

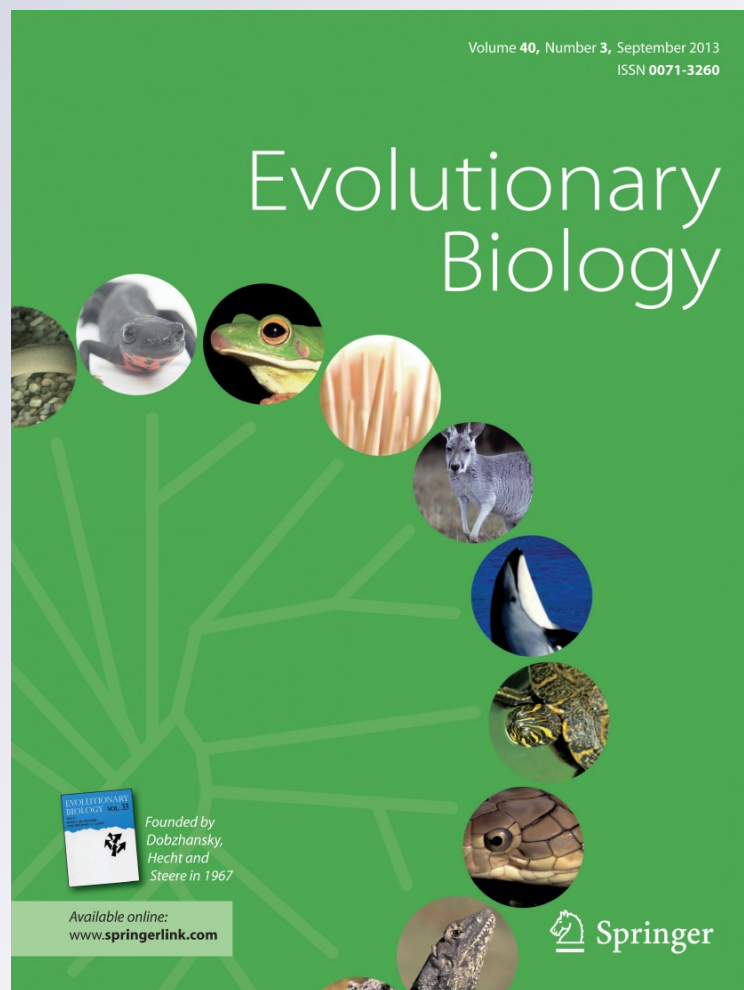
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Adaptive Significance and Long-Term Survival of Asexual Lineages

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Abstract Important questions remain about the long-term survival and adaptive significance of eukaryotic asexual lineages. Numerous papers dealing with sex advantages still continued to compare parthenogenetic populations *versus* sexual populations arguing that sex demonstrates a better fitness. Because asexual lineages do not possess any recombination mechanisms favoring rapid changes in the face of severe environmental conditions, they should be considered as an evolutionary dead-end. Nevertheless, reviewing literature dealing with asexual reproduction, it is possible to draw three stimulating conclusions. (1) Asexual reproduction in eukaryotes considerably differs from prokaryotes which experience recombination but neither meiosis nor syngamy. Recombination and meiosis would be a driving force for sexual reproduction. Eukaryotes should therefore be considered as a continuum of sexual organisms that are more or less capable (and sometimes incapable) of sexual reproduction. (2) Rather than revealing ancestral eukaryotic forms, most known lineages of asexual eukaryotes have lost sex due to a genomic conflict affecting their sexual capacity. Thus, it could be argued that hybridization is a major cause of their asexuality. Asexuality may have evolved as a reproductive mechanism reducing conflict within organisms. (3) It could be proposed that, rather than being generalists, parthenogenetic hybrid lineages could be favored when exploiting peculiar restricted ecological niches, following the “frozen niche variation” model. Although hybrid events may result in sex loss, probably caused by genomic conflict, asexual hybrids

could display new original adaptive traits, and the rapid colonization of environments through clonal reproduction could favor their long-term survival, leading to evolutionary changes and hybrid speciation. Examination of the evolutionary history of asexual lineages reveals that evolutionary processes act through transitional stages in which even very small temporary benefits may be enough to counter the expected selective disadvantages.

Keywords Frozen niche variation · Hybrid · Parthenogenesis · Red Queen · Sexual conflict · Speciation

Introduction

Although sexual reproduction is widely spread out among eukaryotes, the maintenance of asexual populations remains a major evolutionary issue. Deleterious mutations are expected to accumulate in asexual lineages and therefore contribute in limiting their long-term persistence (Keightley and Eyre-Walker 2000). Nevertheless, the putative evolutionary advantages of a costly mechanism such as sexual reproduction have been debated for decades (Barton and Charlesworth 1998) and sex is often considered as a late evolutionary acquisition.

Sexual reproduction promotes high genetic variety, whereas clonal reproduction produces identical genomes between descendants. Thus, most of the theories supporting a presumed benefit of sexual strategies have proposed that sexual reproduction enlarges the genetic diversity in the lineages in which natural selection acts (see Bernstein et al. 1984; Maynard-Smith 1978; Kondrashov 1994; Rice 2002; Lesbarrères 2011). This benefit would be mainly due to genetic recombination that generates numerous changes in

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genomes (Kondrashov 1994; Hadany and Feldman 2005). The claimed importance of recombination has even led many authors to consider as identical sex and genetic recombination (Otto 2009). The recombination of genes is indeed shared in both eukaryotic and prokaryotic phyla, suggesting both an ancient origin and a common function. As a result, sex can be considered as a nearly universal mechanism because of the ubiquity of gene recombination in living species, and genetic recombination could have been imposed as a mechanism for diversifying through evolutionary history.

Nevertheless, the mechanisms of sexual reproduction are not confined only to recombination. Recombination is only fragmentary in bacteria and archaea and all prokaryotes ignore the mechanisms of reductional meiosis and of syngamy (Vos 2009), essential characteristics of sexual eukaryotes. Recombination is a chemical process rooted in DNA exchange, while sex appears as a biological process (Penny 1985; Cavalier-Smith 2002). Thus, sex can be defined as an evolutionary mechanism that combines a total recombination of genomes, the development of meiosis, gametogenesis and a process of cell fusion called syngamy. This operational definition restricts sex to eukaryotes (Normark et al. 2003). Consequently, sex in eukaryotes significantly differs from the bacterial recombination (Redfield 2001; Lodé 2012a). The three basic characteristics of sexual reproduction are found in almost all eukaryotes, while prokaryotes are chiefly reproduced by binary fission (Lawrence 1999). This fact may suggest both the establishment of a common evolutionary mechanism in all eukaryotes and an ancient divergence with the other groups of prokaryotes (Lodé 2011, 2012b). The lack of intermediate organisms in the prokaryote-to-eukaryote transitions could indicate that recombination and sexual reproduction have accelerated the basic divergence. In addition, numerous eukaryotes privileged anisogamy, introducing male and female divergence.

However, some eukaryotes exhibit different reproductive mechanisms, such as parthenogenesis or scissiparity, and some are thought to be as exclusively asexual, though they are rare exceptions. The existence of these asexual organisms raises a crucial question about the evolutionary processes that led to the establishment of sexual reproduction and many of asexual lineages are the subject of experimental studies dealing with the potential benefits of sex (Egel 2000; Agrawal 2009). What can these exceptions tell us about evolutionary processes?

Putative Advantages of Asexual Reproduction

In fact, it is somewhat surprising to consider that so few eukaryotes show asexual reproduction. Although the

concept of species in asexual organisms has been questioned (Hillis 2007) since sexual isolation is considered the basic mechanism of speciation (de Queiroz 2005), a large majority of the species practicing partial recombination with neither meiosis nor syngamy are prokaryotes (Vos 2009). Asexual reproduction is observed in protists, in yeast or in plants but there are also many examples of animals that have interested researchers (Halkett et al. 2005). Rotifers, for instance, are a group of dioecous animals, but males are unknown in several species so that bdelloid rotifers asexually produce diploid eggs that only develop into females (Birky 2004). In some annelids, mollusks and arthropods, asexual reproduction is often the preferred mode of reproduction. Finally, asexual reproduction also exists in some vertebrates such as fish and lizards for example (Schultz 1971). The diversity of concerned species suggests that those showing asexual reproduction therefore do not have a common evolutionary origin and that their asexuality could be dependent on factors specific to the species' life history.

The possible evolutionary advantages of asexual reproduction have been discussed (see Butlin and Griffiths 1993). For example, the optional parthenogenetic reproduction of aphids is usually associated with severe and changing climatic conditions and seems to be a response to environmental stresses (Suomalainen 1962; Suomalainen et al. 1976). In social hymenoptera, parthenogenetic reproduction is generally limited to the production of males because they are haploid, but there are some cases of female-producing parthenogenesis (Slobodchikoff and Daly 1971; review in Wenseleers and Van Oystaeyen 2011). Reproduction by scissiparity or binary fission is found both in plants, protists, cnidarians and annelids, which however can also have sexual phases. Gynogenesis and hybridogenesis could be considered as forms of parthenogenesis that require sperm to initiate embryogenesis, with no fecundation (gynogenesis) or excluding the paternal genome (hemiclinal hybridogenesis) (Schmidt 1993; Beukeboom and Vrijenhoek 1998; Vorburger 2001; Pagano et al. 2003; Schmeller et al. 2005). Hybridogenetic lineages realize a hemiclinal transmission of genes since they discard one complete genome of either parental species.

Nonetheless, the reason why asexual reproduction can be maintained in such a variety of different groups remains enigmatic. It has been shown that sexual species may suffer a double constraint, called the “two-fold cost of sex” (Maynard-Smith 1978; Williams 1975; Uyenoyama 1984). Asexual lineages avoid both the cost of meiosis and the cost of males (Lively and Lloyd 1990). Therefore, an asexual population has an intrinsic capacity to grow exponentially, the asexual lineage doubling in the population with each generation.

Consequently, from a purely numerical point of view, asexual populations should outcompete sexual species to

extinction when they are in a similar ecological situation (Schley et al. 2004). Because of the obvious evolutionary benefits that asexual populations have over sexual species, it is difficult to understand why asexual lineages have not invaded the most stable environments. Referring only to adaptive advantages, it is hard to understand why phasmids have privileged asexual reproduction, including parthenogenesis and hybridogenesis (Passamonti et al. 2004; Ghiselli et al. 2007), while related species, such as dragonflies or mantis, exhibit sexual reproduction.

The Red Queen

It has been hypothesized that species reproducing asexually might suffer from greater parasite load than sexual species. The “Red Queen model” asserts that sexual recombination could offer an immediate benefit (Hamilton 1980; Hamilton et al. 1990). By mixing genes from different individuals, the resulting diversity of descendants could be an efficient response to pathogen and parasite selection. Sexual reproduction, and especially recombination, may increase the anti-parasite advantage in the sexual lineages, thus the parasite load should be higher in asexual populations (Ladle 1992).

Numerous field studies have supported some of these predictions (Hakoyama et al. 2001; Lively and Jokela 2002; Lively 2009). For instance, it has been found that sexual *Poeciliopsis* fish species survive a parasite load more successfully than asexual fish populations (Lively et al. 1990; Mateos et al. 2002). Examining the parasite load in *Carassius* fish living sympatrically, Hakoyama et al. (2001) found that sexual *Carassius* had a significantly lower load of parasites than asexual populations. Similarly, the parasite loads and juvenile mortality in a parthenogenic freshwater gastropod *Campeloma limum* were found to be significantly higher in autodiploid parthenogens, but the variance of prevalence was also higher in autodiploid parthenogens, suggesting that unparasitized parthenogens have temporarily escaped these virulent parasites (Johnson 2000). A survey of the freshwater ostracod *Eucypris virens* has also revealed that very few populations support parasite infections (Bruvo et al. 2011). Similarly, a host-parasite model by Howard and Lively (1994) showed the coexistence of sexual and asexual lineages, even under moderate levels of virulence.

By contrast, some clonal species have revealed great adaptive potential. In daphnia, tests have failed to find evidence that parasite load is able of causing synergistic epistasis between mutations in their hosts (Salathé and Ebert 2003; Haag et al. 2003). Tobler and Schlupp (2005), when testing the Red Queen prediction using four populations of the sexual fish species *Poecilia latipinna* and its asexual relative *Poecilia Formosa*, detected no differences

in parasite load. Indeed, sexual recombination could disrupt favorable gene combinations more often than it generates them. Further, asexual geckos exhibited lower parasite infestations than sexual relatives (Hanley et al. 1995; Brown et al. 1995; Kearney and Shine 2005). Natural hybrids often show very high levels of heterozygosity, thus, it has been hypothesized that asexual vertebrates may have a higher resistance to parasites owing to their hybrid origin (Brown et al. 1995).

Genetic diversity is present in asexual populations through a variety of different clones (Lushai et al. 2003), and asexual groups do not diversify less rapidly than sexual species (Barracough et al. 2003). For instance, the pattern of diversification found in bdelloid rotifers is suggestive of their adaptive radiation rather than reflecting neutral divergence and genetic drift (Fontaneto et al. 2007). Similarly, in parthenogenetic populations of the oribatid mite, either asexual or sexual lineages may show a comparable rate of speciation (Heethoff et al. 2007).

Analyzing 101 eukaryotic phylogenies, Venditti et al. (2010) concluded that the Red Queen model of a species losing a race in a selective environment should be replaced by a view linking speciation to rare stochastic events. Reviewing plant/pathogen interactions, Clay and Kover (1996) also found that gene-for-gene interactions are generally not consistent with the Red Queen hypothesis.

Finally, in bacteria reproducing asexually, there is no evidence of meiosis, but co-evolution with viruses determines the frequency of mutation rates (Pal et al. 2007). This suggests that the parasite-host co-evolution model (Red Queen) functions as a driver for mutation frequency even when sex is not implicated.

Benefit of Recombination

Since asexual reproduction results in clonal progeny, it was assumed that this reduced diversity, linked to a lack or an incomplete recombination could reduce the fitness of asexual populations. The absence of recombination in asexual organisms results in accumulation of deleterious mutations, while recombination in sexual populations is known to achieve a “Muller’s Ratchet” (Muller 1964; Felsenstein 1974). Furthermore, sexual species would be advantaged because they produce a wide variety of descendants, whereas asexual populations only have a clonal progeny with a reduced ability to adapt to changing environments (Kondrashov 1994; Penny 1985; Kondrashov 1993; de Visser and Elena 2007). Thus, genetic recombination is thought to be an essential mechanism that favors the long-term survival of a species. Further, sexual genomes contain many genes, each containing many strongly epistatic nucleotides (Watson et al. 2011).

The advantage of recombination was assessed in *Escherichia coli* microbial cultures by introducing the F plasmid carrying *Rec* genes for conjugation (Cooper 2007). All recombining lineages showed greater fitness than non-recombining lineages. In yeast populations, Goddard et al. (2005) found that sexual lineages exhibited the best fitness in selective conditions. Similarly, Morran et al. (2011) showed that co-evolution with a bacterial pathogen (*Serratia marcescens*) resulted in significantly increased outcrossing in mating populations of the nematode *Caenorhabditis elegans*.

Nonetheless, asexual organisms occupy larger ranges, survive at higher latitudes and altitudes and have a greater ability to colonize than their sexual relatives (Kearney 2005; Hörandl et al. 2008). Furthermore, even bacteria may obtain new genes by direct transfer from other bacteria, promoting their adaptation to a changing environment (Ochman et al. 2005; Pal et al. 2007). McDaniel et al. (2010) found high genetic transfer in marine bacteria which demonstrated the widespread capability of variance and adaptation in bacteria with no sexual practices. Finally, several species with clonal genomes have revealed great adaptive potential (Loxdale and Lushai 2003; Pagano et al. 2008). As a result, it is quite possible to conclude that asexual organisms with no sexual recombination may show a better adaptive potential than expected.

In fact, considerable confusion is still attached to the term “asexual” reproduction. The consequences of sexual reproduction have been tested by comparing a wide variety of sexual species and their “asexual” relatives, which often exhibit very different life-histories. The “asexual” organisms are species in which sexual reproduction has never been observed or species that practice asexual reproduction alternatively or sometimes optionally. Thus, the definition of asexual reproduction is typically based on negative evidence. Numerous species can be considered as obligate sexual but it is difficult to say that there are obligate asexual species. Although they consist in all-females lineages, parthenogenetic species are considered as “asexual” species as well as some organisms showing scissiparity or hemiclonal reproduction. Thus “asexual” reproduction includes situations that greatly contrast. Some species have developed reproduction through scissiparity or binary fission and reconstruction of new organic tissues.

The situation is further complicated because many “asexual” organisms have retained a capacity for sexual reproduction. This is the case in the haploid–diploid hymenoptera or in aphids for instance. In monogonate rotifer species, both reproduction by parthenogenesis and sexual reproduction take place during the life cycle (Fontaneto et al. 2007). Therefore, these species are rather facultative sexual species in which reproductive mechanisms differ according to the environmental context. Even species that do not use obvious sexual reproduction may still show some

characteristics of sex. Most asexual lineages are dioecus, and, despite a change in syngamy, individuals may have almost normal meiosis but not until complete reductional division (meiosis II) and sometimes may even show a complete meiosis.

If recombination is shared by many prokaryotic organisms, meiosis and syngamy mechanisms are found only in eukaryotes (Vos 2009). It might be thought that, in most cases, “asexual” eukaryotes experienced both a deterioration of meiosis mechanisms and a lack of syngamy. Nonetheless, repeated accumulation of mutations and lack of recombination in an asexual population should result in a “Meselson effect” whereby one organism is affected by high sequence divergence of two different genomes because alleles at a single locus evolve independently of each other (Mark-Welch and Meselson 2000; Butlin 2002). Thus, it remains difficult to identify what benefits asexual lineages can derive from the absence of meiosis and syngamy. In addition, many asexual organisms are phylogenetically related to other sexual species and can live under relatively similar environmental conditions.

Intragenomic Conflict and Asexual Reproduction

A better comprehension of what asexual organisms are is needed in order to understand the importance of asexual reproduction in evolutionary history. It is often useful to distinguish between the evolutionary forces favoring the origin and the subsequent elaboration and maintenance of a trait. Even very weak advantages can select for the maintenance of sex, if the process is the result of a series of separate events (Lodé 2011).

The sexual cycle of eukaryotes is often supposed to have arisen from the infection of eukaryotic cells by prokaryotic genome parasites (Bell 1993). Based on supposed primitive microbial eukaryotes such as protists which have often been assumed to be asexual organisms, it has usually been accepted that the ancestors of all eukaryotes were asexual or, at least, facultatively sexual isogamous organisms (Normark et al. 2003; Ramesh et al. 2005). Nevertheless, most of the support for this alleged primitive asexuality derives from the lack of observing sex or motile organisms considered as males. It could be noticed that anisogamy is not a mandatory requirement for sex, although it is often privileged in sexual organisms. After recombination and meiosis, isogamy should be a probable primitive step for sex. Although there is some evidence suggesting that current asexual organisms originated from ancient asexual organisms (Chaplin et al. 1994; Schön et al. 1998), considerable contradictory evidence suggests that they were originally sexual species (Judson and Normark 1996; Normark et al. 2003; Mark-Welch et al. 2004; Matheos and

Vrijenhoek 2007). The small number of asexual lineages seems to indicate that asexual eukaryotes are species that have lost sex rather than archaic species that have survived until today. Thus, it might be possible to accept the hypothesis that the ancestor of eukaryotes had certain primitive characteristics of a sexual being, such as recombination and meiosis (Lodé 2011, 2012a). Indeed, most eukaryotic species exhibited sexual reproduction while asexual eukaryotes are not organized in a continuum but are found scattered throughout the tree of life.

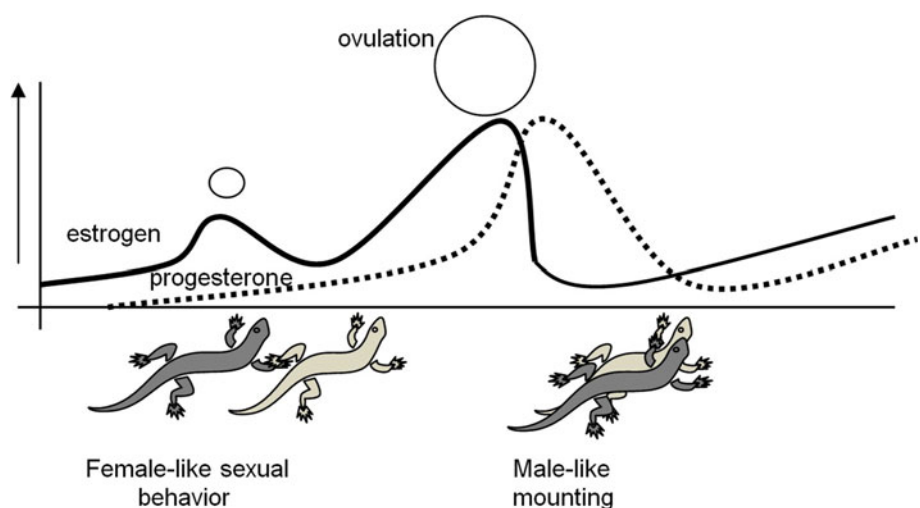
In fact, the various forms of asexual reproduction might stem from casual factors affecting some species rather than being the result of a common process. This could lead us to assume that asexual reproduction depends much more on the individual life histories of each species, and could result in peculiar adaptive conditions. The association of such different species in only one category such as “asexual reproduction” may be artificial and does not give a general explanation for the evolutionary process.

“Asexual” eukaryotes mainly reproduce by apomixis, a mechanism in which diploid eggs produced by mitotic division develop parthenogenetically into females. Thus, in eukaryotes, a species is expected to reproduce “asexually” when no functional males are detected. However, recently, male darwinulid ostracods were found although this family was considered as an exclusively ancient asexual group (Smith et al. 2006). Reviewing the literature on ciliates, Dunthorn and Katz (2010) concluded that the putative asexuality of this lineage is an observational artifact; so many microbial eukaryotes could actually be secretly sexual. Numerous plants produce asexual seeds but have a sexual male function. Oribatid mites can show a reversal from “obligate” asexual forms to sexual forms (Domes et al. 2007), but sexuality might have been lost repeatedly (Goldberg and Igc 2008). Similarly, evidence for a sexual stage was observed in the supposedly “obligatory” asexual

fungi *A. fumigatus* (Dyer and Paoletti 2005) revealing that “asexual” eukaryotes may have something to do with sex.

Eukaryotic organisms with “asexual” reproduction clearly show an alteration of the reproductive mechanisms involved in sexual reproduction. Many “asexual” lineages are genetically related to sexual species and mostly possess sexual ancestors. Some worm species reproducing asexually by scissiparity have revealed hybrid origins, and epigamy was their ancestral reproductive state (Lunt 2008; Nygren and Sundberg 2003). Asexual fungal species have sexual ancestors and may also be cryptically sexual (Sun and Heitman 2011). Parthenogenetic species, such as phasmids (Passamonti et al. 2004), *Poeciliid* fishes (Lamatsch et al. 2007), unisexual *Aspidoscelis/Cnemidophorus* lizards (Parker and Selander 1976; Crews et al. 1986, Cullum 2000), hybridogenetic water frogs (Vorburger 2001; Pagano et al. 2003; Schmeller et al. 2005) and fishes (Schartl et al. 1995; Angers and Schlosser 2007) are believed to use clonal or hemiclinal asexual reproduction, but have sexual ancestors and exhibited numerous traits shared by gonochoristic species (i.e. separate sexes in separate individuals). In *Timema* stick insects, parthenogens are evolved spontaneously from sexually reproducing species (Schwander and Crespi 2008). Asexual bdelloids are probably allotetraploids resulting from ancient hybridization events. Reconstructions of rotifer phylogenies suggest that sexual reproduction has been lost during their evolutionary history on at least three different occasions (Mark-Welch and Meselson 2000). In *Equisetum*, female gametophytes became hermaphroditic or males when cultured in the presence of sucrose (Guillon and Raquin 2002). Finally, some amphibians and many reptiles depend on environmental cues to determine sex and in some fish, this process can persist throughout life, so Crews (2012) argued that most eukaryotic lineages evolved from bisexual ancestors that could adopt both male and female roles related to their ovarian cycle (Fig. 1.).

Fig. 1 Sexual behavior in the diploid parthenogenetic lizard *Aspidoscelis/Cnemidophorus uniparens* related to the ovarian cycle (based on Woolley et al. 2004)



Thus, it could be said that sexual reproduction became “facultative” in eukaryotic organisms showing a decline in sexual fertility or losing sex during their evolutionary history, although they have sexual ancestry.

Asexual organisms may arise by mutation or loss of some key genes (Lattorff et al. 2005), but hybridization events give rise to conflicts of genomes due to a lesser genetic compatibility between the protagonists. Indeed, hybrid sterility or incompatibilities have been a focus in reproductive isolation and speciation, especially since the Haldane rule (1922) states that the sterility of heterogametic sex is the most affected by hybridization. In angiosperms, polyploidy and gene interactions should be a cause of asexual development (Quarin et al. 2001). Parthenogenetic stick insects should have a hybrid origin (Schwander and Crespi 2008). In fact, most unisexual populations have generally originated from hybridization with sexual species (Simon et al. 2003; Woolley et al. 2004; Kearney 2005; Mable 2007; Matheos and Vrijenhoek 2007), thus it could be argued that hybridization is a major cause of asexuality in eukaryotes.

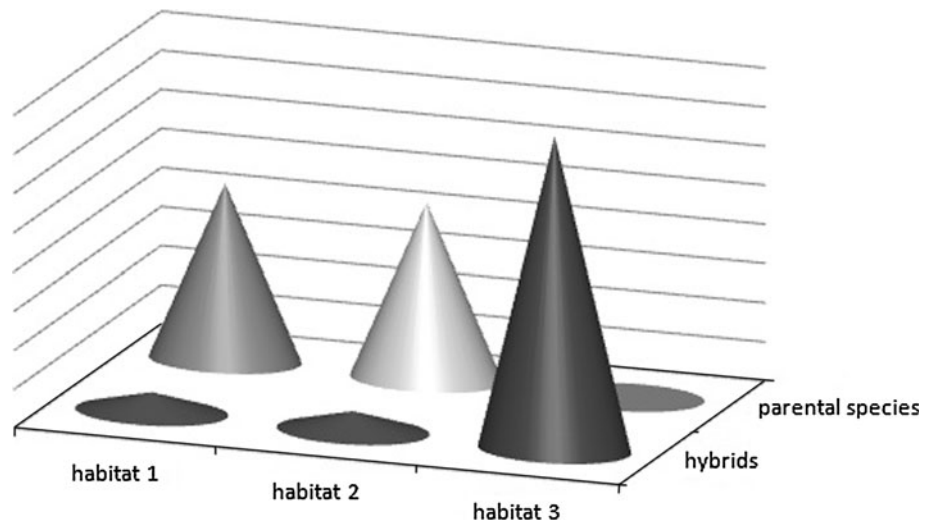
Asexual lineages lost sex after a genomic shock leading to the adoption of a form of endomitosis reproduction, sometimes with a normal meiosis preceded by a replication. Numerous mechanisms may have evolved to reduce conflict within organisms, such as separation between germ and somatic lines, or the uniparental transmission of mitochondria. Calling attention to the role of hybridization in angiosperms, Carman (1997, 2007) hypothesized that a heterochrony in the expression of genes involved in reproduction could cause apomeiotic development of the embryo leading to asexual lineages. Hybridization between individuals showing an asynchronous expression of genes could result in a disorder in the stages of development, via epigenetic modification in polyploids. These conflicts of genomes particularly affect meiosis and segregation distortion, some alleles being over-represented in the gametes. Although this possibility has been discussed (Coyne and Orr 1993) meiotic drive is known to affect sexual reproduction (Wilkinson and Fry 2001) and to contribute to hybrid sterility (see McDermott and Noor 2010 for a review), and thus is an important mechanism for possible speciation (Presgraves 2007; Phadnis and Orr 2009). Hybrid sterility and reduced fertility probably share common genetic factors. Some polyploid hybrid organisms with a disrupted meiosis can only reproduce “asexually”, which emphasizes the importance of genome conflict affecting meiotic sex. Most asexual eukaryotic organisms are parthenogenetic hybrids, and the changes in their reproduction modes could originate in the conflict-related genetic perturbations of the genome. Molecular mechanisms counteracting the accumulation of deleterious mutations must be important for asexual relatives to persist in the long-term. However, in most lineages, the

“Meselson effect” seems to be countered, probably because of the efficiency of DNA repair mechanisms (Martens et al. 2003; Schaefer et al. 2006; Schön and Martens 2003).

In sexual organisms, gamete dimorphism is considered as an adaptation that increases gamete encounter rates and recombination opportunities (Czárán and Hoesktra 2004). Nevertheless, anisogamy also introduces the sexual conflict (Rice 2000; Bjork and Pitnik 2006), which in turn, could favor a reversal towards asexuality (Lodé 2011). Hybrid lineages could therefore be affected by genetic factors selecting for asexuality but they could also find some favorable survival aptitude under certain environmental conditions. Because they possess both biological traits of their two parents, the resulting single cross hybrids are supposed to display intermediate phenotypes. A hypothesis, known as “the general purpose genotype model” (Baker and Stebbins 1965), argues that hybrids could be generalists. Their broad tolerance range could be favorable for the evolution of clones in temporary changing conditions (Schultz 1971; Lynch 1984). The hybrid’s genotype fits a broad ecological niche so it should exhibit a similar fitness level in both parental and intermediate niches. In hemiclinal water frog, some empirical evidence may be consistent with a generalist use of habitats but data are not univocal (Pagano et al. 2008 for instance). Rather than showing a generalist strategy, numerous parthenogenetic species adopt more or less specialized ecological niches, and numerous empirical observations do not support the “general purpose genotype” hypothesis (Robinson et al. 2002; Vorburger et al. 2003; Pagano et al. 2008). As a result, asexual hybrids can hardly compete with parental species in selective environments; therefore their lineages should decline in the long-term.

Alternatively, hybrids could exploit a different restricted range of resources along the environmental gradient, and hence, only occupy a narrow ecological niche, following the model developed by Vrijenhoek (1994, 1998) on hybrid zones. The “frozen niche variation” model predicts that hybrids could benefit by occupying niches that differ from their parental species and cannot be used (frozen niche, Fig. 2.). Thus, it could be proposed that, rather than being generalists, parthenogenetic hybrid lineages could be favored when exploiting peculiar restricted ecological niches. Indeed, an “asexual” hybrid progeny may extend part of the ecological valence of their sexual parental species by experiencing different ecological conditions. Although hybridization events have resulted in sex loss, probably due to intragenomic conflict, “asexual” hybrids are likely to show new selective traits. These original adaptive traits and the rapid colonization of new and sometimes extreme environments through asexual reproduction could favor the maintenance of these asexual lineages, and even lead to hybrid speciation (Seehausen 2004; Mallet 2007; Rieseberg and Willis 2007).

Fig. 2 “Frozen niche variation” model predicting that hybrids could benefit by occupying niches that differ from their two parental species and cannot be used leading to putative hybrid speciation (from Vrijenhoek 1998)



Conclusion

Hybridization seems to have a key role in the origins of asexual eukaryotes. In any case, it seems that, rather than providing an evolutionary benefit, “asexual reproduction” in eukaryotes is influenced by processes involving genomic conflict, thus leading some species to abandon a former sexual reproductive mechanism. The existence and the origin of “asexual” eukaryotes that have lost meiotic sex therefore greatly differ from the primitive absence of sex in prokaryotes. While the fragmentary and the total genetic recombination were put in place very early in evolution, meiosis, gametogenesis and syngamy appear as three fundamental characteristics of eukaryotes. Sexual specific traits evolved to attract the opposite sex and thereby favor reproduction.

Sexual reproduction is the basic characteristic promoting the fundamental divergence between eukaryotes and prokaryotes (Lodé 2011, 2012c). Thus, it could be hypothesized that sex (i.e. total recombination, meiosis, gametogenesis and syngamy) would be a driving force for eukaryote evolution.

Little is known about the determinants of parthenogenesis. Parthenogenetic species often exhibit all the characteristics of anisogamy. In numerous plants, apomixy occurs with a meiosis in which one division is suppressed. It has been proposed that the reversal of sexuality is only controlled by a single dominant locus (Dujardin and Hanna 1989; Lattorff et al. 2005) entailing the suppression of recombination. Sex-determining mechanisms are however very diverse, even including environmental cues (Marin and Baker 1998; Crews and Bull 2009), and even species without sex chromosomes could develop into males or females and behave in a gamete-appropriate manner (Woolley et al. 2004).

Eukaryotic species with “asexual” reproduction probably derive from hybridization events between sexual species. These hybridization events have triggered an evolutionary loss of sex through genome conflict and meiotic drive but it is

probable that numerous species may have kept the potential to reproduce by sexual means. The presence of male darwinulids calls into question the hypothesis that “asexual” eukaryotes are ancient asexual groups that have reproduced without sex for over 200 million years (Smith et al. 2006). As a result, that reproduction in numerous eukaryotes is obligate and primitively “asexual” cannot be known for certain. Even if they are not facultatively sexual, eukaryotic organisms should be considered as a continuum of organisms that are more or less capable (and sometimes incapable) of sexual reproduction.

Mechanisms of hybridization and horizontal gene transfers occurred in evolutionary processes and it is assumed that, mainly in primitive prokaryotes, horizontal transfers play an important role in speciation (Lawrence 1999; Parnell et al. 2010; Martin, 2011; Arnold 1996). These events may also produce a reticulate evolution in eukaryotes (Matheos and Vrijenhoek 2007; Christin et al. 2012; Genner and Turner 2012; Gilbert et al. 2012). Hybridization events seem sufficient to disrupt such a delicate mechanism as sexual meiosis and could affect sexual reproduction at a higher level than the cellular level, like the specific mate recognition system, often allowing the cost of males to be avoided.

Because asexual reproduction is supposed to be deleterious in the long run (Keightley and Eyre-Walker 2000; Arkhipova and Meselson 2004), the survival of these “asexual” eukaryotes however addresses critical evolutionary issues. Most studies dealing with asexual lineages focused on their potential evolutionary disadvantages, mainly supporting the idea that deleterious mutation accumulation should shorten their life span (Henry et al. 2012). However, examination of the evolutionary history of asexual lineages reveals that evolutionary processes act through transitional stages in which even very small temporary benefits may be enough to counter the expected

selective disadvantages. Here, I emphasize that, although asexual eukaryotes are thought to be penalized by genetic incompatibilities, they may display evolutionary advantages such as local adaptations, following the “frozen niche variation” model. Thus, although hybrid events result in sex loss, probably caused by genomic conflict, asexual hybrids could have new adaptive traits and the rapid colonization of new environments through clonal reproduction could favor their long-term survival. Therefore, asexuality may have evolved as a reproductive mechanism for reducing conflict within organisms.

New avenues of research should detail the molecular basis of asexuality and should specify the phylogenetic origin of different groups in order to clarify what asexual eukaryotes have in common. Tests are now available to look for genetic signatures for meiosis or for asexual reproduction (Normark et al. 2003; Schurko and Logsdon 2008). Such works should allow a better understanding of eukaryotic specificities to be developed.

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