of parthenogens. An efficient method to assess the lability of sexual reproduction at different taxonomic levels is to survey breeding system variation among taxa within a particular group. For example, high rates of transition to unisexuality are found in aphids and ostracods. This results in a vast number of species in which bisexual and unisexual lineages coexist: 37% of a sample of 270 aphid species (Moran, 1992), and 57% of a sample of 286 ostracod species (Butlin, Schön & Griffiths, 1998) show coexisting bisexual and unisexual lineages.

The consequences of a polyphyletic origin of unisexual lines are several. First, polyphyly contributes to an increase in the genetic diversity in the pool of unisexual lines. Second, it leads to the emergence of unisexual lines that could differ in their genetic profile from one another, and from their bisexual ancestors (e.g. heterozygosity), which also depends on the mechanisms involved in the loss of sex (see below). Third, transitions to unisexuality are often accompanied by changes in life-history traits, phenotype and ecological life style compared to the bisexual ancestors. All of these consequences of the loss of sex are likely to influence not only the outcome of the competition with bisexual congeners in the short term, but also the evolutionary fate of unisexual lineages in the longer term.

MODES OF ORIGIN OF PARTHENOGENETIC LINEAGES

There are several ways in which parthenogenetic lineages could arise. As stated before, depending on the mechanism leading to the loss of sex, newly emerging unisexual lineages may differ greatly in their genotypic and phenotypic attributes compared to bisexual congeners. Therefore, it will likely be necessary to modify ideas about the relative costs and benefits of sexual and parthenogenetic reproduction because the assumption that 'all else is equal' between bisexuals and their unisexual descendants is not valid in many cases. The major modes of origin of parthenogenetic animal lineages are presented hereafter (Fig. 3).

SPONTANEOUS ORIGIN

Spontaneous loss of sex may occur through mutations in the genes involved in the production of sexual forms and successful meiosis. An important issue is the extent to which the resulting parthenogenetic lineage will be reproductively isolated from its sexual ancestor. At one extreme, a mutation might occur that fixes a single genotype into a strict

Table 1. Type of parthenogenesis, ploidy level, number and mode of origin of unisexual taxa in vertebrates and invertebrates

Phylum	Class/Order	Parthenogenetic taxa	Mode of reproduction	Ploidy	Number of origin	Mode of origin	Reference		
Platyhelminthes	Turbellaria	<i>Dugesia polychroa</i>	gynogenetic	2n-4n	polyphyletic	contagious	Pongratz <i>et al.</i> (1998)		
		Bdelloidea	apomictic	2n	monophyletic	?	Mark Welch & Meselson (2000)		
		<i>Octolasion tyrtaeum</i>	apomictic	2n-4n	polyphyletic?	contagious	Jaenike & Selander (1979)		
		Lasaea	gynogenetic	3n-6n	polyphyletic	hybrid	O'Foighil & Smith (1995), Taylor & O'Foighil (2000)		
Arthropoda	Gastropoda	<i>Campeloma</i>	apomictic	2n	polyphyletic	spontaneous	Johnson & Leefe (1999)		
		<i>Potamopyrgus antipodarum</i>	apomictic	3n	polyphyletic	hybrid	Johnson & Leefe (1999)		
	Ostracoda	Darwinulidae	apomictic	2n	polyphyletic	polyphyletic	spontaneous	Dybdahl & Lively (1995)	
		<i>Cyprinotus incongruens</i>	apomictic	2n	monophyletic	?	Schön <i>et al.</i> (1998)		
		<i>Eucypris virens</i>	apomictic	2n-4n	polyphyletic	spontaneous	Turgeon & Hebert (1994)		
		<i>Daphnia pulex</i>	apomictic	2n	polyphyletic	contagious	Turgeon & Hebert (1994)		
		<i>D. middendorffiana</i>	apomictic	2n	polyphyletic	contagious	Schön <i>et al.</i> (2000)		
		<i>Trichoniscus pusillus</i>	apomictic	polyploid	polyphyletic	hybrid	Hebert (1981), Crease <i>et al.</i> (1989)		
		<i>Artemia</i>	apomictic/automictic	3n	polyphyletic	hybrid	Dufresne & Hebert (1994)		
		<i>Rhopalosiphum padi</i>	apomictic/automictic	2n-5n	polyphyletic?	hybrid	Theisen <i>et al.</i> (1995)		
Coleoptera	Homoptera	<i>Aramigus tessellatus</i>	apomictic	2n	polyphyletic	hybrid	Browne (1992)		
		<i>Polydrusus mollis</i>	apomictic	2n	polyphyletic	hybrid	Delmotte <i>et al.</i> (2003)		
		<i>Otiorynchus saber</i>	apomictic	2n	polyphyletic	spontaneous	Delmotte <i>et al.</i> (2001)		
		<i>Solenobia triquetrella</i>	automictic	2n	polyphyletic	contagious	Simon <i>et al.</i> (1996)		
		<i>Aramigus tessellatus</i>	apomictic	3n	polyphyletic	hybrid?	Normark (1996)		
		<i>Polydrusus mollis</i>	apomictic	2n,3n	polyphyletic	hybrid?	Tomiuk <i>et al.</i> (1994)		
		<i>Otiorynchus saber</i>	apomictic	3n,4n	polyphyletic	hybrid	Tomiuk & Loeschke (1992)		
		<i>Solenobia triquetrella</i>	automictic	2n-4n	polyphyletic	hybrid?	Lokki <i>et al.</i> (1974), Tomiuk & Loeschke (1991)		
		Hymenoptera	Orthoptera	<i>Alsophila pometaria</i>	gynogenetic	2n	polyphyletic	spontaneous	Harshman & Futuyama, 1985)
				<i>Lysiphlebus</i>	apomictic?	2n	polyphyletic	hybrid?	Belshaw <i>et al.</i> (1999)
<i>Venturia canescens</i>	apomictic			2n	polyphyletic	contagious	Schneider <i>et al.</i> (2002)		
<i>Warramaba virgo</i>	apomictic			2n	polyphyletic	hybrid	Honeycutt & Wilkinson (1989)		
<i>Bacillus lyceorum</i>	apomictic			3n	polyphyletic?	hybrid	Mantovani (1998)		
<i>Timema</i>	apomictic			?	polyphyletic	hybrid?	Law & Crespi (2002)		
<i>Phoxinus</i>	gynogenetic			2n,3n	monophyletic?	hybrid	Elder & Schlosser (1995)		
<i>Poecilopsis</i>	hybridogenetic			2n	polyphyletic	hybrid	Quattro <i>et al.</i> (1992)		
Sauria	Phasmatoptera			<i>Cnemidophorus</i>	gynogenetic	3n	polyphyletic	hybrid	Vrijenhoek (1993)
				<i>Lacerta unisexualis</i>	automictic	2n,3n	polyphyletic	hybrid	Avise <i>et al.</i> (1992)
		<i>Lacerta armeniaca</i>	automictic	2n	monophyletic?	hybrid	Fu <i>et al.</i> (1998)		
		<i>Heteronotoa binoei</i>	automictic	2n	polyphyletic?	hybrid	MacCulloch <i>et al.</i> (1995)		
Chordata	Amphibia	<i>Ambystoma</i>	gynogenetic	3n	polyphyletic	hybrid	Moritz (1991)		
		<i>Rana esculenta</i>	hybridogenetic	2n	polyphyletic	hybrid	Spolsky <i>et al.</i> (1992) Avise <i>et al.</i> (1992)		

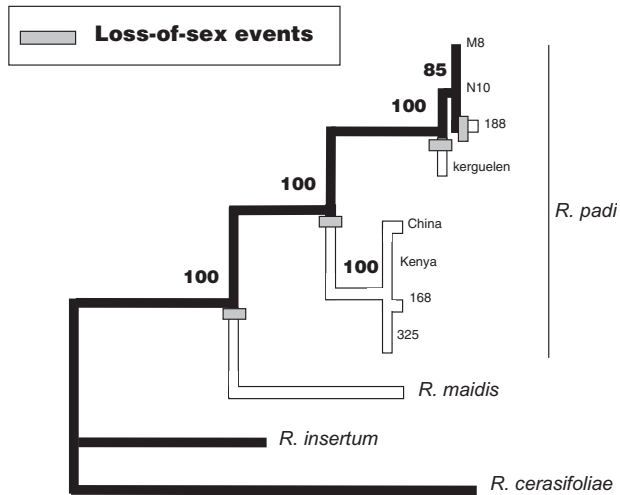


Figure 2. Phylogenetic relationships between cyclic (black lines) and obligate (white lines) parthenogens of the aphid *Rhopalosiphum padi*. The phylogeny, based on 1006 bp of the mitochondrial cytochrome *b* gene, reveals at least three independent losses of sex in this species. The numbers at the nodes are bootstrap percentages (from Delmotte *et al.*, 2001).

parthenogenetic lineage. Alternatively, mutation might initiate a lineage that produces a mix of sexual and parthenogenetic offspring, or a lineage that produces males and parthenogenetic females (Butlin *et al.*, 1998; Simon, Risper & Sunnucks, 2002). In many animal species, a small proportion of unfertilized eggs develop spontaneously into zygotes (tycho-parthenogenesis), providing opportunities to select for parthenogenesis in the laboratory and in nature (Kramer & Templeton, 2001). Selection experiments on several bisexual *Drosophila* species have shown that some strains are able to produce up to 6% of viable offspring from unfertilized eggs (Stalker, 1954; Carson, 1967). Spontaneous origins of parthenogenetic lineages have been demonstrated in a wide range of invertebrates including ostracods, snails, *Daphnia*, aphids and moths (Table 1).

In cyclically parthenogenetic invertebrates, parthenogenetic and sexual generations alternate regularly in the life cycle. However, transitions to obligate (strict) parthenogenesis often occur in such organisms and could result from several mechanisms. For example, genes that suppress meiosis have been suspected in *Daphnia* (Hebert, 1981; Innes & Hebert, 1988). In aphids, gene modifications that alter the responsiveness to sex-inducing environmental conditions might account for spontaneous origins of parthenogenetic lineages. This might involve periodicity genes or genes that regulate hormonal expression (Simon *et al.*, 2002).

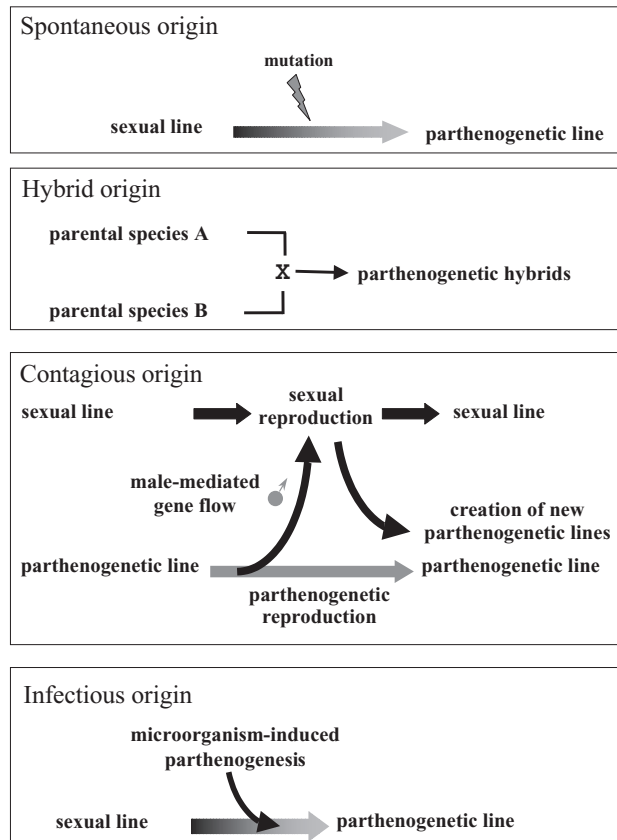


Figure 3. Main modes of origin of parthenogenetic lineages in animals. See text for explanations.

HYBRID ORIGIN

Interspecific hybridization can disrupt meiosis and create opportunities for the selection of cytological processes that rescue egg production (Vrijenhoek, 1998). Hybridization is a major route to parthenogenesis in animals, and most, if not all, unisexual vertebrates have a hybrid origin (Avisé *et al.*, 1992). Although the mode of origin of parthenogenesis is more diverse in invertebrates, hybridization leading to parthenogenetic lineages is a very frequent event and has been demonstrated in snails, crustaceans and many insects such as weevils, stick insects and grasshoppers (Table 1).

Parthenogenetic hybrids resulting from crosses between two bisexual species possess high heterozygosity and alleles typical of the two parental species. This genotypic architecture is convenient not only to detect the hybrid origin of the parthenogenetic lineages, but also to identify the parental species (when they have not gone extinct) and the direction of the crosses by combining nuclear and maternally inherited markers.

The cytogenetic processes that disrupt meiosis in parthenogenetic lineages may sometimes lead to an

incomplete loss of sex. For example, the fish genus *Poeciliopsis* contains six unisexual taxa that have resulted from crosses between *P. monacha* Miller and four other bisexual species. Three of these unisexual hybrids are gynogenetic triploids while the remaining are hybridogenetic diploids (Vrijenhoek, 1998). As a result, unisexual *Poeciliopsis* still require insemination from bisexual relatives, which consequently constrains their habitat range (Beukeboom & Vrijenhoek, 1998). In a similar way, many parthenogenetic lineages retain the potential to produce males. Whether this residual male production is a side-effect of the complex cytogenetic processes leading to parthenogenetic hybrids is unknown.

Initial hybridization between bisexual animal species usually leads to the production of diploid parthenogenetic lineages. However, it has been established that both plant and animal polyploids often have a hybrid ancestry (Dufresne & Hebert, 1994). Indeed, the majority of unisexual vertebrates (64% according to Avise *et al.*, 1992) and invertebrates that have arisen via hybridization are polyploids. It is thought that the most common route to triploidy in parthenogens is the fertilization of a parthenogenetically produced diploid egg by the sperm of a male from the bisexual ancestor (intraspecific) or from a closely related species (interspecific). Further backcrossing by polyploid parthenogens can lead to even higher ploidy levels. In some cases, hybridization is thought to occur between sexual females and males produced by parthenogenetic lineages. This is a separate issue and is developed in the next section.

CONTAGIOUS ORIGIN

Parthenogenetic lineages may arise secondarily from pre-existing parthenogenetic lineages as a result of incomplete reproductive isolation between sexuals and parthenogens. Indeed, hybridization between parthenogenetic females and the males of either the same or closely related species is thought to be the major route to polyploidy in unisexuals. Moreover, as mentioned earlier, many parthenogenetic lineages are still able to produce males while a few others can produce a mixture of sexual and parthenogenetic females.

Parthenogenetically produced males have been observed in freshwater flatworms (Pongratz *et al.*, 1998), earthworms (Jaenike & Selander, 1979), ostracods (Turgeon & Hebert, 1994; Butlin *et al.*, 1998), brine shrimp (Browne, 1992), snails (Samadi *et al.*, 1997), *Daphnia* (Hebert, 1981), wasps (Plantard *et al.*, 1998; Belshaw *et al.*, 1999), and aphids (Blackman, 1972; Simon, Blackman & Le Gallic, 1991). Intermediate lineages that invest in both sexual and parthenogenetic reproduction at the

same time are also known in aphids (Dedryver *et al.*, 1998) and ostracods (Martens, 1998). This gene flow between sexual and parthenogenetic lineages allows the spread of unisexuality genes in a contagious fashion that could rapidly convert sexual into parthenogenetic lineages. In addition, occasional gene exchange with sexual lineages may be important for the persistence of otherwise parthenogenetic lineages. Under such events, new parthenogenetic genotypes are generated by recombination, slowing the accumulation of deleterious mutation and increasing genetic diversity in parthenogenetic populations.

Jaenike & Selander (1979) first modelled the spread of a dominant gene in sexual populations that causes parthenogenetic development of eggs while allowing normal spermatogenesis. They predicted that such a gene would spread to fixation, while there would be concomitant selection for the reduction of male allocation. These theoretical results were validated in their study of parthenogenetic earthworms. Theoretical consequences of the spread of unisexuality genes were further developed and validated in *Daphnia* (Hebert, 1981; Innes & Hebert, 1988) and in aphids (Rispe & Pierre, 1998; Rispe *et al.*, 1998; Dedryver *et al.*, 2001).

Despite the high potential of this contagious mechanism to generate parthenogenetic lineages, its actual incidence in the wild is largely unknown and could be limited by at least three factors:

- (1) Parthenogenetically produced males must be functional. Many parthenogenetic populations of *Artemia* contain a small number of males but when they are crossed to sexual females in the laboratory, no offspring are obtained, although the males are capable of producing sperm (Browne, 1992). Similarly, non-functional males are occasionally produced by some species of apomictic ascid mites (Norton & Palmer, 1991).
- (2) Parthenogenetically produced males must successfully mate with conspecific sexual females: they might be less adept at seeking the other sex or be out-competed by sexually produced males.
- (3) Parthenogenetically produced males must transmit their parthenogenetic genes to their offspring, which should result in the creation of new parthenogenetic lineages. In both *Daphnia* and aphids, it has been demonstrated in the laboratory that matings between parthenogenetically produced males and females from sexual lineages generate both sexual and parthenogenetic lineages (e.g. Innes & Hebert, 1988 for *Daphnia* and Blackman, 1972 for aphids).

This is good evidence that contagious parthenogenesis could operate in these invertebrates, but it still needs to be confirmed in the field.

INFECTIOUS ORIGIN

A further possible mode of origin of parthenogenetic lineages is through infection by vertically inherited microorganisms. Induction of parthenogenesis is mainly accomplished by *Wolbachia*, a member of the Proteobacteria. It is known to induce parthenogenesis in parasitoid wasps such as *Trichogramma* as well as thrips and mites (Werren, 1997; Stouthammer *et al.*, 1993; Weeks, Reynolds & Hoffman, 2002). Females infected with *Wolbachia* reproduce parthenogenetically, but sexual reproduction can be restored by treatment with antibiotics. Recently, other bacteria that are unrelated to the Proteobacteria have been shown to induce parthenogenesis in *Encarsia*, a genus of parasitoid wasps (Zchori-Fein *et al.*, 2001), and in a mite species (Weeks, Marec & Breeuwer, 2001). These recent findings suggest that parthenogenesis induction may be a relatively frequent event, although it has only been found so far in haplodiploid organisms. Unfertilized infected eggs, which would normally develop as haploid males, develop as diploid females. Diploidy is restored either by gamete duplication, that leads to complete homozygosity, or by an unknown cytogenetic mechanism that maintains heterozygosity (Weeks *et al.*, 2002).

MULTIPLE MODES OF ORIGIN

While parthenogenetic lineages are generated by a single mechanism in some species (e.g. hybrid origin of unisexual vertebrates), parthenogenetic lineages of other species can arise through several mechanisms. It has been shown, for example, that parthenogenetic lineages of ostracods often have a dual origin since diploid clones originate from the spontaneous loss of sex while polyploid clones arise from hybridization between parthenogenetic females and males from the same or closely related species (Chaplin, Havel & Hebert, 1994). Similarly, diploid parthenogenetic lineages of the freshwater snail *Campeloma* originate by spontaneous loss of sex while triploid parthenogenetic lineages originate by hybridization (Johnson & Leefe, 1999). Obligate parthenogenesis occurs in all species of the *Daphnia pulex* (Leydig) complex. Diploid clones within this complex have arisen spontaneously or via contagious spread, while polyploid clones often have a hybrid origin (Dufresne & Hebert, 1994). Another example is the case of the aphid *R. padi*; biological and phylogenetic evidence shows that parthenogenetic lineages can arise from three distinct origins: spontaneous, hybrid or contagious (Simon, Leterme & Latorre, 1999; Delmotte *et al.*, 2001; Delmotte *et al.*, 2003). These are extreme examples, but they show that sexual reproduction is a rather labile genetic system that could lead to many situations where sexual popula-

tions coexist with a pool of polyphyletic and diverse parthenogenetic lineages. As a consequence, short-term benefits of sex are likely to be higher than its 'two-fold' cost, in order to compensate for such intense competition with parthenogenesis.

GENETIC AND ECOLOGICAL ATTRIBUTES OF PARTHENOGENS

GENOTYPIC ARCHITECTURE

The genotypic architecture of parthenogens is mainly shaped by: (1) the mode and rhythm of emergence of parthenogenetic lineages and (2) the age of parthenogenetic lineages and their responsiveness to selection. The effects of these factors can be envisaged at two levels: individual/genotype and population.

At the individual/genotype level, high heterozygosity is expected in parthenogenetic lineages that arose from interspecific hybridization. Many of those parthenogenetic hybrids also show ploidy shifts, which could result in a very complicated genetic make-up. However, increasing heterozygosity is also expected in old parthenogenetic lineages as a result of differential mutation accumulation in the two alleles (in the case of diploid unisexuals) through time. As discussed earlier, it is possible to discriminate between these two sources of heterozygosity (see also Normark, Judson & Moran, 2003). In sharp contrast to parthenogenetic hybrids, parthenogenetic lineages that have a spontaneous automictic origin may be highly homozygous while those that have an infectious or spontaneous apomictic origin will show, at the time of their formation, genotypes similar to those of their sexual ancestors. Of course, allele divergence through time under clonal reproduction also applies in such parthenogenetic lineages which gradually leads to genetic differentiation from their sexual ancestors. Lastly, contagious parthenogenesis results in the introgression of alleles from sexual into parthenogenetic lineages. If some of the offspring of males of parthenogenetic lineages remain sexual, the gene flow would even be bi-directional (Fig. 3). Thus, repeated gene flow between male-producing parthenogens and their sexual relatives should limit the extent of genetic differentiation between the two reproductive modes.

There are several factors that determine the level of genotypic diversity among populations of parthenogens. According to Vrijenhoek (1998), most of the diversity seen in parthenogenetic lineages arises from multiple origins from sexual ancestors, rather than from other processes such as mutation accumulation within parthenogenetic lineages. If this is true, the parthenogenetic component of a sexual-unisexual species complex should encompass many phylogenetically distant parthenogenetic lineages rather than a few

highly related ones. This hypothesis has never been tested properly, although empirical data suggest that the relative importance of these two factors in generating clonal diversity differs considerably between parthenogenetic taxa. Mutation accumulation is the major, if not the only factor responsible for genetic diversification in the asexual rotifer class, Bdelloidea, which includes approximately 360 species (Mark Welch & Meselson, 2000). By contrast, the two factors seem to contribute equally to the clonal diversity observed in obligately parthenogenetic populations of the aphid *R. padi* (Delmotte *et al.*, 2001, 2002). Hence, the use of clonal diversity as a measure of the age of clonal lineages, as proposed by some authors (e.g. Fu *et al.*, 1998), seems unrealistic.

Factors other than mode of origin and mutation accumulation may influence the level of genetic diversity in parthenogenetic populations. Rare sex and other recombination events such as chromosomal rearrangement, gene conversion and mitotic crossing over may increase genetic variation, although the extent of such phenomena is poorly known. The fitness of clones and subsequent clonal turn over (i.e. the ecological success and longevity of clones) are also important considerations. New clones may be generated at a high rate but rapidly eliminated by natural selection. As a result, the genetic diversity usually measured in the field has already been eroded by the operation of selection. The fact that parthenogenetic populations are sympatric to or isolated from sexual congeners might also influence their level of genetic diversity (Martens, 1998; Pongratz *et al.*, 1998). For example, genetic diversity in parthenogenetic populations of planarians of the genus *Dugesia* that are sympatric with their sexual relatives is twice as great as that in isolated populations (Pongratz *et al.*, 1998). A similar pattern has been observed in *Daphnia* populations (Hebert *et al.*, 1989). This seems to indicate that transitions from sexual to parthenogenetic reproduction are a rather frequent event, but also that newly created clones are not always successful.

ECOLOGICAL LIFE STYLE OF PARTHENOGENS

Generally, parthenogenetic lineages are categorized as 'generalists' or 'specialists' depending on whether they have a wide niche and broad environmental tolerance, or high fitness in a limited range of environments. There have been numerous attempts to determine which ecological factors favour specialized clones in certain circumstances and generalized clones in others. This literature, which has been reviewed in recent papers (e.g. Vrijenhoek, 1998; Parker & Niklasson, 1999), will not be discussed here. Rather, attention will focus on the influence of the mode of clonal

origin on the ecological and phenotypic attributes of parthenogens.

It has been suggested that parthenogenetic lineages arising from hybridization enjoy hybrid vigour (heterosis), which in turn confers high fitness in a broad range of environments (White, 1978; Lynch, 1984). For instance, it has been reported that parthenogenetic hybrids in frogs (*Rana*) and fish (*Poeciliopsis*) have enhanced ecological tolerance relative to their sexual counterparts (discussed in Vrijenhoek, 1998). Yet, this hypothesis suffers three major flaws. There are numerous counter-examples showing reduction in viability of parthenogenetic hybrids that may result from cytogenetic accidents (Templeton, 1983). In addition, the strong association between parthenogenesis and polyploidy makes it difficult to test for heterosis as polyploidy *per se* is also thought to confer an ecological advantage in 'marginal' habitats (e.g. Dufresne & Hebert, 1994). Moreover, the ecological success of a few parthenogenetic hybrids is likely to hide the failure of the many others that were quickly purged by natural selection. This was verified in laboratory experiments on *Poeciliopsis*: while most parthenogenetic hybrids synthesized were sterile and less viable than non-hybrid offspring, several hybrid lineages were as fit as their sexual progenitors (Wetherington, Schenck & Vrijenhoek, 1987). At the other extreme, the imposition of complete homozygosity can also generate high variance in viability and fecundity among offspring produced by some forms of automixis (Templeton, 1982). Conversely, the fitness of parthenogens generated by infectious or contagious spread, or by spontaneous apomixis may fall within the range typically seen for the sexual populations from which they were derived (Dybdahl & Lively, 1995; Rispe, Simon & Pierre, 1996).

Another important consideration is that the modes of origin and type of parthenogenesis have their own influence on the geographical distribution of parthenogenetic lineages. It is clear that the distribution of unisexuals reproducing by sperm-dependent parthenogenesis (e.g. gynogenesis, hybridogenesis) is constrained by the requirement for conspecific sexual populations (Beukeboom & Vrijenhoek, 1998). In the same way, contagious parthenogenesis can only influence clonal diversity if male-producing parthenogens are in close geographical proximity to their sexual relatives. This could explain why isolated parthenogenetic populations are less variable than those that are sympatric to sexual ones (Martens, 1998; Pongratz *et al.*, 1998).

An important assumption of the two-fold cost of sex is that all else should be equal between sexual and parthenogenetic lineages (Maynard Smith, 1971). It has already been shown that strong genotypic differences can exist between the two reproductive modes.

In addition, sexual and parthenogenetic lineages can differ phenotypically, in particular in life-history traits. These phenotypic differences are often realized very shortly after the formation of new parthenogenetic lineages from their sexual progenitors. For example, it has been shown that the transition from sexual to parthenogenetic reproduction in tycho-parthenogenetic *Drosophila* is accompanied by an increased mortality but shorter generation time relative to their sexual counterparts (Kramer & Templeton, 2001). There are many other examples showing differences in morphology, physiology, life history and behaviour between parthenogenetic and conspecific sexual lineages that indicate potential for ecological diversification in parthenogens (Vrijenhoek, 1998). It is thus likely that the 'all else is equal' assumption is hardly ever met.

CONCLUSIONS AND FUTURE DIRECTIONS

It is clear that parthenogenetic taxa very often have multiple origins from their sexual ancestors and that this has important consequences for both their short- and long-term success. Although there are a few well-supported examples of the long-term persistence and diversification of unisexual lineages, the majority of such lineages occupy the terminal branches of phylogenetic trees suggesting that they are relatively young on an evolutionary time scale. One of the major questions still to be answered is why most unisexual lineages do not endure, and how those few that do have managed to overcome the barriers to long-term persistence. Work on extant unisexual lineages shows that they can be ecologically very successful with broad geographical ranges that overlap and/or are more extensive than those of the sexual ancestor. Why then, do individual unisexual lineages generally seem to have such short evolutionary life-spans?

It has been argued that the accumulation of deleterious mutations (mutational meltdown through Muller's ratchet) ultimately restricts the lifespan of lineages that have lost the genetic mechanisms (such as recombination) to purge the genome of these mutations (Muller, 1964; Felsenstein, 1974; Lynch *et al.*, 1993). However, there is currently little empirical evidence that the 'mutational load' of clonal lineages does indeed increase faster than that of sexual populations over time. There is evidence for Muller's ratchet in the asexually inherited organelle genomes of plants and animals, which accumulate deleterious mutations faster than nuclear genes (Lynch, 1996, 1997; Lynch & Blanchard, 1998). Deleterious mutation accumulation has also been demonstrated in maternally inherited endosymbiotic bacteria (Moran, 1996; Wernegreen & Moran, 1999). Storhas *et al.* (2000) found increased embryo mortality in obligate parthenogenetic strains

of the freshwater flatworm *Schmidtea polychroa* Ball (formerly *Dugesia polychroa* Schmidt; Tricladida; Platyhelminthes), possibly resulting from deleterious mutations. Although it will undoubtedly be a very difficult task, an important focus of future research should be to measure the mutational load of unisexual lineages and their sexual relatives as has been done in sexual and anciently apomictic rotifers (Mark Welch & Meselson, 2001). Empirical support for the operation of Muller's ratchet in the nuclear genomes of parthenogens would then direct attention to the ancient unisexual lineages to determine how they have managed to 'escape'. For example, are mutation rates substantially lower in these organisms, do they have more efficient mechanisms of DNA repair, or is recombination somehow operating?

The occurrence of parthenogenesis in a wide array of animal taxa highlights the lability of the sexual reproductive system. Moreover, the existence of tycho-parthenogenesis and taxa in which transitions to unisexuality are frequent suggests that the genetic basis of the loss of sex need not be complex, or involve a large number of genes. However, the genes involved in transitions to unisexuality are poorly known. Progress in the field of genomics will facilitate the identification of the individual genes that are responsible for the loss of sex. Future research can then be directed towards the discovery of the mechanisms by which these genes cause such reproductive transitions. The results of this research may also provide insight into the mechanisms that prevent taxa such as mammals and birds from developing parthenogenetic modes of reproduction in the wild.

Finally, there is still a need to improve our knowledge of the ecological interactions between parthenogens and their sexual relatives. Although theory suggests that parthenogenetic females should out-compete sexual females reproductively, there are many cases of coexistence between conspecific sexual and unisexual lineages. Measurements of the relative fitness of unisexual lineages and their sexual relatives in both the field and the laboratory are required for a wide array of taxa to determine the nature and relative importance of the ecological factors that influence interactions within and between the two groups. For example, the parthenogens might not take the full demographic advantage of avoiding the cost of males because they suffer more from intra-group competition than sexual congeners (Case & Taper, 1986; Doncaster, Pound & Cox, 2000). A better understanding of the evolutionary consequences of losing sexuality will most likely emerge from model organisms because the precise molecular and cellular mechanisms of the loss of sex, the resulting genetic differences between sexual and parthenogenetic lineages, and the mechanisms that translate these

genetic differences into phenotypes can all be studied simultaneously.

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