
Parthenogenesis and Natural Clones

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GLOSSARY

amphimixis Sexual reproduction; the mixing of the genes from two distinct individuals; involving the recombinational effects of meiotic reduction and fusion of gametes.

apomixis Asexual reproduction without chromosome reduction or fusion of gametes; ameiotic parthenogenesis; retains parental heterozygosity.

automixis Asexual reproduction with chromosomal reduction but without fusion of gametes; meiotic parthenogenesis; rapidly leads to complete homozygosity.

endoduplication Duplication of the entire chromosomal set without cell division prior to meiosis.

gynogenesis Sperm-dependent parthenogenesis; sperm are used to activate embryogenesis but fusion of egg and sperm nuclei does not occur; pseudogamy.

hemiclone A haploid clonal genome that is transmitted without recombination by hybridogenetic females.

hybridogenesis The perpetuation of a hybrid genotype (AB) by hemiclonal inheritance in which the maternal genome (A) is transmitted to eggs; the paternal genome (B) is discarded during oogenesis and restored by true fertilization with sperm from males of a sexual host species B.

pseudo gamy Sperm-dependent parthenogenesis in plants; pollen is required to activate seed development, but the seed nucleus is produced clonally.

tychoparthenogenesis Occasional or accidental parthenogenetic development in unfertilized eggs.

Parthenogenesis (virgin birth) is reproduction via eggs but without sex. Eggs develop into new individ-

uals without fertilization by sperm. Parthenogenetic lineages occur in many plant and animal taxa, and they may flourish under a variety of ecological conditions. Nevertheless, individual clones are believed to be evolutionary dead ends, because they lack the ability to respond genetically to changes in their physical and biotic environments.

I. PARTHENOGENESIS AND ASEXUAL REPRODUCTION

Reproduction does not require sex, or amphimixis, a complex process that involves two basic elements: (i) meiotic reduction-chromosomal segregation, assortment, and crossing over that generate an immense variety of haploid gametes; and (ii) syngamy-fusion of gametes that produces unique new individuals in each generation. Mixing the genotypes from different individuals (recombination) is the essential characteristic of sex in eukaryotic organisms, and circumvention of these processes leads to parthenogenesis and cloning.

Vegetative reproduction (budding, fragmentation, fission, etc.) is common in plants and some invertebrate animals. Although comparable to parthenogenesis in producing clones, vegetative modes of reproduction should be distinguished because they do not involve egg production and meiotic processing of chromosomes. Chromosome processing may be necessary to reset imprinted DNA methylation patterns and restore developmental totipotency in some organisms. Additionally, fertilized seeds and eggs (and subsequent larvae) are often the essential dispersal phase of many plants and animals. In most cases, vegetative propagules tend to remain close to the parent organism. Corals ordinarily reproduce by budding, but they employ sexual reproduction to

produce planula larvae, the dispersal phase of the life cycle. In an ecological sense, vegetative reproduction is more appropriately compared with growth than reproduction.

Cyclical parthenogenesis alternates between sexual and asexual egg production. Because cyclical parthenogens engage in periodic recombination, they are facultatively sexual. The cladoceran waterflea, *Daphnia pulex*, produces a new assemblage of clones after each cycle of sexual reproduction. Sexual reproduction generally is stimulated by high density or other forms of stress and is used to produce the overwintering eggs. However, some populations occurring at high latitudes and in more permanent bodies of water have given rise to obligately parthenogenetic lineages that no longer reproduce sexually.

True parthenogenesis is a strictly clonal form of reproduction that transmits the female's diploid (or polyploid) genome to eggs, which develop spontaneously into genetically identical daughters. The terminology favored by botanists is more precise in its distinction among cytological mechanisms involved in the production of eggs. The term apomixis (ameiotic parthenogenesis) is used to describe zygote production without chromosomal reduction (some researchers include vegetative reproduction under apomixis). Some apomicts eliminate the reductional division (meiosis I) and produce nonrecombinant eggs with a single equational division (meiosis II). Other ameiotic methods of egg production are known and the primary genetic consequences are strict clonal inheritance and retention of the maternal level of heterozygosity.

In contrast, automixis (meiotic parthenogenesis) restores diploidy by fusing various meiotic products. For example, some free-living *Rhabditis* nematodes fuse the second polar body with the egg nucleus. In most cases, automixis is comparable to self-fertilization and quickly leads to complete homozygosity. Some automicts produce normal haploid ova and then duplicate the generative nucleus in a subsequent mitotic division. Fusion of these mitotic products restores diploidy but leads to complete homozygosity in one step. Once automicts are completely homozygous, inheritance is effectively clonal.

Most parthenogenetic animals are functionally apomictic. They retain elements of meiosis while

circumventing chromosomal recombination and reduction. For example, parthenogenetic whiptail lizards of the genus *Cnemidophorus* duplicate the entire chromosomal complement prior to meiosis, a process known as endoduplication. Because synapsis occurs between the duplicated pairs of chromosomes, meiotic recombination is genetically inconsequential. Eggs contain a functionally nonrecombinant version of the maternal genotype. A great variety of functionally apomictic mechanisms are known. Their common theme is the circumvention of reduction and recombination. Many parthenogenetic animals arose as hybrids, and functional apomixis effectively preserves their hybrid genotypes. Why functionally apomictic animals are more common than true apomicts is not understood. Perhaps, chromosomal processing during prophase of meiosis I is necessary for normal embryonic development.

Sperm-dependent modes of parthenogenetic reproduction also are known. Dandelions in North America (they were introduced from Europe) are pseudogamous apomicts: Pollination is necessary to activate development of endosperm tissue in the seed, but the generative nucleus develops apomictically. Pseudogamy is more commonly called gynogenesis in animals (Fig. 1). Despite the need for sperm, pseudogamous inheritance is strictly maternal and clonal. The fall cankerworm moth, *Alsophila pometaria*, has pseudogamous lineages that use sperm from males of a coexisting sexual lineage, but gynogenetic fish such as the Amazon molly, *Poecilia formosa*, use sperm from males of closely related sexual species. The need for sperm produces a kind of host-parasite relationship between sexually reproducing sperm donors and all-female gynogens. However, pseudogamous planarians are hermaphrodites, and they can use their own sperm. Although pseudogamous forms are not parthenogenetic in the strict sense (i.e., virgin birth), genetic consequences are the same: Syngamy does not occur and inheritance is clonal. Nevertheless, sperm-dependent versus sperm-independent forms of parthenogenesis function under very different ecological constraints.

Hybridogenesis, an unusual form of matrilineal inheritance that perpetuates a hybrid genotype, combines elements of parthenogenesis and sexual reproduction. The hybridogenetic fish *Poeciliopsis*

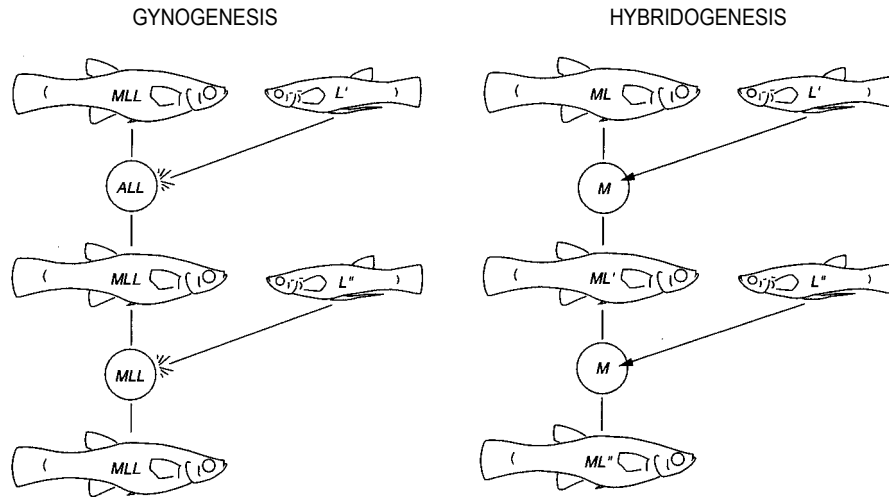


FIGURE 1 Gynogenetic and hybridogenetic reproduction in all-female fish (genus *Poeciliopsis*) of hybrid origin. The letters *M* and *L* represent whole chromosome sets from the sexually reproducing progenitors, *P. monacha* and *P. lucida*. The triploid gynogen, *P. monacha-2 lucida* (or *MLL*), has one set of monacha chromosomes and two sets of lucida chromosomes; and the diploid hybridogen, *P. monacha-lucida* (or *ML*) has one set of chromosomes from each species. Both the gynogen and hybridogen are pictured mating with males of *P. lucida*. During gynogenesis, the entire triploid genome, *MLL*, is transmitted between generations without recombination. Different markers associated with the sperm source (*L*, *L'*, *L''*, etc.) are not incorporated or expressed in the offspring. During hybridogenesis, only the haploid *M* genome (hemiclone) is transmitted to eggs. The paternal *L* genome is replaced in each generation.

monacha-lucida is a hybrid between the sexual species *P. monacha* and *P. lucida*. It is easier to describe hybridogenesis if we substitute the letters *M* and *L* for monacha and lucida chromosome sets of the hybrid (Fig. 1). Just before meiosis, these *ML* hybrids discard the *L* chromosomes. Functional eggs contain only a nonrecombinant *M* set that must fuse with sperm provided by *P. lucida* males, producing a new hybrid, *ML'*. New paternal genomes (*L*, *L'*, *L''*, etc.) are (i) drawn anew from the sexual gene pool in each generation, (ii) paired with the *M* genome, (iii) fully expressed in *ML* hybrids, and then (iv) discarded. The *M* genome is called a hemiclone because it comprises only half of the organism's chromosomal complement, and it is cloned. Populations of *P. monacha-lucida* usually contain several hemiclones, marked by distinct *M* genomes that were independently derived from *P. monacha*. The European water frog, *Rana esculenta*, also is hybridogenetic. Hybridogenesis is also found in some insects, but overall it is a rare form of clonal reproduction.

Numerous variations exist on these basic themes of clonal reproduction and parthenogenesis in plants and animals. The reference by Suomalainen and co-workers (1987) provide a useful summary of what is known about cytogenetic mechanisms.

II. ORIGINS OF PARTHENOGENS

Most plant and animal parthenogens (agamospecies or parthenoforms) have arisen relatively recently from sexual progenitors. Additionally, a large proportion of parthenogens are polyploids and many are interspecific hybrids. In the majority of cases, the sexual progenitors are extant and living sympatrically or parapatrically with the parthenogens (see Section III).

A. Spontaneous Origins

Meiotic parthenogens arise spontaneously in many plant and animal species. *Tychoparthenogenesis* (occasional development of unfertilized eggs) may be

avored in colonizing species that often find themselves at low density and without mates. Artificial selection can improve the rate of tycho-parthenogenesis in *Drosophila mercatorum*, which suggests that automictic species such as *D. mangabierai* may have arisen spontaneously from tycho-parthenogenetic ancestors. Nevertheless, the transition to automixis may be difficult if the sexual ancestors carry deleterious recessive mutations. Selection will rapidly eliminate automictic lineages that are homozygous for such mutations and fix the "lucky" lineages that lack them. Colonization, founder events, and small population sizes can purge the genetic load of the sexual progenitors and facilitate the transition to automixis.

B. Hybrid Origins

Many apomictic and functionally apomictic parthenogens arose as interspecific hybrids. All known asexual vertebrates are hybrids, as are many insects. The strong association between asexuality and hybrid origins led some researchers to suggest that cloning fixes heterosis (hybrid vigor) that may confer broad ecological tolerance. Although evidence exists for broad tolerance to physical stresses in some asexual plants, fish, and frogs, the phenomenon may be a consequence of interclonal selection for the best hybrid combinations rather than heterosis per se. Experimental studies with laboratory-synthesized hybridogenetic fish (*P. monacha-lucida*; Fig. 1) revealed that most hybrids were inferior to the parental forms; however, a small proportion of hybrid combinations had relatively high fitness. Fitness was not a consequence of heterosis; it was a consequence of the combining properties of parental genomes. Inferences about heterosis and fitness from comparative studies of natural parthenogens and their sexual counterparts are likely to be biased because we only see the successful genomic combinations in nature and not the failures that were purged by selection.

The association between parthenogenesis and hybridization may be a consequence of hybrid dysgenesis. Interspecific hybridization often leads to disruption of meiosis and sterility. Natural selection will preserve the lucky cytogenetic accidents that rescue egg production and restore or retain diploidy. Hybridization is one of a number of dysgenic pro-

cesses that can produce windows of opportunity for the selection of ameiotic or functionally apomictic reproduction.

C. Parthenogenesis and Polyploidy

The majority of unisexual vertebrates, insects, and plants are polyploids. Although some researchers have suggested that elevated ploidy may produce superior genetic combinations, the association between polyploidy and parthenogenesis may also result from dysgenic processes. Accidental fertilization of a diploid (unreduced) egg will produce triploid progeny that typically are sterile. Such events create another window of opportunity for the selection of lucky cytological accidents that rescue egg production.

Prior establishment of functionally apomictic diploids can facilitate the elevation of ploidy because it removes the sterility barrier. For example, the triploid gynogenetic fish *P. monacha-2 lucida* ($3n = 72$; Fig. 1) arose by addition of a second *lucida* genome ($n = 24$) to a *P. monacha-lucida* ($2n = 48$) hybrid. For most polyploids, we do not know whether unisexuality or polyploidy came first or if they arose together. If some of these polyploids outperform their diploid counterparts, enhanced performance may be a product of interclonal selection and fixation of the best genomic combinations from sexual ancestors rather than a direct consequence of elevated ploidy.

III. ECOLOGICAL CONSIDERATIONS

All other things being equal (i.e., survival, fecundity, niche requirements, etc.), an all-female lineage should rapidly replace its sexual relatives because a parthenogenetic female produces two daughters for every one produced by an equivalent sexual female. This twofold "cost of sex" may be exacerbated by numerous additional liabilities, such as the risks and energetic costs associated with finding a mate, courtship, and mating itself. Despite the costs of sex, asexual lineages generally have not completely replaced their sexual counterparts in animal taxa that regu-

larly produce clones. Williams (1975) referred to this ecological and evolutionary problem as the "paradox of sex." Why does biparental sexuality predominate so overwhelmingly despite its costs? Ecological studies that attempt to address this question have focused on the primary assumption behind this paradox—that all else is equal between sexual progenitors and derived asexual lineages.

A. Primary Fitness (Fecundity and Survival)

No investigator has succeeded in comparing the lifetime fertility and survival schedules of closely related sexual and asexual lineages in their natural environments, so it is impossible to say that everything else is equal with respect to primary fitness (fertility and survival). Some field and laboratory investigations have obtained data on components of fitness, although few generalizations can be drawn from the current studies. Gynogenetic and hybridogenetic *Poeciliopsis* have fecundities that are similar to those of their sexual counterparts. All-female reproduction is limited, however, by the availability of sperm from the sexual hosts. Parthenogenetic flies (*Drosophila*) and lizards (*Lacerta*) exhibit lower hatching rates than comparable sexual species. Finally, automictic lineages tend to have low hatching success, perhaps due to expression of deleterious recessive genes and inbreeding depression.

Survival differences have been observed in field and laboratory studies. Some unisexual fish (*Phoxinus eos-neogaeus*) and frogs (*R. esculenta*) may be more tolerant of thermal stresses than their sexual counterparts, but the differences do not appear to be generalizable. The roles of hybridity and selection for resistant clones are confounded in these organisms. Studies of survival under stress in *Poeciliopsis* revealed considerable variation among clones and no consistent advantage over the sexual counterparts for the various kinds of stress tested.

B. Geographical Parthenogenesis and General-Purpose Genotypes

Parthenogens should have superior colonizing abilities because they do not have to find mates when

they initially occur at low density. Some researchers argue that parthenogens are general-purpose genotypes (jack-of-all-trades) that have wider ecological tolerances than their sexual counterparts. Other researchers argue that parthenogens are narrowly adapted fugitive species that escape from competition with their sexual ancestors. Biogeographical studies reveal that parthenogens are more frequent at the margins of a species range, at extreme latitudes, at higher altitudes, and in regularly disturbed communities—a pattern known as geographical parthenogenesis. It is unclear in most cases, however, whether this pattern is due to enhanced colonization abilities of parthenogens, an inability to compete with sexual progenitors in ecologically central areas, or an increased tolerance of ecologically marginal conditions.

Many widespread apomictic weeds appear to have general-purpose genotypes that can tolerate a wide range of environmental conditions. Selection in a varying environment should favor clones that fluctuate least in fitness. General-purpose clones may not be the best genotype in a particular set of circumstances but, more important, they avoid being the worst during many circumstances. Although the wide geographical distribution of many asexual plants and animals is often cited as supporting the general-purpose genotype hypothesis, such taxa may be composed of numerous cryptic (hidden) clones, each with different environmental tolerances, as found in some asexual waterfleas, brine shrimp, snails, and topminnows. Furthermore, a wide geographical distribution alone may not be sufficient evidence for general-purpose genotypes because a single widespread clone might occupy a narrow but universally available niche. For example, humans introduced dandelion (*Taraxacum officinale*) clones to North America and their success is a consequence of human habitat disruption (grassy lawns).

The fugitive species aspect of geographical parthenogenesis does not apply to sperm-dependent parthenogens. Their colonization and competitive abilities are constrained by the need for sperm from coexisting sexual hosts. Outcompeting or geographically escaping the sexual host will lead to their own reproductive failure. Hybridogenetic and gynogenetic fish (*Poeciliopsis*) have relatively limited ranges

encompassed within the geographical limits of their sexual relatives and hosts, whereas some parthenogens, such as the cockroach *Pycnoscelus surinamensis*, have immense distributions, all outside the range of the putative sexual ancestors.

C. Niche Requirements

The niches of parthenogenetic clones and their sexual counterparts appear to differ in many cases. A sexual population should have greater niche breadth than a single clone if the differences between genotypes contribute to a wider use of resources. For example, it is difficult to imagine a single jack-of-all-trades human clone (if humans were to be cloned) that has the breadth of talents of the entire human population from which it was drawn. The difference in niche breadth between a sexual population and a single clone will result in asymmetrical competition, in which the sexual lineage has a greater competitive impact on the clone than vice versa. However, an assemblage of ecologically divergent clones may equal or exceed the niche breadth of the sexual ancestors, leading to symmetrical competition and, perhaps, competitive exclusion of the sexuals.

Computer simulations of these ideas revealed that clonal invasion of the sexual niche proceeds from the margins to the center of the resource distribution. According to the frozen niche-variation model, a diverse array of clonal genotypes is frozen from the sexual gene pool. Interclonal selection will eliminate clones that overlap substantially with one another and the sexual ancestors and fix an assemblage of clones that maximally exploits the range of available resources. Sexual and clonal forms can coexist as long as competition remains asymmetrical and the combined niche of the clones is less than that of the sexuals.

Some hybrid parthenogens appear to occupy a weakly contested intermediate niche between the parental forms. However, hybrids are not necessarily intermediate for all niche-related characters. For example, some clones of the hybridogenetic fish *P. monacha-lucida* exhibit dominant phenotypes and extreme trophic behaviors. Hybridity does not necessarily constrain unisexual organisms to ecological intermediacy. Evidence also exists for niche separa-

tion between diploid and polyploid parthenogens in several taxa.

IV. EVOLUTIONARY CONSIDERATIONS

Asexual lineages may flourish briefly in some environments, but most appear to be dead ends with limited adaptive potential. From a phylogenetic perspective, obligately asexual plants and animals are little more than buds at the ends of branches that are fundamentally sexual. The rotifer class Bdelloidea is a notable exception. Although they appear to be strictly asexual, bdelloids have diversified into hundreds of morphologically distinct species that are classified into several families. We know of few other asexual taxa that have diversified in a similar way.

Bdelloids notwithstanding, numerous theories exist concerning the genetic, ecological, and evolutionary benefits of sex. Theories about the origin of recombination and meiosis in eukaryotic organisms are poorly understood and beyond the scope of this article. However, factors that favored the origin of sex (e.g., recombinational repair of DNA damage) need not be the same as those that currently maintain sex in higher organisms. Critical reviews of current hypotheses are provided in several of the listed references. Some major ideas related to the maintenance of sex in higher organisms are outlined in the following sections.

A. The Fisher-Muller Hypothesis (Sex Accelerates Evolution)

Adaptation by natural selection requires heritable genetic variation, and sexuality generates a new array of genotypes in each generation. Having more variation, sexual species should be able to adapt more quickly in a changing environment than asexual species. In the early 1930s, Ronald Fisher and Hermann Muller restated this hypothesis in genetic terms. Good mutations occur rarely (e.g., let the mutation rate, μ , be 10^{-8}). The probability of two good mutations arising simultaneously in the same asexual lineage is the vanishingly small product of these numbers (A^2 or 10^{-16}). It is more likely that two good mutations will come together in the same clone if

the first mutation spreads to near fixation before the second mutation arises in the same lineage. In a sexual population, however, the mutations can arise simultaneously in different individuals, and mixis will bring them together as each spreads to fixation.

Although the idea that sex is good for evolution seems intuitively satisfying, it suffers from several fundamental problems. It provides an advantage to sexual populations but not to the individuals that participate in sex. Sexual individuals will not spread at the expense of clones, unless the individuals also gain an advantage that compensates for the cost of males or meiosis. Furthermore, it is hard to see how sex could spread for the purpose of accelerating evolution of the species if evolution itself has no purpose. Evolution is a consequence of heritable variation among individuals and natural selection; it has no goals. Furthermore, evolving rapidly does not necessarily guarantee evolutionary success. Some "living fossils" such as *Limulus*, the horseshoe crab, and *Lingula*, an articulated brachiopod, have changed very little morphologically for hundreds of millions of years.

B. Muller's Ratchet (Sex Is a Way to Get Rid of Bad Mutations)

In 1960, Muller recognized another problem with the Fisher-Muller theory: The vast majority of expressed mutations are slightly deleterious. Recombination uncouples mutations and facilitates purging the bad ones. Muller suggested that slightly deleterious mutations will accumulate in asexual lineages and hitchhike along with the rare good mutations. Clones with the lowest genetic load may be lost due to genetic drift in finite populations. Except for the exceedingly rare back-mutation, the expected fate of an asexual population is to ratchet forward with deteriorating fitness. Other researchers have examined this problem in greater mathematical detail and refer to the mutational meltdown of clones. Despite the attractiveness of this argument, the evolutionary time scale for Muller's ratchet makes it difficult to imagine how it can compensate for the twofold cost of sex on an ecologically relevant time scale (but see Section IV,D).

C. The Tangled Bank (Sex Increases Niche Breadth)

Genotypic differences among individuals of a sexual species may contribute to more effective utilization of natural resources. In a heterogeneous environment, a sexual parent that produces diverse progeny may leave more offspring than a clonal parent that produces only one specialized type of offspring. Competition should be lower among the diverse sexual offspring than among clonal offspring. Thus, sexuals may gain a slight advantage over individual clones in a heterogeneous environment, but they may be eclipsed and replaced by an ecologically diverse assemblage of clones. Without considerable demographic stochasticity that leads to the random loss of clones, it is hard to see how this model can compensate for the twofold cost of sex.

D. The Red Queen (Sex Is Needed to Stay in Coevolutionary Race with Biological Enemies)

A consensus seems to be emerging that coevolutionary pressures from biological enemies (parasites, predators, and competitors) may provide sufficient ecological compensation for the costs of sex. Rapidly evolving microparasites (bacteria, viruses, etc.), because of their short generation times and vast numbers, will rapidly evolve means to avoid immune surveillance and exploit the most common host phenotypes. This provides rare host phenotypes a temporary advantage, until they rise in frequency and become the targets of newly evolved mechanisms of parasitic attack. Fitness of the host is frequency dependent, always favoring rare and different phenotypes, a cycle that maintains genetic polymorphism. Such a process would favor the parents of diverse offspring by spreading the risks of survival. This benefit is even more evident for species that brood their young and thereby increase the risk of contagion.

Red Queen processes may also facilitate the advance of Muller's ratchet. Frequency-dependent fitness will cause clones to cycle in abundance. Clones are more susceptible to random extinction when they are rare, and these losses may also remove clones

with the smallest load of deleterious mutations. Working together, the Red Queen and Muller's ratchet may result in a rapid decay of fitness that may account for the maintenance of sex on ecological time scales.

V. PARTHENOGENS AS STUDY ORGANISMS

Comparative studies of sexual and asexual organisms have provided considerable insight into the adaptive benefits of sex. Just as a physician studies deficiencies and diseases to understand the functioning of normal health, evolutionary biologists and ecologists study parthenogenetic clones as deviations from the normal sexual processes. Understanding the conditions under which asexuals prosper has provided insight into the short-term limitations of biparental sex. The overall biogeographical patterns of asexual organisms have likewise allowed biologists to reject some of models for the benefits of sex.

Efforts are also under way to compare the evolutionary longevity of closely related sexual and asexual taxa. Analyses of mitochondrial and nuclear genes provide a general picture that most asexual taxa, except bdelloid rotifers perhaps, arose recently and are relatively short-lived. Few asexual taxa have diversified to the extent that a taxonomist would be tempted to erect new species, genera, or families. For the most part, clonal diversity in asexual populations can be explained by recurrent origins of new clones from extant sexual progenitors. This observation leads to a surprising conclusion that the ecological success of many asexual taxa may depend on

periodic recruitment of new genotypes from the sexual gene pool. Thus, sex, and periodic recombination, may also be essential for the ecological success and persistence of asexual populations.

See Also the Following Articles

ASEXUAL REPRODUCTION; CLONING; HYBRIDIZATION; MEIOSIS

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