

1 **Adaptive significance and long-term survival of asexual**
2 **lineages**

3

4 **Lodé Thierry**

5 UMR-CNRS 6552 ETHOS, Campus de Beaulieu, Université de Rennes 1, France

6 *thierry.lode@univ-rennes1.fr*

7

8

9

10 Running title: survival of asexual lineages

11 **Abstract**

12 Important questions remain about the long-term survival and adaptive significance of eukaryotic
13 asexual lineages. Numerous papers dealing with sex advantages still continued to compare
14 parthenogenetic populations *versus* sexual populations arguing that sex demonstrates a better
15 fitness. Because asexual lineages do not possess any recombination mechanisms favoring
16 rapid changes in the face of severe environmental conditions, they should be considered as an
17 evolutionary dead-end.

18 Nevertheless, reviewing literature dealing with asexual reproduction, it is possible to draw three
19 stimulating conclusions. 1) Asexual reproduction in eukaryotes considerably differs from
20 prokaryotes which experience recombination but neither meiosis nor syngamy. Recombination
21 and meiosis would be a driving force for sexual reproduction. Eukaryotes should therefore be
22 considered as a continuum of sexual organisms that are more or less capable (and sometimes
23 incapable) of sexual reproduction. 2) Rather than revealing ancestral eukaryotic forms, most
24 known lineages of asexual eukaryotes have lost sex due to a genomic conflict affecting their
25 sexual capacity. Thus, it could be argued that hybridization is a major cause of their asexuality.
26 Asexuality may have evolved as a reproductive mechanism reducing conflict within organisms.
27 3) It could be proposed that, rather than being generalists, parthenogenetic hybrid lineages
28 could be favored when exploiting peculiar restricted ecological niches, following the “frozen
29 niche variation” model. Although hybrid events may result in sex loss, probably caused by
30 genomic conflict, asexual hybrids could display new original adaptive traits, and the rapid
31 colonization of environments through clonal reproduction could favor their long-term survival,
32 leading to evolutionary changes and hybrid speciation. Examination of the evolutionary history
33 of asexual lineages reveals that evolutionary processes act through transitional stages in which
34 even very small temporary benefits may be enough to counter the expected selective
35 disadvantages.

36
37 **Keywords** asexual advantage - frozen niche variation - hybrid - meiotic drive - parthenogenesis
38 - prokaryotes - recombination - Red Queen - scissiparity - sexual conflict - speciation

39

40 **Introduction**

41

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

48

49 Sexual reproduction promotes high genetic variety, whereas clonal reproduction produces
50 identical genomes between descendants. Thus, most of the theories supporting a presumed
51 benefit of sexual strategies have proposed that sexual reproduction enlarges the genetic
52 diversity in the lineages in which natural selection acts (see Bernstein et al. 1984; Maynard-
53 Smith 1978; Kondrashov 1994; Rice 2002; Lesbarrères 2012). This benefit would be mainly due
54 to genetic recombination that generates numerous changes in genomes (Kondrashov 1994;
55 Hadany and Feldman 2005). The claimed importance of recombination has even led many
56 authors to consider as identical sex and genetic recombination (Otto 2009). The recombination
57 of genes is indeed shared in both eukaryotic and prokaryotic phyla, suggesting both an ancient
58 origin and a common function. As a result, sex can be considered as a nearly universal
59 mechanism because of the ubiquity of gene recombination in living species, and genetic
60 recombination could have been imposed as a mechanism for diversifying through evolutionary
61 history.

62

63 Nevertheless, the mechanisms of sexual reproduction are not confined only to recombination.
64 Recombination is only fragmentary in bacteria and archaea and all prokaryotes ignore the
65 mechanisms of reductional meiosis and of syngamy (Vos 2009), essential characteristics of
66 sexual eukaryotes. Recombination is a chemical process rooted in DNA exchange, while sex

67 appears as a biological process (Penny 1985; Cavalier-Smith 2002). Thus, sex can be defined
68 as an evolutionary mechanism that combines a total recombination of genomes, the
69 development of meiosis, gametogenesis and a process of cell fusion called syngamy. This
70 operational definition restricts sex to eukaryotes (Normark et al. 2003). Consequently, sex in
71 eukaryotes significantly differs from the bacterial recombination (Redfield 2001; Lodé 2012a).
72 The three basic characteristics of sexual reproduction are found in almost all eukaryotes, while
73 prokaryotes are chiefly reproduced by binary fission (Lawrence 1999). This fact may suggest
74 both the establishment of a common evolutionary mechanism in all eukaryotes and an ancient
75 divergence with the other groups of prokaryotes (Lodé 2011, Lodé 2012b). The lack of
76 intermediate organisms in the prokaryote-to-eukaryote transitions could indicate that
77 recombination and sexual reproduction have accelerated the basic divergence. In addition,
78 numerous eukaryotes privileged anisogamy, introducing male and female divergence.

79
80 However, some eukaryotes exhibit different reproductive mechanisms, such as
81 parthenogenesis or scissiparity, and some are thought to be as exclusively asexual, though they
82 are rare exceptions. The existence of these asexual organisms raises a crucial question about
83 the evolutionary processes that led to the establishment of sexual reproduction and many of
84 asexual lineages are the subject of experimental studies dealing with the potential benefits of
85 sex (Egel 2000; Agrawal 2009). What can these exceptions tell us about evolutionary
86 processes?

87

88 **1. Putative advantages of asexual reproduction**

89

90 In fact, it is somewhat surprising to consider that so few eukaryotes show asexual reproduction.
91 Although the concept of species in asexual organisms has been questioned (Hillis 2007) since
92 sexual isolation is considered the basic mechanism of speciation (de Queiroz 2005), a large
93 majority of the species practicing partial recombination with neither meiosis nor syngamy are
94 prokaryotes (Vos 2009). Asexual reproduction is observed in protists, in yeast or in plants but

95 there are also many examples of animals that have interested researchers (Halkett et al. 2005).
96 Rotifers, for instance, are a group of dioecous animals, but males are unknown in several
97 species so that bdelloid rotifers asexually produce diploid eggs that only develop into females
98 (Birky 2004). In some annelids, mollusks and arthropods, asexual reproduction is often the
99 preferred mode of reproduction. Finally, asexual reproduction also exists in some vertebrates
100 such as fish and lizards for example (Schultz 1971). The diversity of concerned species
101 suggests that those showing asexual reproduction therefore do not have a common
102 evolutionary origin and that their asexuality could be dependent on factors specific to the
103 species' life history.

104
105 The possible evolutionary advantages of asexual reproduction have been discussed (see Butlin
106 and Griffiths 1993). For example, the optional parthenogenetic reproduction of aphids is usually
107 associated with severe and changing climatic conditions and seems to be a response to
108 environmental stresses (Suomalainen 1962, 1976). In social hymenoptera, parthenogenetic
109 reproduction is generally limited to the production of males because they are haploid, but there
110 are some cases of female-producing parthenogenesis (Slobodchikoff and Daly 1971; review in
111 Wenseleers and Van Oystaeyen 2011). Reproduction by scissiparity or binary fission is found
112 both in plants, protists, cnidarians and annelids, which however can also have sexual phases.
113 Gynogenesis and hybridogenesis could be considered as forms of parthenogenesis that require
114 sperm to initiate embryogenesis, with no fecundation (gynogenesis) or excluding the paternal
115 genome (hemiclinal hybridogenesis) (Schmidt 1993; Beukeboom and Vrijenhoek 1998;
116 Vorburger 2001; Pagano et al. 2003; Schmeller et al. 2005). Hybridogenetic lineages realize a
117 hemiclinal transmission of genes since they discard one complete genome of either parental
118 species.

119
120 Nonetheless, the reason why asexual reproduction can be maintained in such a variety of
121 different groups remains enigmatic. It has been shown that sexual species may suffer a double
122 constraint, called the "two-fold cost of sex" (Maynard-Smith 1978; Williams 1975; Uyenoyama
123 1984). Asexual lineages avoid both the cost of meiosis and the cost of males (Lively and Lloyd

124 1990). Therefore, an asexual population has an intrinsic capacity to grow exponentially, the
125 asexual lineage doubling in the population with each generation.

126
127 Consequently, from a purely numerical point of view, asexual populations should outcompete
128 sexual species to extinction when they are in a similar ecological situation (Schley et al. 2004).
129 Because of the obvious evolutionary benefits that asexual populations have over sexual
130 species, it is difficult to understand why asexual lineages have not invaded the most stable
131 environments. Referring only to adaptive advantages, it is hard to understand why phasmids
132 have privileged asexual reproduction, including parthenogenesis and hybridogenesis
133 (Passamonti et al. 2004; Ghiselli et al. 2007), while related species, such as dragonflies or
134 mantis, exhibit sexual reproduction.

135

136 **2. The Red Queen**

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

144
145 Numerous field studies have supported some of these predictions (Hakoyama et al. 2001; Lively
146 and Jokela 2002; Lively 2009). For instance, it has been found that sexual *Poeciliopsis* fish
147 species survive a parasite load more successfully than asexual fish populations (Lively et al.
148 1990; Mateos et al. 2002). Examining the parasite load in *Carassius* fish living sympatrically,
149 Hakoyama et al. (2001) found that sexual *Carassius* had a significantly lower load of parasites
150 than asexual populations. Similarly, the parasite loads and juvenile mortality in a parthenogenic
151 freshwater gasteropod *Campeloma limum* were found to be significantly higher in autodiploid

152 parthenogens, but the variance of prevalence was also higher in autodiploid parthenogens,
153 suggesting that unparasitized parthenogens have temporarily escaped these virulent parasites
154 (Johnson 2000). A survey of the freshwater ostracod *Eucypris virens* has also revealed that
155 very few populations support parasite infections (Bruvo et al. 2011). Similarly, a host-parasite
156 model by Howard and Lively (1994) showed the coexistence of sexual and asexual lineages,
157 even under moderate levels of virulence.

158
159 By contrast, some clonal species have revealed great adaptive potential. In daphnia, tests have
160 failed to find evidence that parasite load is able of causing synergistic epistasis between
161 mutations in their hosts (Salathé and Ebert 2003; Haag et al. 2003). Tobler and Schlupp (2005),
162 when testing the Red Queen prediction using four populations of the sexual fish species
163 *Poecilia latipinna* and its asexual relative *Poecilia Formosa*, detected no differences in parasite
164 load. Indeed, sexual recombination could disrupt favorable gene combinations more often than
165 it generates them. Further, asexual geckos exhibited lower parasite infestations than sexual
166 relatives (Hanley et al. 1995; Brown et al. 1995; Kearney and Shine 2005). Natural hybrids often
167 show very high levels of heterozygosity, thus, it has been hypothesized that asexual vertebrates
168 may have a higher resistance to parasites owing to their hybrid origin (Brown et al. 1995).

169
170 Genetic diversity is present in asexual populations through a variety of different clones (Lushai
171 et al. 2003), and asexual groups do not diversify less rapidly than sexual species (Barraclough
172 et al. 2003). For instance, the pattern of diversification found in bdelloid rotifers is suggestive of
173 their adaptive radiation rather than reflecting neutral divergence and genetic drift (Fontaneto et
174 al. 2007). Similarly, in parthenogenetic populations of the oribatid mite, either asexual or sexual
175 lineages may show a comparable rate of speciation (Heethoff et al. 2007).

176
177 Analyzing 101 eukaryotic phylogenies, Venditti et al. (2010) concluded that the Red Queen
178 model of a species losing a race in a selective environment should be replaced by a view linking
179 speciation to rare stochastic events. Reviewing plant/pathogen interactions, Clay and Kover

180 (1996) also found that gene-for-gene interactions are generally not consistent with the Red
181 Queen hypothesis.

182
183 Finally, in bacteria reproducing asexually, there is no evidence of meiosis, but co-evolution with
184 viruses determines the frequency of mutation rates (Pal et al. 2007). This suggests that the
185 parasite-host co-evolution model (Red Queen) functions as a driver for mutation frequency even
186 when sex is not implicated.

187

188

189 **3. Benefit of recombination**

190 Since asexual reproduction results in clonal progeny, it was assumed that this reduced diversity,
191 linked to a lack or an incomplete recombination could reduce the fitness of asexual populations.
192 The absence of recombination in asexual organisms results in accumulation of deleterious
193 mutations, while recombination in sexual populations is known to achieve a “Muller’s Ratchet”
194 (Muller 1964; Felsenstein 1974). Furthermore, sexual species would be advantaged because
195 they produce a wide variety of descendants, whereas asexual populations only have a clonal
196 progeny with a reduced ability to adapt to changing environments (Kondrashov 1994; Penny
197 1985; Kondrashov 1993; de Visser and Elena 2007). Thus, genetic recombination is thought to
198 be an essential mechanism that favors the long-term survival of a species. Further, sexual
199 genomes contain many genes, each containing many strongly epistatic nucleotides (Watson et
200 al. 2011).

201

202 The advantage of recombination was assessed in *Escherichia coli* microbacterial cultures by
203 introducing the F plasmid carrying *Rec* genes for conjugation (Cooper 2007). All recombining
204 lineages showed greater fitness than non-recombining lineages. In yeast populations, Goddart
205 et al. (2005) found that sexual lineages exhibited the best fitness in selective conditions.
206 Similarly, Morran et al. (2011) showed that co-evolution with a bacterial pathogen (*Serratia*

207 *marcescens*) resulted in significantly increased outcrossing in mating populations of the
208 nematode *Caenorhabditis elegans*.

209
210 Nonetheless, asexual organisms occupy larger ranges, survive at higher latitudes and altitudes
211 and have a greater ability to colonize than their sexual relatives (Kearney 2005; Hörandl et al.
212 2008). Furthermore, even bacteria may obtain new genes by direct transfer from other bacteria,
213 promoting their adaptation to a changing environment (Ochman et al. 2005; Pal et al. 2005).
214 McDaniel et al. (2010) found high genetic transfer in marine bacteria which demonstrated the
215 widespread capability of variance and adaptation in bacteria with no sexual practices. Finally,
216 several species with clonal genomes have revealed great adaptive potential (Loxdale and
217 Lushai 2003; Pagano et al. 2008). As a result, it is quite possible to conclude that asexual
218 organisms with no sexual recombination may show a better adaptive potential than expected.

219
220 In fact, considerable confusion is still attached to the term “asexual” reproduction. The
221 consequences of sexual reproduction have been tested by comparing a wide variety of sexual
222 species and their “asexual” relatives, which often exhibit very different life-histories. The
223 “asexual” organisms are species in which sexual reproduction has never been observed or
224 species that practice asexual reproduction alternatively or sometimes optionally. Thus, the
225 definition of asexual reproduction is typically based on negative evidence. Numerous species
226 can be considered as obligate sexual but it is difficult to say that there are obligate asexual
227 species. Although they consist in all-females lineages, parthenogenetic species are considered
228 as “asexual” species as well as some organisms showing scissiparity or hemiclinal
229 reproduction. Thus “asexual” reproduction includes situations that greatly contrast. Some
230 species have developed reproduction through scissiparity or binary fission and reconstruction of
231 new organic tissues.

232
233 The situation is further complicated because many “asexual” organisms have retained a
234 capacity for sexual reproduction. This is the case in the haploid-diploid hymenoptera or in
235 aphids for instance. In monogonate rotifer species, both reproduction by parthenogenesis and

236 sexual reproduction take place during the life cycle (Fontaneto et al. 2007). Therefore, these
237 species are rather facultative sexual species in which reproductive mechanisms differ according
238 to the environmental context. Even species that do not use obvious sexual reproduction may
239 still show some characteristics of sex. Most asexual lineages are dioecus, and, despite a
240 change in syngamy, individuals may have almost normal meiosis but not until complete
241 reductional division (meiosis II) and sometimes may even show a complete meiosis.

242
243 If recombination is shared by many prokaryotic organisms, meiosis and syngamy mechanisms
244 are found only in eukaryotes (Vos 2009). It might be thought that, in most cases, “asexual”
245 eukaryotes experienced both a deterioration of meiosis mechanisms and a lack of syngamy.
246 Nonetheless, repeated accumulation of mutations and lack of recombination in an asexual
247 population should result in a “Meselson effect” whereby one organism is affected by high
248 sequence divergence of two different genomes because alleles at a single locus evolve
249 independently of each other (Mark-Welch and Meselson 2000; Butlin 2002). Thus, it remains
250 difficult to identify what benefits asexual lineages can derive from the absence of meiosis and
251 syngamy. In addition, many asexual organisms are phylogenetically related to other sexual
252 species and can live under relatively similar environmental conditions.

253

254

255 **4. Intragenomic conflict and asexual reproduction**

256

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

262

263 The sexual cycle of eukaryotes is often supposed to have arisen from the infection of eukaryotic
264 cells by prokaryotic genome parasites (Bell 1993). Based on supposed primitive microbial

265 eukaryotes such as protists which have often been assumed to be asexual organisms, it has
266 usually been accepted that the ancestors of all eukaryotes were asexual or, at least,
267 facultatively sexual isogamous organisms (Normark et al. 2003; Ramesh et al. 2005).
268 Nevertheless, most of the support for this alleged primitive asexuality derives from the lack of
269 observing sex or motile organisms considered as males. It could be noticed that anisogamy is
270 not a mandatory requirement for sex, although it is often privileged in sexual organisms. After
271 recombination and meiosis, isogamy should be a probable primitive step for sex. Although there
272 is some evidence suggesting that current asexual organisms originated from ancient asexual
273 organisms (Chaplin et al. 1994; Schön et al. 1998), considerable contradictory evidence
274 suggests that they were originally sexual species (Judson and Normark 1996; Normak et al.
275 2003; Mark-Welch et al. 2004; Matheos and Vrijenhoek 2007). The small number of asexual
276 lineages seems to indicate that asexual eukaryotes are species that have lost sex rather than
277 archaic species that have survived until today. Thus, it might be possible to accept the
278 hypothesis that the ancestor of eukaryotes had certain primitive characteristics of a sexual
279 being, such as recombination and meiosis (Lodé 2011; 2012a). Indeed, most eukaryotic species
280 exhibited sexual reproduction while asexual eukaryotes are not organized in a continuum but
281 are found scattered throughout the tree of life.

282
283 In fact, the various forms of asexual reproduction might stem from casual factors affecting some
284 species rather than being the result of a common process. This could lead us to assume that
285 asexual reproduction depends much more on the individual life histories of each species, and
286 could result in peculiar adaptive conditions. The association of such different species in only
287 one category such as “asexual reproduction” may be artificial and does not give a general
288 explanation for the evolutionary process.

289
290 “Asexual” eukaryotes mainly reproduce by apomixis, a mechanism in which diploid eggs
291 produced by mitotic division develop parthenogenetically into females. Thus, in eukaryotes, a
292 species is expected to reproduce “asexually” when no functional males are detected. However,
293 recently, male darwinulid ostracods were found although this family was considered as an

294 exclusively ancient asexual group (Smith et al. 2006). Reviewing the literature on ciliates,
295 Dunthorn and Katz (2010) concluded that the putative asexuality of this lineage is an
296 observational artifact; so many microbial eukaryotes could actually be secretly sexual.
297 Numerous plants produce asexual seeds but have a sexual male function. Oribatid mites can
298 show a reversal from “obligate” asexual forms to sexual forms (Domes et al. 2007), but sexuality
299 might have been lost repeatedly (Goldberg and Igic 2008). Similarly, evidence for a sexual
300 stage was observed in the supposedly “obligatory” asexual fungi *A. fumigatus* (Dyer and
301 Paoletti 2005) revealing that “asexual” eukaryotes may have something to do with sex.

302
303 Eukaryotic organisms with “asexual” reproduction clearly show an alteration of the reproductive
304 mechanisms involved in sexual reproduction. Many “asexual” lineages are genetically related to
305 sexual species and mostly possess sexual ancestors. Some worm species reproducing
306 asexually by scissiparity have revealed hybrid origins, and epigamy was their ancestral
307 reproductive state (Lunt 2008; Nygren and Sundberg 2003). Asexual fungal species have
308 sexual ancestors and may also be cryptically sexual (Sun and Heitman 2011). Parthenogenetic
309 species, such as phasmids (Passamonti et al. 2004), *Poeciliid* fishes (Lamatsch et al. 2007),
310 unisexual *Aspidoscelis/Cnemidophorus* lizards (Parker and Selander 1976; Crews et al. 1986,
311 Cullum 2000), hybridogenetic water frogs (Vorburger 2001; Pagano et al. 2003; Schmeller et al.
312 2005) and fishes (Schartl et al. 1995; Angers and Schlosser 2007) are believed to use clonal or
313 hemiclonal asexual reproduction, but have sexual ancestors and exhibited numerous traits
314 shared by gonochoristic species (*i.e.* separate sexes in separate individuals). In *Timema* stick
315 insects, parthenogens are evolved spontaneously from sexually reproducing species
316 (Schwander and Crespi 2008). Asexual bdelloids are probably allotetraploids resulting from
317 ancient hybridization events. Reconstructions of rotifer phylogenies suggest that sexual
318 reproduction has been lost during their evolutionary history on at least three different occasions
319 (Mark-Welch and Meselson 2000). In *Equisetum*, female gametophytes became hermaphroditic
320 or males when cultured in the presence of sucrose (Guillon & Raquin 2002). Finally, some
321 amphibians and many reptiles depend on environmental cues to determine sex and in some
322 fish, this process can persist throughout life, so Crews (2012) argued that most eukaryotic

323 lineages evolved from bisexual ancestors that could adopt both male and female roles related to
324 their ovarian cycle (Fig. 1.).

325
326 Thus, it could be said that sexual reproduction became “facultative” in eukaryotic organisms
327 showing a decline in sexual fertility or losing sex during their evolutionary history, although they
328 have sexual ancestry.

329
330 Asexual organisms may arise by mutation or loss of some key genes (Lattorff et al. 2005), but
331 hybridization events give rise to conflicts of genomes due to a lesser genetic compatibility
332 between the protagonists. Indeed, hybrid sterility or incompatibilities have been a focus in
333 reproductive isolation and speciation, especially since the Haldane rule (1922) states that the
334 sterility of heterogametic sex is the most affected by hybridization. In angiosperms, polyploidy
335 and gene interactions should be a cause of asexual development (Quarin et al. 2001).
336 Parthenogenetic stick insects should have a hybrid origin (Schwander and Crespi 2008). In fact,
337 most unisexual populations have generally originated from hybridation with sexual species
338 (Simon et al. 2003; Wooley et al. 2004; Kearney 2005; Mable 2007; Matheos and Vrijenhoek
339 2007), thus it could be argued that hybridization is a major cause of asexuality in eukaryotes.

340
341 Asexual lineages lost sex after a genomic shock leading to the adoption of a form of
342 endomitosis reproduction, sometimes with a normal meiosis preceded by a replication.
343 Numerous mechanisms may have evolved to reduce conflict within organisms, such as
344 separation between germ and somatic lines, or the uniparental transmission of mitochondria.
345 Calling attention to the role of hybridization in angiosperms, Carman (1997; 2007) hypothesized
346 that a heterochrony in the expression of genes involved in reproduction could cause apomeiotic
347 development of the embryo leading to asexual lineages. Hybridization between individuals
348 showing an asynchronous expression of genes could result in a disorder in the stages of
349 development, via epigenetic modification in polyploids. These conflicts of genomes particularly
350 affect meiosis and segregation distortion, some alleles being over-represented in the gametes.
351 Although this possibility has been discussed (Coyne and Orr 1993) meiotic drive is known to

352 affect sexual reproduction (Wilkinson and Fry 2001) and to contribute to hybrid sterility (see
353 McDermott and Noor 2010 for a review), and thus is an important mechanism for possible
354 speciation (Presgraves 2007; Phadnis and Orr 2009). Hybrid sterility and reduced fertility
355 probably share common genetic factors. Some polyploid hybrid organisms with a disrupted
356 meiosis can only reproduce “asexually”, which emphasizes the importance of genome conflict
357 affecting meiotic sex. Most asexual eukaryotic organisms are parthenogenetic hybrids, and the
358 changes in their reproduction modes could originate in the conflict-related genetic perturbations
359 of the genome. Molecular mechanisms counteracting the accumulation of deleterious mutations
360 must be important for asexual relatives to persist in the long-term. However, in most lineages,
361 the “Meselson effect” seems to be countered, probably because of the efficiency of DNA repair
362 mechanisms (Martens et al. 2003; Schaefer et al. 2006; Schön and Martens 2003).

363
364 In sexual organisms, gamete dimorphism is considered as an adaptation that increases gamete
365 encounter rates and recombination opportunities (Czárán and Hoesktra 2004). Nevertheless,
366 anisogamy also introduces the sexual conflict (Rice 2000; Bjork and Pitnik 2006), which in turn,
367 could favor a reversal towards asexuality (Lodé 2011). Hybrid lineages could therefore be
368 affected by genetic factors selecting for asexuality but they could also find some favorable
369 survival aptitude under certain environmental conditions. Because they possess both biological
370 traits of their two parents, the resulting single cross hybrids are supposed to display
371 intermediate phenotypes. A hypothesis, known as “the general purpose genotype model” (Baker
372 and Stebbins 1965), argues that hybrids could be generalists. Their broad tolerance range could
373 be favorable for the evolution of clones in temporary changing conditions (Schultz 1971; Lynch
374 1984). The hybrid’s genotype fits a broad ecological niche so it should exhibit a similar fitness
375 level in both parental and intermediate niches. In hemiclonal water frog, some empirical
376 evidence may be consistent with a generalist use of habitats but data are not univocal (Pagano
377 et al. 2008 for instance). Rather than showing a generalist strategy, numerous parthenogenetic
378 species adopt more or less specialized ecological niches, and numerous empirical observations
379 do not support the “general purpose genotype” hypothesis (Robinson et al. 2002; Vorburger et

380 al. 2003; Pagano et al. 2008). As a result, asexual hybrids can hardly compete with parental
381 species in selective environments; therefore their lineages should decline in the long-term.

382
383 Alternatively, hybrids could exploit a different restricted range of resources along the
384 environmental gradient, and hence, only occupy a narrow ecological niche, following the model
385 developed by Vrijenhoek (1994; 1998) on hybrid zones. The “frozen niche variation” model
386 predicts that hybrids could benefit by occupying niches that differ from their parental species
387 and cannot be used (frozen niche, Fig. 2.). Thus, it could be proposed that, rather than being
388 generalists, parthenogenetic hybrid lineages could be favored when exploiting peculiar
389 restricted ecological niches. Indeed, an “asexual” hybrid progeny may extend part of the
390 ecological valence of their sexual parental species by experiencing different ecological
391 conditions. Although hybridization events have resulted in sex loss, probably due to
392 intragenomic conflict, “asexual” hybrids are likely to show new selective traits. These original
393 adaptive traits and the rapid colonization of new and sometimes extreme environments through
394 asexual reproduction could favor the maintenance of these asexual lineages, and even lead to
395 hybrid speciation (Seehausen 2004; Mallet 2007; Rieseberg and Willis 2007).

396

397

398 **Conclusion**

399

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

409
410 Sexual reproduction is the basic characteristic promoting the fundamental divergence between
411 eukaryotes and prokaryotes (Lodé 2011, Lodé 2012c). Thus, it could be hypothesized that sex
412 (*i.e.* total recombination, meiosis, gametogenesis and syngamy) would be a driving force for
413 eukaryote evolution.

414
415 Little is known about the determinants of parthenogenesis. Parthenogenetic species often
416 exhibit all the characteristics of anisogamy. In numerous plants, apomixy occurs with a meiosis
417 in which one division is suppressed. It has been proposed that the reversal of sexuality is only
418 controlled by a single dominant locus (Dujardin and Hanna 1989; Lattorff et al. 2005) entailing
419 the suppression of recombination. Sex-determining mechanisms are however very diverse,
420 even including environmental cues (Marin & Backer 1998, Crews & Bull 2009), and even
421 species without sex chromosomes could develop into males or females and behave in a
422 gamete-appropriate manner (Woolley et al. 2004).

423
424 Eukaryotic species with “asexual” reproduction probably derive from hybridization events
425 between sexual species. These hybridization events have triggered an evolutionary loss of sex
426 through genome conflict and meiotic drive but it is probable that numerous species may have
427 kept the potential to reproduce by sexual means. The presence of male darwinulids calls into
428 question the hypothesis that “asexual” eukaryotes are ancient asexual groups that have
429 reproduced without sex for over 200 million years (Smith et al. 2006). As a result, that
430 reproduction in numerous eukaryotes is obligate and primitively “asexual” cannot be known for
431 certain. Even if they are not facultatively sexual, eukaryotic organisms should be considered as
432 a continuum of organisms that are more or less capable (and sometimes incapable) of sexual
433 reproduction.

434
435 Mechanisms of hybridization and horizontal gene transfers occurred in evolutionary processes
436 and it is assumed that, mainly in primitive prokaryotes, horizontal transfers play an important
437 role in speciation (Lawrence 1999; Parnell et al. 2010; Martin, 2011; Arnold 1996). These

438 events may also produce a reticulate evolution in eukaryotes (Matheos and Vrijenhoek 2007;
439 Christin *et al.* 2012; Genner and Turner 2012; Gilbert *et al.* 2012). Hybridization events seem
440 sufficient to disrupt such a delicate mechanism as sexual meiosis and could affect sexual
441 reproduction at a higher level than the cellular level, like the specific mate recognition system,
442 often allowing the cost of males to be avoided.

443
444 Because asexual reproduction is supposed to be deleterious in the long run (Keightley and
445 Eyre-Walker 2000; Arkhipova and Meselson 2004), the survival of these “asexual” eukaryotes
446 however addresses critical evolutionary issues. Most studies dealing with asexual lineages
447 focused on their potential evolutionary disadvantages, mainly supporting the idea that
448 deleterious mutation accumulation should shorten their life span (Henry *et al.* 2012). However,
449 examination of the evolutionary history of asexual lineages reveals that evolutionary processes
450 act through transitional stages in which even very small temporary benefits may be enough to
451 counter the expected selective disadvantages. Here, I emphasize that, although asexual
452 eukaryotes are thought to be penalized by genetic incompatibilities, they may display
453 evolutionary advantages such as local adaptations, following the “frozen niche variation” model.
454 Thus, although hybrid events result in sex loss, probably caused by genomic conflict, asexual
455 hybrids could have new adaptive traits and the rapid colonization of new environments through
456 clonal reproduction could favor their long-term survival. Therefore, asexuality may have evolved
457 as a reproductive mechanism for reducing conflict within organisms.

458
459 New avenues of research should detail the molecular basis of asexuality and should specify the
460 phylogenetic origin of different groups in order to clarify what asexual eukaryotes have in
461 common. Tests are now available to look for genetic signatures for meiosis or for asexual
462 reproduction (Normark *et al.* 2003; Schurko and Logsdon 2008). Such works should allow a
463 better understanding of eukaryotic specificities to be developed.

464

465

466 **Acknowledgments**

467 I would like to thank David Crews and two anonymous referees for helpful suggestions.

468

469 **References**

470 Agrawal, A. F. (2009). Differences between selection on sex versus recombination in red queen
471 models with diploid hosts. *Evolution*, 63, 2131–2141.

472 Angers, B., & Schlosser, I. J. (2007). The origin of *Phoxinus eos-neogaeus* unisexual hybrids.
473 *Molecular Ecology*, 16, 4562–4571.

474 Arkhipova, I., & Meselson, M. (2004). Deleterious transposable elements and the extinction of
475 asexuals. *Bioessays*, 27, 76-85.

476 Arnold, M. L. (1996). *Natural Hybridization and Evolution*. New York: Oxford University Press.

477 Baker, H. G., & Stebbins, G. I. (1965). *The genetics of colonizing species*. New York: Academic
478 Press.

479 Barraclough, T. G., Birky, Jr. C. W., & Burt, A. (2003). Diversification in sexual and asexual
480 organisms. *Evolution*, 57, 2166-2172.

481 Barton, N. H., & Charlesworth, B. (1998). Why Sex and Recombination? *Science*, 281, 1986-
482 1990.

483 Bell, G. (1993). The sexual nature of eukaryote genomes. *Journal of Heredity*, 84, 351-359.

484 Bernstein, H., Byerly, H. C., Hopf, F. A., & Michod, R. E. (1984). Origin of sex. *Journal of*
485 *Theoretical of Biology*, 110, 323–351.

486 Beukeboom, L., & Vrijenhoek, R. C. (1998). Evolutionary genetics and ecology of sperm-
487 dependent parthenogenesis. *Journal of Evolutionary Biology*, 11, 755–782.

488 Birky, W. C., Jr. (2004). Bdelloid rotifer revisited. *Proceedings of the National Academy of*
489 *Sciences USA*, 101, 2651-2652.

490 Bjork, A., & Pitnik, S. (2006). Intensity of sexual selection along the anisogamy-isogamy
491 continuum. *Nature*, 441, 742-745.

hal-00860811, version 1 - 11 Sep 2013

- 492 Brown, S. G., Kwan S., & Shero, S. (1995). The parasitic theory of sexual reproduction,
493 parasitism in unisexual and bisexual geckos. *Proceedings of the Royal Society of London B*,
494 260, 317-320.
- 495 Bruvo, R., Adolfsson S., Symonova R., Lamatsch D. K., Schön I., Jokela J., et al. (2011). Few
496 parasites, and no evidence for Wolbachia infections in a freshwater ostracod inhabiting
497 temporary ponds. *Biological Journal of the Linnaean Society of London*, 102, 208–216.
- 498 Butlin, R. (2002). The costs and benefits of sex, new insights from old asexual lineages. *Nature*
499 *Reviews of Genetics*, 3, 311-317.
- 500 Butlin, R. K., & Griffiths, H. I. (1993). Ageing without sex? *Nature*, 364, 680.
- 501 Carman, J. G. (1997). Asynchronous expression of duplicate genes in angiosperms may cause
502 apomixis, bispory, tetraspory, and polyembryony. *Biological Journal of the Linnaean Society of*
503 *London*, 61, 51-94.
- 504 Carman, J. G. (2007). Do duplicate genes cause apomixes? In E. Hörandl, U. Grossniklaus, P.
505 J. van Dijk & T. F. Sharbel (Eds.), *Apomixis, Evolution, mechanisms and perspectives* (pp. 63-
506 91). Liechtenstein: Gantner Rugell.
- 507 Cavalier-Smith, T. (2002). Origins of the machinery of recombination and sex. *Heredity*, 8, 125-
508 141.
- 509 Chaplin, J. A., Havel, J. E., & Hebert, P. D. N. (1994). Sex and ostracods. *Trends in Ecology*
510 *and Evolution*, 9, 435-439.
- 511 Christin, P. A., Edwards, E. J., Besnard, G., Boxall, S. F., Gregory, R., Kellogg, E. A., et al.
512 (2012). Adaptive evolution of C4 Photosynthesis through recurrent lateral gene transfer. *Current*
513 *Biology*, 22, 445-449.
- 514 Clay, K., & Kover, P. X. (1996). The Red Queen Hypothesis and plant/pathogen interactions.
515 *Annuals Reviews of Phytopathology*, 34, 29-50.
- 516 Cooper, T. F. (2007). Recombination speeds adaptation by reducing competition between
517 beneficial mutations in populations of *Escherichia coli*. *PLoS Biology*, 59, e225.
- 518 Coyne, J. A., & Orr, H. A. (1993). Further evidence against meiotic-drive models of hybrid
519 sterility. *Evolution*, 47, 685-687.

- 520 Crews, D., Grassman, M., & Lindzey J. (1986). Behavioral facilitation of reproduction in sexual
521 and unisexual whiptail lizards, *Proc Natl Acad Sci USA*, *83*, 9547–9550.
- 522 Crews, D. (2012). The (bi)sexual brain. *Embo reports* (in press).
- 523 Crews, D., & Bull J. J. (2009). Mode and tempo in environmental sex determination in
524 vertebrates. *Seminar Cell Development Biology*, *20*, 251–255.
- 525 Cullum, A. (2000). Phenotypic variability of physiological traits in populations of sexual and
526 asexual whiptail lizards (genus *Cnemidophorus*). *Evolutionary Ecology Research*, *2*, 841-855.
- 527 Czárán, T. L., & Hoesktra, R. F. (2004). Evolution of sexual asymmetry. *BMC Evolutionary*
528 *Biology*, *4*, 34.
- 529 de Queiroz, K. (2005). Ernst Mayr and the modern concept of species. *Proceedings of the*
530 *National Academy of Sciences USA*, *102*, 6600–6607.
- 531 de Visser, J. A. G. M., & Elena, S. F. (2007). The evolution of sex, Empirical insights into the
532 roles of epistasis and drift. *Nature Reviews of Genetics*, *8*, 139-149.
- 533 Domes, K., Norton, R. A., Maraun, M., & Scheu, S. (2007). Revolution of sexuality breaks
534 Dollo's law. *Proceedings of the National Academy of Sciences USA*, *104*, 7139-7144.
- 535 Dujardin, M., & Hanna, W. W. (1989). Developing apomictic pearl millet characterization of a
536 BC3 plant. *Journal of Genetic Breeding*, *43*, 145-151.
- 537 Dunthorn, M., & Katz, L. (2010). Secretive ciliates and putative asexuality in microbial
538 eukaryotes. *Trends in Microbiology*, *18*, 183-188.
- 539 Dyer, P. S., & Paoletti, M. (2005). Reproduction in *Aspergillus fumigatus*, sexuality in a
540 supposedly asexual species? *Medical Mycology Supplement*, *43*, S7-S14.
- 541 Egel, R. (2000). Fission yeast on the brink of meiosis. *BioEssays*, *22*, 854–860.
- 542 Felsenstein, J. (1974). The evolutionary advantage of recombination. *Genetics*, *78*, 737-756.
- 543 Fontaneto, D., Herniou, E. A., Boschetti, C., Caprioli, M., Melone, G., Ricci, C., et al. (2007).
544 Independently evolving species in asexual bdelloid rotifers. *Plos Biology*, *5*, e87.
- 545 Genner, M. J., & Turner, G. F. (2012). Ancient hybridization and phenotypic novelty within Lake
546 Malawi's Cichlid fish radiation. *Molecular Biology and Evolution*, *29*, 195-206.

- 547 Ghiselli, F., Milani, L., Scali, V., & Passamonti, M. (2007). The *Leptynia hispanica* species
 548 complex (Insecta Phasmida), polyploidy, parthenogenesis, hybridization and more. *Molecular*
 549 *Ecology*, 16, 4256–4268.
- 550 Gilbert, C., Hernandez, S. S., Flores-Benabib, J., Smith, E. N., & Feschotte, C. (2012). Rampant
 551 horizontal transfer of *SPIN* transposons in Squamate Reptiles. *Molecular Biology and*
 552 *Evolution*, 29, 503-515.
- 553 Goddard, M. R., Godfray, H. C. J., & Burt, A. (2005). Sex increases the efficacy of natural
 554 selection in experimental yeast populations. *Nature*, 434, 636–640.
- 555 Goldberg, E. E. & Igic, B. (2008). On phylogenetic tests of irreversible evolution. *Evolution*, 62,
 556 2727-2741.
- 557 Guillon, J.M. & Raquin, C. (2002) Environmental sex determination in the genus *Equisetum* :
 558 sugars induce male sex expression in cultured gametophytes. *International Journal of Plant*
 559 *Science*, 163, 825-830.
- 560 Haag, C. R., Sakwinska, O. & Ebert, D. (2003). Test of synergistic interactions between
 561 infection and inbreeding in *Daphnia magna*. *Evolution*, 57, 777–783.
- 562 Hadany, L. & Feldman, M. W. (2005). Evolutionary traction, the cost of adaptation and the
 563 evolution of sex. *Journal of Evolutionary Biology*, 18, 309–314.
- 564 Hakoyama, H., Nishimura, T., Matsubara, N., & Iguchi, K. (2001). Difference in parasite load
 565 and nonspecific immune reaction between sexual and gynogenetic forms of *Carassius auratus*.
 566 *Biological Journal of the Linnaean Society of London*, 72, 401–407.
- 567 Haldane, J. B. S. (1922). Sex ratio and unisexual sterility in hybrid animals. *Journal of Genetics*,
 568 12, 101-109.
- 569 Halkett, F., Simon, J.-C., & Balloux, F. (2005). Tackling the population genetics of clonal and
 570 partially clonal organisms. *Trends in Ecology and Evolution*, 20, 194–201.
- 571 Hamilton, W. D. (1980). Sex versus non-sex versus parasite. *Oikos*, 35, 282–290.
- 572 Hamilton, W. D., Axelrod, R., & Tanese, R. (1990). Sexual reproduction as an adaptation to
 573 resist parasites (a review). *Proceedings of the National Academy of Sciences USA*, 87, 3566–
 574 3573.

- 575 Hanley, K. A., Fisher, R. N., & Case, T. J. (1995). Lower mite infestations in an asexual gecko
576 compared with its sexual ancestors. *Evolution*, *49*, 418-426.
- 577 Heethoff, M., Domes, K., Laumann, M., Maraun, M., Norton, R. A., & Scheu, S. (2007). High
578 genetic divergences indicate ancient separation of parthenogenetic lineages of the oribatid mite
579 *Platynothrus peltifer* (Acari, Oribatida). *Journal of Evolutionary Biology*, *20*, 392-402.
- 580 Henry, L., Schwander, T., & Crespi, B. J. (2012). Deleterious mutation accumulation in asexual
581 *Timema* stick insects. *Molecular Biology and Evolution*, *29*, 401-408.
- 582 Hillis, D. M. (2007). Asexual evolution, can species exist without sex? *Current Biology*, *17*,
583 R543–R544.
- 584 Hörandl, E., Cosendai, A.-C., & Temsch, E. (2008). Understanding the geographic distributions
585 of apomictic plants, a case for a pluralistic approach. *Plant Ecology and Diversity*, *2*, 309-320
- 586 Howard, R. S. & Lively, C. M. (1994). Parasitism, mutation accumulation and the maintenance
587 of sex. *Nature*, *367*, 554-557.
- 588 Johnson, S. J. (2000). Populations structure, parasitism and survivorship of sexual and asexual
589 autodiploid parthenogenetic *Campeloma limum*. *Evolution*, *54*, 167-175.
- 590 Judson, O. P., & Normark, B. B. (1996). Ancient asexual scandals. *Trends in Ecology and*
591 *Evolution*, *11*, A41-A46.
- 592 Kearney, M. (2005). Hybridization, glaciation and geographical parthenogenesis. *Trends in*
593 *Ecology and Evolution*, *20*, 495.
- 594 Kearney, M., & Shine, R. (2005). Lower fecundity in parthenogenetic geckos than sexual
595 relatives in the Australian arid zone. *Journal of Evolutionary Biology*, *18*, 609-618.
- 596 Keightley, P. D., & Eyre-Walker, A. (2000). Deleterious mutations and the evolution of sex.
597 *Science*, *290*, 331–333.
- 598 Kondrashov, A. S. (1993). Classification of hypotheses on the advantage of amphimixis. *Journal*
599 *of Heredity*, *84*, 372-387.
- 600 Kondrashov, A. S. (1994). The asexual ploidy cycle and the origin of sex. *Nature*, *370*, 213-216.
- 601 Ladle, R. J. (1992). Parasites and sex, catching the red queen. *Trends in Ecology and*
602 *Evolution*, *7*, 405-408.

- 603 Lamatsch, D. K., Lampert, K. P., Fischer, P., Epplen, J. T., Nanda, I., Schmid, M., et al. (2007).
604 Automictic reproduction in interspecific hybrids of poeciliid fish. *Current Biology*, 17, 1948-1953.
- 605 Lattorff, H. M. G., Moritz, R. F. A., & Fuchs, S. (2005). A single locus determines thelytokous
606 parthenogenesis of laying honeybee workers (*Apis mellifera capensis*). *Heredity*, 94, 533-537.
- 607 Lawrence, J. G. (1999). Gene transfer, speciation, and the evolution of bacterial genomes.
608 *Current Opinion Microbiology*, 2, 519–523.
- 609 Lesbarrères, D. (2011). Sex or no sex, reproduction is not the question. *BioEssays*, 33, 818.
- 610 Lively, C. M. & Lloyd, D. G. (1990). The cost of biparental sex under individual selection.
611 *American Naturalist*, 135, 489-500.
- 612 Lively, C. M. (2009). The maintenance of sex, host–parasite coevolution with density-dependent
613 virulence. *Journal of Evolutionary Biology*, 22, 2086-2093.
- 614 Lively, C. M., & Jokela, J. (2002). Temporal and spatial distributions of parasites and sex in a
615 freshwater snail. *Evolutionary Ecological Research*, 4, 219–226
- 616 Lively, C. M., Craddock, C., & Vrijenhoek, R. C. (1990). Red queen hypothesis supported by
617 parasitism in sexual and clonal fish. *Nature*, 344, 864-867.
- 618 Lodé, T. (2011). Sex is not a solution for reproduction, the libertine bubble theory. *BioEssays*,
619 33, 419-422.
- 620 Lodé, T. (2012a). Sex and the origin of genetic exchanges. *Trends in Evolutionary Biology*,
621 2012, 4 e1.
- 622 Lodé, T. (2012b). For quite a few chromosomes more: the origin of eukaryotes. *Journal of*
623 *Molecular Biology*, 423, 135–142.
- 624 Lodé, T. (2012c). Have sex or not? Lessons from bacteria. *Sexual Development*, 6, 325-328.
- 625 Loxdale, H. D., & Lushai, G. (2003). Rapid changes in clonal lines, the death of a 'sacred cow'.
626 *Biological Journal of the Linnaean Society*, 79, 3-16.
- 627 Lunt, D. H. (2008). Genetic tests of ancient asexuality in root knot nematodes reveal 536 recent
628 hybrid origins. *BMC Evolutionary Biology*, 8, 194.
- 629 Lushai, G., Loxdale, H. D., & Allen, J. A. (2003). The dynamic clonal genome and its adaptive
630 potential. *Biological Journal of the Linnaean Society of London*, 79, 193-208.

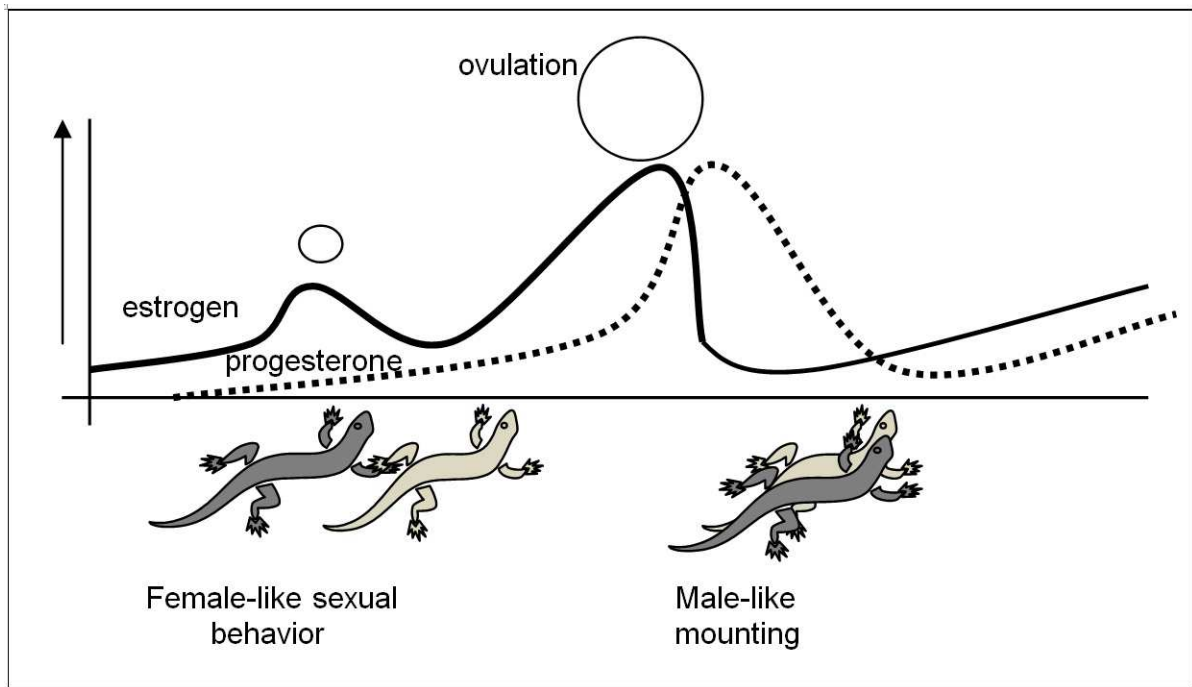
- 631 Lynch, M. (1984). Destabilizing hybridization, general-purpose genotypes, and geographic
 632 parthenogenesis. *Quaternary Review of Biology*, 59, 257-290.
- 633 Mable, K. (2007). Sex in the postgenomic era. *Trends in Ecology and Evolution*, 2, 559-561.
- 634 Mallet, J. (2007). Hybrid speciation. *Nature*, 446, 279-283.
- 635 Marin, I., & Baker, B. S. (1998) The evolutionary dynamics of sex determination. *Science*, 281,
 636 1990–1994.
- 637 Mark-Welch, D., & Meselson, M. (2000). Evidence for the evolution of bdelloid rotifers without
 638 sexual reproduction or genetic exchange. *Science*, 288, 1211-1215.
- 639 Mark-Welch, J. L., Mark-Welch, D. B., & Meselson, M. (2004). Cytogenetic evidence for asexual
 640 evolution of bdelloid rotifers. ? *Proceedings of the National Academy of Sciences USA*, 101,
 641 1618-1621.
- 642 Martens, K., Rossetti, G., & Home, D. J. (2003). How ancient are ancient asexuals?
 643 *Proceedings of the National Academy of Sciences USA*, 270, 723-729.
- 644 Martin, W. F. (2011). Early evolution without a tree of life. *Biology Direct*, 6, 36.
- 645 Matheos, M., & Vrijenhoek, R. C. (2007). Ancient versus reticulate origin of hemiclinal lineage.
 646 *Evolution*, 56, 985-992.
- 647 Maynard-Smith, J. (1978). *The evolution of sex*. Cambridge University Press, Cambridge, UK.
- 648 McDaniel, L. D., Young, E., Delaney, J., Ruhnau, F., Ritchie, K. B., & Paul, J. H. (2010). High
 649 frequency of horizontal gene transfer in the oceans. *Science*, 330, 50.
- 650 McDermott, S. R., & Noor, M. A. F. (2010). The role of meiotic drive in hybrid male sterility.
 651 *Philosophical Transactions of the Royal Society B*, 365, 1265-1272.
- 652 Morran, L. T., Schmidt, O. G., Gelarden, I. A., Parrish II, R. C., & Lively, C. M. (2011). Running
 653 with the red queen, host-parasite coevolution selects for biparental sex. *Science*, 333, 216-218.
- 654 Muller, H. J. 1964. The relation of mutation to mutational advance. *Mutation Research*, 1, 2-9.
- 655 Normark, B. B., Judson, O. P., & Moran, N. A. (2003). Genomic signatures of ancient asexual
 656 lineages. *Biological Journal of the Linnaean Society of London*, 79, 69–84.
- 657 Nygren, A., & Sundberg, P. (2003). Phylogeny and evolution of reproductive modes in
 658 *Autolytinae Syllidae*, Annelida. *Molecular Phylogeny and Evolution*, 29, 235-249.

- 659 Ochman, H., Lerat, E., & Daubin, V. (2005). Examining bacterial species under the specter of
660 gene transfer and exchange. *Proceedings of the National Academy of Sciences USA*, *102*,
661 6595-6599.
- 662 Otto, S. P. (2009). The evolutionary enigma of sex. *American Naturalist*, *174*, S1–14.
- 663 Pagano, A., Lesbarrères, D., O'hara, R., Crivelli, A., Veith, M., Lodé, T., & Schmeller, D. S.
664 (2008). Geographical and ecological distributions of frog hemiclones suggest occurrence of both
665 “General Purpose Genotype” and “Frozen Niche Variation” clones. *Journal of Zoological*
666 *Systems in Evolutionary Research*, *46*, 162-168.
- 667 Pagano, A., Dubois, A., Lesbarrères, D., & Lodé, T. (2003). Frog alien species, a way for
668 genetic invasion ? *Comptes-Rendus Biologies*, *326*, 85-92
- 669 Pal, C., Macia, M., Oliver, A., Schacher, I., & Buckling, A. (2007). Coevolution with viruses
670 drives the evolution of bacterial mutation rates. *Nature*, *450*, 1079-1081.
- 671 Parker, Jr E. D., & Selander, R. K. (1976). The organization of genetic diversity in the
672 parthenogenetic lizard *Cnemidophorus tesselatus*. *Genetics*, *84*, 791-805.
- 673 Parnell, J. J., Rompato, G., Latta IV, L. C., Pfrender, M. E., Van Nostrand, J. D., He, Z., Zhou,
674 J., Andersen, G., Champine, P., Balasubramanian, G., & Weimer, B. C. (2010). Functional
675 biogeography as evidence of gene transfer in hypersaline microbial communities. *PLoS One*, *5*,
676 e12919. doi,10.1371/journal.pone.0012919
- 677 Passamonti, M., Mantovani, B., & Scali, V. (2004). Phylogeny and karyotype evolution of the
678 Iberian *Leptynia attenuata* species complex (Insecta Phasmatodea). *Molecular Phylogeny and*
679 *Evolution*, *30*, 87–96.
- 680 Penny, D. (1985). The evolution of *meiosis* and sexual reproduction. *Biological Journal of the*
681 *Linnaean Society of London*, *25*, 209–220.
- 682 Phadnis, N., & Orr, H. A. (2009). A single gene causes both male sterility and segregation
683 distortion in *Drosophila* hybrids. *Science*, *323*, 376-379.
- 684 Presgraves, D. C. (2007). Speciation genetics, epistasis, conflict and the origin of species.
685 *Current Biology*, *17*, R125-R127.

- 686 Quarin, C. L., Espinoza, F., Martinez, E. J., Pessino, S. C., & Bovo, O. A. (2001). A rise of ploidy
687 level induces the expression of apomixis in *Paspalum notatum*. *Sex Plant Reproduction*, *13*,
688 243-249.
- 689 Ramesh, M. A., Malik, S., & Logsdon, J. M. (2005). A phylogenomic inventory of meiotic genes,
690 evidence for sex in *Giardia* and an early eukaryotic origin of meiosis. *Current Biology*, *15*, 185-
691 191.
- 692 Redfield, R. (2001). Do bacteria have sex? *Nature Reviews of Genetics*, *2*, 634–639.
- 693 Rice, W. R. (2000). Dangerous liaisons. *Proceedings of the National Academy of Sciences*
694 *USA*, *97*, 12953-12955.
- 695 Rice, W. R. (2002). Experimental tests of the adaptive significance of sexual recombination.
696 *Nature Reviews of Genetics*, *3*, 241–251.
- 697 Rieseberg, L., & Willis, J. H. (2007). Plant speciation. *Science*, *317*, 910-914.
- 698 Robinson, M. T., Weeks, A. R., & Hoffmann, A. A. (2002). Geographic patterns of clonal
699 diversity in the earth mite species *Pentthaleus major* with particular emphasis on species
700 margins. *Evolution*, *56*, 1160-1167.
- 701 Salathé, P., & Ebert, D. (2003). The effects of parasitism and inbreeding on the competitive
702 ability in *Daphnia magna*, evidence for synergistic epistasis. *Journal of Evolutionary Biology*, *16*,
703 976–985.
- 704 Schaefer, I., Domes, K., Heethoff, M., Schneider, K., Schön, I., Norton, R. A., et al. (2006). No
705 evidence for the “Meselson effect” in parthenogenetic oribatid mites (Oribatida, Acari). *Journal*
706 *of Evolutionary Biology*, *19*, 184-193.
- 707 Schartl, M., Wilde, B., Schlupp, I., & Parzefall, J. (1995). Evolutionary origin of a parthenoform,
708 the Amazon Molly *Poecilia formosa*, on the basis of a molecular genealogy. *Evolution*, *49*, 827-
709 835.
- 710 Schley, D., Doncaster, C., & Slutkin, T. (2004). Population models of sperm-dependent
711 parthenogenesis. *Journal of Theoretical Biology*, *229*, 559–572.
- 712 Schmeller, D. S., O'Hara, R., & Kokko, H. (2005). Male adaptive stupidity, male mating pattern
713 in hybridogenetic frogs. *Evolutionary Ecological Research*, *7*, 1039–1050

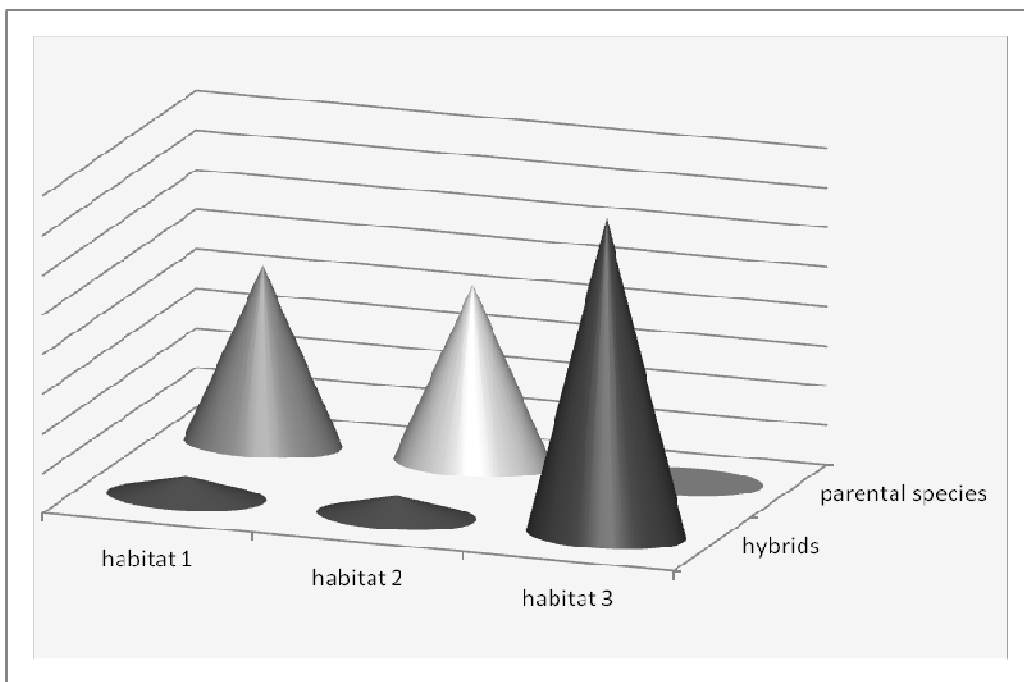
- 714 Schmidt, B. R. (1993). Are hybridogenetic frogs cyclical parthenogens? *Trends in Ecology and*
715 *Evolution*, 8, 271–273.
- 716 Schön, I., & Martens, K. (2003). No slave to sex. *Proceedings of the Royal Society of London B*,
717 270, 827-833.
- 718 Schön, I., Butlin, R. K., Griffiths, H. I., & Martens, K. (1998). Slow evolution in an ancient
719 asexual ostracod. *Proceedings of the Royal Society of London B*, 265, 235-242.
- 720 Schultz, R J. (1971). Special adaptive problems associated with unisexual fishes. *American*
721 *Zoologist*, 11, 351–360.
- 722 Schurko, A. M., & Logsdon, Jr J. M. (2008). Using a *meiosis* detection toolkit to investigate
723 ancient asexual "scandals". *BioEssays*, 30, 579-589.
- 724 Schwander, T., & Crespi, B. J. (2008). Multiple direct transitions from sexual reproduction to
725 apomictic parthenogenesis in *Timema* stick insects. *Evolution*, 63, 84-103.
- 726 Seehausen, O. (2004). Hybridization and adaptive radiation. *Trends in Ecology and Evolution*,
727 19, 198-207.
- 728 Simon, J. C., Delmotte, F., Rispe, C., & Crease, T. (2003). Phylogenetic relationships between
729 parthenogens and their sexual relatives, the possible routes to parthenogenesis in animals.
730 *Biological Journal of the Linnaean Society of London*, 79, 151-163.
- 731 Slobodchikoff, C. N., & Daly, H. V. (1971). Systematic and evolutionary implications of
732 parthenogenesis in the Hymenoptera. *American Zoologist*, 11, 273-282.
- 733 Smith, R. J., Kamiya, T., & Horne, D. J. (2006). Living males of the 'ancient asexual'
734 Darwinulidae (Ostracoda, Crustacea). *Proceedings of the National Academy of Sciences USA*,
735 273, 1569-1578.
- 736 Sun, S., & Heitman, J.(2011). Is sex necessary ? *BMC Biology*, 9, 56.
- 737 Suomalainen, E. (1962). Significance of Parthenogenesis in the Evolution of Insects. *Annual*
738 *Review of Entomology*, 7, 349-366.
- 739 Suomalainen, E., Saura, E., & Lokki, J. (1976). Evolution of parthenogenetic insects.
740 *Evolutionary Biology*, 9, 209–257.
- 741 Tobler, M., & Schlupp, I. (2005). Parasites in sexual and asexual mollies *Poecilia*, *Poeciliidae*,
742 *Teleostei*, a case for the Red Queen? *Biology Letters*, 1, 166-168.

- 743 Uyenoyama, M. K. (1984). On the evolution of parthenogenesis, A genetic representation of the
744 "cost of meiosis". *Evolution* 38, 87-102.
- 745 Venditti, P. C., Meade, A., & Pagel, M. (2010). Phylogenies reveal new interpretation of
746 speciation and the Red Queen. *Nature*, 463, 349-352.
- 747 Vorburger, C. (2001). Heterozygous fitness effects of clonally transmitted genomes in
748 waterfrogs. *Journal of Evolutionary Biology*, 14, 602-610.
- 749 Vorburger, C., Sunnucks, P., & Ward, S. A. (2003). Explaining the coexistence of asexuals with
750 their sexual progenitors, no evidence for general-purpose genotypes in obligate parthenogens
751 of the peach-potato aphid, *Myzus persicae*. *Ecology Letters*, 6, 1091-1098.
- 752 Vos, M. (2009). Why do bacteria engage in homologous recombination? *Trends in Microbiology*,
753 17, 226–232.
- 754 Vrijenhoek, R. C. (1994). Unisexual fish, model systems for studying ecology and evolution.
755 *Annual Review of Ecological System*, 25, 71-96.
- 756 Vrijenhoek, R. C. (1998). Animal clones and diversity. Are natural clones generalists or
757 specialists? *Bioscience*, 48, 617-628.
- 758 Watson, R. A., Weinreich, D. M. & Wakeley, J. (2011). Genomes structure and the benefit of
759 sex. *Evolution*, 65, 523-536.
- 760 Wenseleers, T., & Van Oystaeyen, A. (2011). Unusual modes of reproduction in social insects:
761 Shedding light on the evolutionary paradox of sex. *BioEssays*, 33, 927-937.
- 762 Wilkinson, G. S., & Fry, C. L. (2001). Meiotic drive alters sperm competitive ability in stalk-eyed
763 flies. *Proceedings of the Royal Society of London B*, 268, 2559-2564.
- 764 Williams, G. C. (1975). *Sex and evolution*. Princeton: Princeton University Press.
- 765 Woolley S. C., Sakata J. T., & Crews D. (2004). Tracing the Evolution of Brain and Behavior
766 Using Two Related Species of Whiptail Lizards: *Cnemidophorus uniparens* and *Cnemidophorus*
767 *inornatus*. *ILAR Journal*, 45, 46-53.



768
769
770
771
772

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



773
774
775
776
777

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)