

GENETIC AND ECOLOGICAL CONSTRAINTS ON THE ORIGINS AND ESTABLISHMENT OF UNISEXUAL VERTEBRATES

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Unisexual "species" of vertebrates are taxonomically rare because their origins from sexual ancestors and their establishment in nature are subject to severe genetic, developmental, and ecological constraints. Interspecific hybridization appears necessary to disrupt normal meiotic oogenesis, thereby leading to nonrecombinant all-female reproduction, but hybridization can also disrupt normal developmental processes. Most new hybrids typically exhibit depressed fertility, survival, and developmental stability. There is no evidence for spontaneous heterosis in newly synthesized unisexual hybrids. The enhanced fitness characteristics of some naturally occurring unisexuals is due to interclonal selection eliminating low-fitness clones and leaving only the high-fitness clones.

New unisexual lineages must also face a series of ecological and evolutionary constraints. The establishment of gynogenetic and hybridogenetic unisexuals requires a suitable host species whose males can be exploited as mates. Furthermore, the establishment of new unisexual hybrids might be constrained by competition from the parental species and existing clonal lineages. The demise of clonal lineages might be accelerated by disappearing clonal subniches, destabilizing hybridization, and Muller's ratchet. Individual clones probably suffer a relatively high extinction rate.

The argument that asexual lineages are "evolutionary dead-ends" appears to be supported by recent genetic studies. If unisexual organisms play a significant evolutionary role, it may be to serve as temporary vehicles for novel gene combinations. Occasionally such novel combinations might reestablish sexual reproduction and thereby produce a new species. A newly discovered sexual species of *Poeciliopsis* may be the first example of this scenario.

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INTRODUCTION

Approximately 50 unisexual "species" of vertebrates have been recognized during the past half century. Nearly all arose from interspecific matings leading to hybrid genotypes sustained by nonrecombinant reproductive processes including true parthenogenesis, gynogenesis, and hybridogenesis (Vrijenhoek et al., this volume). In many localities, these all-female "species" are ecologically very successful, often outnumbering the bisexual (i.e., dioecious, sexually reproducing) species from which they arose. Whenever an all-female lineage arises, it should, all other things being equal, rapidly replace its bisexual ancestors, which must bear the cost of producing males (Clanton, 1934; Williams, 1975; Maynard Smith, 1978). Despite this obvious demographic advantage, all-female lineages have not completely replaced their bisexual ancestors on broad geographical scales. Therefore, we must question the assumption that all other things (genetic, developmental, and ecological) are equal. Furthermore, when considered from a taxonomic perspective, we must acknowledge that morphologically distinct unisexual "species" are relatively rare, comprising little more than 0.1% of all the named species of vertebrates. The broader phylogenetic picture strongly suggests that unisexual species are evolutionary "dead-ends" (White, 1978) and "no-hopers" (Darlington, 1939).

It may seem blasphemous to begin a volume on unisexual vertebrates by drawing attention to their taxonomic rarity

and apparent evolutionary hopelessness. My intent, however, is to focus on the unique opportunities that unisexual organisms provide for exploring a broad range of evolutionary, genetic, and ecological questions. Examination of unusual processes opens a window to understanding what is common and what is normal. We learn about human health by studying innumerable disorders and diseases, and we learn about the function of normal genes by studying the phenotypic consequences of mutations. To understand the functional properties of outcrossing, biparental sexuality, we must study the consequences of aberrant reproductive processes. My purpose in this chapter is to examine genetic, developmental, and ecological constraints that limit the origins, establishment, and persistence of unisexual populations.

IT IS HARD TO BECOME A UNISEXUAL VERTEBRATE

Meiosis is a tightly coordinated and extremely conservative process that shows little variation among sexually reproducing, diploid eukaryotes. The genetic recombination (segregation, assortment, crossing-over) that occurs during normal meiosis produces a broad diversity of **haploid** gametes. Thus, the origin of a clonally reproducing unisexual lineage depends on some event that disrupts or circumvents recombination during meiosis. It is hard to become a unisexual organism be-

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cause alteration of meiosis often leads to infertility or complete sterility (see **Templeton**, 1982).

Hybrid origins of unisexual vertebrates.- The hybrid nature of most unisexual vertebrates is well documented by morphological, cytogenetic, and electrophoretic studies (Vrijenhoek et al., this volume, and references therein). The coupling between hybridity and unisexuality probably occurs because interspecific hybridization often disrupts normal meiosis (Schultz, 1969; White, 1978; Wetherington et al., 1987; Dawley, 1987; Moritz et al., this volume; but see Cuellar, 1974). Cytological mechanisms that circumvent or preclude synapsis between heterospecific chromosomes might rescue egg production in hybrids and thereby lead to nonrecombinant reproduction (MacGregor and Uzzell, 1964; Cuellar, 1971; Cimino, 1972a, 1972b; Monaco et al., 1984).

In many cases, the sexual ancestors of unisexual hybrids are morphologically or cytogenetically identifiable. Nevertheless, allozyme studies indicate that there is no consistent degree of genetic differentiation between the sexual progenitors of unisexual lineages. For example, the sexual ancestors of *Menidia clarkhubsii* exhibit a Nei's genetic distance (D) of only 0.14, whereas for the sexual ancestors of unisexual *Cnemidophorus*, D averages 0.73 (Echelle et al., 1983; see also Moritz et al., this volume). This range of D values is not surprising, because no consistent level of genetic differentiation is associated with speciation in vertebrates (Nei, 1987). Nei's D values range from 0.01 for some species pairs of birds to 3.00 for some salamander pairs (Avise et al., 1980; Highton and Larson, 1979). Nevertheless, allopatric populations are likely to accumulate genetic differences that may lead to sterility in some hybrids, to various degrees of fertility in other hybrids, and to unisexuality in yet others (Schultz, 1973; Berger, 1971; Vrijenhoek and Schultz, 1974; Turner et al., 1980; Echelle et al., 1983; Hotz et al., 1985; Wetherington et al., 1987). Hybrid induction of unisexuality is ultimately a genetic rather than a taxonomic problem. Cytological and molecular genetic studies of the factors involved in the induction of unisexuality should provide a rich source of new information on chromosomal dynamics during gametogenesis.

Hybridization is clearly the most common vehicle for the origin of unisexual vertebrates, but it might not be the only one. Electrophoretic studies suggest that parthenogenetic forms of the xantusid lizard *Lepidophyma flavimauculatum* might have arisen spontaneously within sexual lineages (R. Bezy, pers. comm.; see also Peccinini-Seale, this volume). Hybridization clearly is not necessary for the origin of many parthenogenetic insects (Suomalainen et al., 1987). Understanding the genetic factors that induce spontaneous parthenogenesis may prove to be an even more difficult but nevertheless rewarding task (see Templeton, 1982).

Synthetic unisexuals.- Schultz (1973) accomplished the first successful synthesis of a unisexual vertebrate in the laboratory. He reproduced the origin of the hybridogenetic fish *Poeciliopsis monacha-lucida* through crosses of *P. monacha* females with *P. lucida* males. Wetherington et al., (1987) found that crosses of *P. monacha* females with *P. occidentalis* males have a higher success rate for producing new hybridogenetic strains. Regardless of the geographical origin of the parents,

all the *monacha* x *occidentalis* hybrids were females, and all the fertile hybrids were also spontaneously hybridogenetic. Hybridogenesis in *Poeciliopsis* appears to be induced by genomic interactions, not specific factors restricted to a few geographical locations. Attempts to reproduce the origin of the gynogenetic fish *Poecilia formosa* through crosses of *P. mexicana* and *P. latipinna* have been unsuccessful, producing only sterile hybrids or hybrids with normal meiosis. Turner et al. (1980) suggested that the specific genomes or individual genes that induced gynogenesis in *Poecilia formosa* might be restricted to a few populations that have not yet been tested or which, perhaps, may no longer exist. Reconstruction of the origins of the hybridogenetic frog *Rana esculenta* through crosses of *Rana ridibunda* x *R. lessonae* also had a strong geographical basis. Some of the *ridibunda* x *lessonae* hybrids were hybridogenetic, and others had normal meiosis (Hotz et al., 1985). Studies of mitochondrial DNA in unisexual lizards also suggest that opportunities for the origin of new unisexual strains may be restricted to a few progenitors or perhaps a few geographical populations (Moritz et al., this volume).

Developmental constraints.- A severe constraint on hybrid origins of unisexual vertebrates results from the need for a delicate balance between the disruption of normal gametogenesis and the coordination of normal development in hybrids (Vrijenhoek and Lerman, 1982; Wetherington et al., 1987). Hybridizing entities must be dissimilar enough to disrupt meiosis and yet not so dissimilar that somatic development of hybrids is also disrupted. Moritz et al. (this volume) call this the "balance" hypothesis. Wetherington et al. (1987) examined developmental abnormalities in laboratory-synthesized hybridogenetic strains of *Poeciliopsis monacha-lucida*. A majority of 16 viable strains exhibited some birth defects in the form of cranial and spinal deformities. Although only a small proportion of the individuals within each strain (maximum 7%) were visibly deformed, these abnormalities were probably symptomatic of a general weakening of developmental homeostasis. We saw no comparable birth defects in the sexual ancestors of these hybrids. Most importantly, the synthetic unisexual hybrids had, on average, significantly lower fertility and survival than the parental strains. Nevertheless, several of the synthetic unisexuals exhibited no evidence of birth defects and their fertility and survival was not different from that of the sexual ancestors. These 16 strains represent the survivors from 33 synthetic strains. The other strains could not be sustained beyond the second or third laboratory generation because of low viability and fertility. Intense fertility and viability "bottlenecks" also occurred during the formation of new parthenogenetic lineages of *Drosophila mercatorum* (Templeton, 1982). Only a few lucky genotypes strike the proper balance between meiotic disruption and developmental coordination.

Sperm-dependence.- Pseudogamy (false fertilization) imposes severe reproductive and ecological constraints on the establishment of gynogenetic fishes and amphibians, because it forces unisexuals into parasitic relationship with a closely related bisexual species. The only truly parthenogenetic vertebrates are reptiles. Why unisexual fishes and amphibians have been unable to shed the burden of sperm-dependence is

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unclear (Uzzell, 1970). We do not know what happens to the sperm pronucleus after activation of gynogenetic eggs, or how nuclear fusion is blocked. Furthermore, we do not know how cleavage is activated in parthenogenetic reptiles. The origin of new parthenogenetic reptiles might be severely constrained because an endogenous mechanism to activate embryogenesis must arise simultaneously with a mechanism that circumvents normal meiosis. Unless both mechanisms are by-products of the same dysgenic event (e.g., hybridization), the origin of new parthenogens seems very unlikely. Despite the considerable effort over the past 50 years, fundamental cytogenetic and ontogenetic processes are still unknown to us. Studies of these aberrant processes in unisexual organisms should serve as excellent tools for elucidating critical aspects of normal fertilization and early development.

Hybridogenetic unisexuals also require sperm from males of a related sexual species, but they are not truly pseudogamous, because the egg and sperm pronuclei fuse and a true hybrid is formed. During hybridogenetic reproduction, only the haploid maternal genome is transmitted to the eggs without recombination (Schultz, 1969; Uzzell and Berger, 1975; Graf and Polls, this volume). This form of reproduction has been called "hemiclinal" (Kallman, cit. in Vrijenhoek et al., 1977). Because hybridogens are also sperm-dependent, they also suffer the pseudogamy constraint.

To appreciate the severity of this constraint, we must imagine a pair of bisexual species with conspecific mating preferences. If, for example, interspecific matings occur once in every 100 courtships, and if the resulting unisexual hybrids are exactly intermediate in their attractiveness to males, the hybrids would be mated once in every 50 courtships. It is difficult to imagine a pseudogamous form successfully invading a bisexual population under such conditions. Special behavioral conditions must exist in the sexual host before pseudogamous unisexuals can become established. For example, traits involved in mate selection might not be additive in some hybrids, placing the hybrids beyond a critical mate-selection threshold. However, behavioral studies with *Poeciliopsis* revealed that the situation is more complex. The unisexuals exploit the dominance hierarchies formed by sexual males (McKay, 1971). Dominant males prevent subordinate males from mating with the preferred bisexual females, and thus the subordinate males defer their mating attempts to unisexual females.

Having invaded a bisexual population, pseudogamous unisexuals face a second peril — the twofold advantage of all-female reproduction should lead to their own demise (Clanton, 1934). Assuming unisexual and bisexual forms occupy equivalent niches, the unisexuals should rapidly replace the bisexuals, thereby eliminating their source of sperm. The persistence of stable unisexual/bisexual complexes has been explored by several investigators (Uzzell, 1964, 1969; Moore and McKay, 1971; Moore, 1976, 1984; Kiester et al., 1981; Keegan-Rogers, 1984; Stenseth et al., 1985). Based on studies of gynogenetic *Poeciliopsis*, Moore (1976) identified three factors affecting the dynamics of this simple host-parasite system: (1) primary fitness (i.e., fertility and survival), (2) the two-fold advantage of all-female reproduction, and (3) a

frequency-dependent mating preference on the part of sexual males. Assuming equal primary fitnesses and equal niches, Moore showed how factors 2 and 3 could lead to a stable equilibrium between unisexual and bisexual forms. When bisexual individuals predominate, the males establish dominance hierarchies, and the subordinate males mate with the unisexuals. As the unisexual females increase in frequency because of their twofold advantage, males become scarce. Solitary males prefer their conspecific bisexual females, and thus unisexual females have a low probability of insemination. At equilibrium the two-fold advantage of unisexuals is balanced by their lowered mating success. The conditions necessary for stable coexistence between a sperm parasite and its sexual host are restrictive (Stenseth et al., 1985; Kirkendall and Stenseth, 1988). Some form of density- or frequency-dependent, unisexual mating success appears to be a general requirement. Also, the assumptions of equal primary fitnesses and completely overlapping ecological niches are probably unrealistic (Vrijenhoek, 1978; Moore, 1984; Schenck and Vrijenhoek, 1986).

IT'S HARD TO FIND A JOB AS A UNISEXUAL VERTEBRATE

Ecological weeds. - The ecological problems faced by unisexual vertebrates have received considerable attention. Pseudogamous unisexuals suffer the most severe constraint, because these sperm parasites cannot escape from, or outcompete, their sexual hosts. True parthenogens, however, are free to play the role of fugitive species, relying on superior colonization ability and a potential for rapid increase attributable to all-female reproduction. Parthenogenetic forms of *Cnemidophorus* may be the zoological equivalents of "weedy species" (Wright and Lowe, 1968), having a high intrinsic rate of increase and exceptional colonizing abilities (Maslin, 1971). The *weeds* hypothesis assumes parthenogens are inferior competitors within the natural habitats of the parental species (Moore, 1984). The successful establishment of weedy parthenogenetic forms depends upon the availability of disturbed (disclimax) or marginal habitats in which the parental forms are inferior competitors (Cuellar, 1977a). Because of worldwide habitat destruction due to human activities, Suomalainen et al. (1987, p. 199) jestingly suggested the future may not be so hopeless for parthenogens that "thrive in disturbed habitats and . . . tolerate pollution better than **bisexuals**."

Hybridization and an intermediate niche. - A variant of the *weeds* hypothesis is the *intermediate niche* hypothesis (Moore, 1984). Because hybrids tend to be intermediate in morphology and presumably other characteristics that would constrain their ability to use food and spatial resources, unisexual hybrids might be best suited for ecotonal regions or intermediate niches in which the parental species are inferior competitors. This hypothesis assumes the parental species are each adapted to different regions along an ecological gradient. Although hybrid intermediacy may play a role in constraining the broad-scale geographical distribution of some unisexual hybrids (Moore, 1984), factors affecting the local distribution

and abundance of individual diploid and triploid unisexual clones are far more complex (Schenck and Vrijenhoek, 1986, this volume).

Heterotic generalists.- Because of the strong coupling between hybridization and unisexuality, some investigators believe unisexual organisms might be heterotic (Schultz, 1971, 1977, 1982; Cole, 1975; White, 1978). The high levels of **heterozygosity** found in unisexual organisms (reviewed by Moore, 1984; Vrijenhoek, 1989) might allow them to exploit a broader range of environmental conditions than their parental species. However, Moore (1984) cautioned that a distinction must be made between hybrid vigor in somatic characteristics and true heterosis in characters affecting Darwinian fitness. Based on his review of the population dynamics and biogeography of unisexual *Poeciliopsis*, Moore (1984) found no substantive evidence for heterotic fitness.

Nevertheless, evidence for hybrid vigor in the form of broad environmental tolerances and rapid growth has been reported for some unisexual strains (Schultz, 1982). When considered in the context of environmental tolerances alone, the *heterosis* hypothesis becomes a special form of the "*general-purpose genotype*" hypothesis (Baker, 1965). Lynch (1984) clarified this hypothesis by stating that general-purpose genotypes have the lowest variance in fitness in a temporally variable environment (i.e., exhibit the highest geometrical mean fitness). The hybridogenetic frog, *Rana esculenta*, appears to have broader options for overwintering survival than either of its parental species gunner and Nopp, 1979). Also, the hybridogenetic fish *P. monacha-lucida* has broader thermal tolerances than either of its parental species, but this result could not be extended to other unisexual forms (Bulger and Schultz, 1979). The triploid gynogenetic form, *P. monacha-2 lucida*, is more heterozygous than the hybridogen but not more tolerant to thermal extremes. Also, *P. monacha-occidentalis* has high heterozygosity, but its thermal tolerance is intermediate to its parental species (Bulger and Schultz, 1982). Broad environmental tolerances are not a generalizable consequence of hybridity in unisexual hybrids.

Wetherington et al. (1987) used synthetic *Poeciliopsis monacha-lucida* strains to test whether the hybrids were spontaneously heterotic for characters related to fitness. In the relatively constant environment of our laboratory, the synthetic hybridogens exhibit, on average, significantly lower survivorship, lower fertility, and higher frequencies of developmental abnormalities than the sexual strains from which they were derived. Although some synthetic strains are comparable to the parental strains for these characteristics, none are better. In contrast, two natural unisexual strains have superior survival. Since all the unisexuals, synthetic and natural, have essentially the same level of heterozygosity, one cannot attribute the qualities found only in the natural strains to heterosis. Instead, the variance among strains is attributable to the different combining abilities of the haploid *monacha* genomes that were "**frozen**" in these strains. Some *monacha* genomes make good combinations with *lucida*, and some do not. The fitness of these unisexual hybrids is a property of the general combining abilities of their hemiclinal *monacha* genomes, not spontaneous heterosis.

Great caution must be exercised in making inferences about the spontaneous fitness and niche breadth of all unisexual hybrids from studies of a few naturally occurring forms. Extant unisexuals are the good combinations, the genotypes that survived in nature because they can compete with or displace the bisexual ancestors from some portion of the available niche (see below). We don't often get to see nature's failures. Laboratory synthesis of more unisexual hybrid forms is needed to establish the generality of this result.

Frozen niche-variation.- Vrijenhoek (1979, 1984a) proposed that the long term success of unisexual populations depends on the opportunity for recruitment of new clones from genetically variable sexual ancestors. Genetic variation for life-history and niche-related characters is frozen and faithfully replicated in new clones. The consequence of interclonal selection is a structured assemblage of clones that can subdivide and efficiently exploit food and spatial resources. Extensive clonal diversity has been found in many unisexual vertebrate populations (reviews in Parker, 1979; Moore, 1984; but see Cuellar, 1977b).

Support for the *frozen niche-variation* model has been found in field and laboratory studies of unisexual *Poeciliopsis*. Our primary observations have been the following: (1) Relative to their sexual progenitors, unisexual populations composed of multiple clones are numerically more successful than monoclonal populations (Vrijenhoek, 1979, 1984b). (2) Multiclinal populations occupy a broader range of microhabitats than monoclonal populations (Vrijenhoek, 1984a). (3) Differences exist among clones in the use of food and spatial resources (Vrijenhoek, 1978; Schenck and Vrijenhoek, 1986, this volume). Additional examples of ecological differentiation among coexisting animal clones have recently been reviewed (Bell, 1982; Lynch, 1984; Vrijenhoek, 1984a, 1989; Case and Taper, 1986; see also, Schultz and Fielding, this volume).

The *frozen niche-variation* model is based on the hypothesis that the sexual ancestors of clonal lineages contain genetic variation for traits affecting niche-breadth. My colleagues and I are using the synthetic *P. monacha-lucida* hybridogens to test this hypothesis. The synthetic hemiclones have frozen significant differences in size at birth and juvenile growth rate (Wetherington, 1988). They exhibit different growth rate reaction norms under high and low quality diets (Wetherington, 1988). Early reproductive investment differs markedly among the strains (Weeks, pers. comm.). We are also examining the synthetic hemiclones for a variety of characteristics including trophic morphology, and foraging and predatory behavior.

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The disappearing niche.- The idea that asexual species are extinction-prone has had a long history (reviewed by Bell, 1982). The absence of genetic recombination in an asexual lineage is believed to prevent adjustments to a constantly changing physical and biotic environment. The concept of a changing environment must be considered in two parts: spatial heterogeneity and temporal variation (Bell, 1982). If individ-

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ual clones of an asexual "species" tend to exploit different patches in a spatially heterogeneous environment, then the longevity of each clone would be a function of the predictability and longevity of its specialized subniche. However, in an environment that changes unpredictably between generations, clonal specialists will rapidly disappear. Such temporal unpredictability should favor the clone with a *general-purpose genotype* (Lynch, 1984). The maintenance of clonal diversity in temporally unpredictable environments requires constant replacement by new clones as old clones are lost. Over the long-term, sexual species are more likely to persist in temporally unpredictable environments, because in each generation they regenerate a broad array of genotypes that exploit ephemeral resources as they appear and disappear (Bell, 1982).

Destabilizing hybridization.- The geographical distribution of some parthenogens may be limited by their inability to block genetic interference by their sexual relatives (Lynch, 1984). Occasional matings of parthenogenetic lizards with one of their sexual ancestors can lead to higher levels of polyploidy and sterility. The disjunct distributions of many parthenogenetic forms and their sexual ancestors may be due to the inability of parthenogens to protect their mode of reproduction from disruptive matings. This interesting constraint on the geographical distribution of parthenogens warrants further investigation. It might also affect the distribution of some hybridogens (Lynch, 1984).

Muller's ratchet.- Muller (1964) proposed that asexual reproduction is like a ratchet mechanism; the fitness of an asexual lineage cannot increase from generation to generation, but instead, it can only decline because of an accumulation of deleterious mutations. The ratchet will advance if the genome-wide mutation rate is high, if selection against new mutations is weak, and if the effective size of the asexual population is small (Maynard Smith, 1978). For vertebrates, the genomic mutation rate is probably high enough that most eggs will carry at least one slightly deleterious mutation (Vrijenhoek, 1984b). Small populations are affected because offspring carrying no new mutations will have a good chance of not occurring in the next generation. Whether the ratchet mechanism really limits unisexual vertebrates is unknown, but if unisexual hybrids have elevated mutation rates due to hybrid dysgenesis (Kidwell et al., 1977), the ratchet mechanism might contribute to a significant reduction in mean fitness over a few hundred generations [see Pamilo et al. (1987) for computer simulations and an analysis of this **problem**]. Evidence for an accumulation of potentially deleterious mutations has been found in hybridogenetic *Poeciliopsis* and *Rana* (Leslie and Vrijenhoek, 1978, 1980; Spinella and Vrijenhoek, 1982; Hotz, 1983; Graf and Polls, this volume). Nevertheless, in regions where endemic clonal origins are possible, the ratchet mechanism probably does not limit unisexual populations, because new clones might arise often enough to replace deteriorating clones.

FROM NO-HOPERS TO HOPEFUL MONSTERS

The conclusion that asexuality *per se* is an evolutionary dead end for higher organisms is well supported by the overall taxo-

omic rarity of asexual "species" of vertebrates and insects (Maynard Smith, 1978; White, 1978). Although morphologically and ecologically diverse clonal lineages have arisen polyphyletically from extant sexual relatives, I am unaware of substantive evidence that any strictly asexual lineage of higher plants or animals has generated morphologically or ecologically discrete descendent forms that also reproduce asexually [bdelloid rotifers and traminine aphids might be exceptions, but careful genetic studies are needed (Maynard Smith, 1986)]. Lynch and Gabriel (1983) found that phenotypic diversification could occur at similar rates in sexual and asexual populations, but the asexual mutation rate had to be at least twice that of the sexual lineage. Elevated mutation rates might occur in asexual lineages, but nevertheless the assumption that most mutations might contribute to adaptive variation is not realistic. Because most new mutations are mildly deleterious (Simmons and Crow, 1977), the ratchet mechanism and associated genetic "hitchhiking" are more likely to cause deterioration of clones (Felsenstein, 1974).

If asexuality contributes anything to the evolution of biological diversity, it might serve as a temporary vehicle for the replication of unusual gene combinations. In his seminal papers on unisexuality, hybridization, and polyploidy in the vertebrates, Schultz (1969, 1980) suggested that asexual reproduction might be a stepping-stone in the evolution of gene duplication and higher ploidy levels. For example, addition of a fourth genome (A) to a clonally reproducing allotriploid form (ABB) may balance meiosis and thereby produce a new sexually reproducing allotetraploid (AABB) species (see also Astaurov, 1969; Vasilev et al., this volume). Perhaps the taxonomically diverse, sexually reproducing tetraploid fishes in the families Salmonidae and Catostomidae arose in this way; but, unfortunately, the evolutionary histories of these fishes are obscured by genetic changes that have accumulated in the 25 to 100 million years since they arose (see Allendorf and Thorgaard, 1984; Ferris, 1984). Unisexuality appears to be involved in the more recent origins of some polyploid cyprinid fishes (Collares-Pereira, 1985; this volume).

A sexual species of unisexual origin.- Given the pessimistic theme expressed in the introduction, it is perhaps fitting that I should conclude this paper by reporting the discovery of a new sexual species whose immediate ancestor was a unisexual vertebrate (a formal description of this new species is in preparation; herein I summarize the salient points). A morphologically distinct, diploid species of *Poeciliopsis* inhabits a marshy area in the headwaters of the Rio Magdalena (Sonora, Mexico). Allozyme studies indicate that it arose from a hybridogenetic form, *P. monacha-occidentalis* hemiclone Ia (Angus, 1980), with which it still occurs. Apparently, the hybridogenetic mechanism broke down, and recombination occurred between the *monacha* and *occidentalis* genomes. This resulted in a new, self-perpetuating, mosaic genotype that reproduces sexually, has normal Mendelian inheritance, and has a 1:1 primary sex-ratio. Crossing experiments revealed that the new species is reproductively isolated from both its hybridogenetic ancestor and *P. occidentalis*. I plan to name this new species in honor of R. Jack Schultz, a foresighted pioneer in this field of research.

Although an apparent contradiction, this discovery clearly

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supports my general thesis that strictly asexual reproduction is an evolutionary dead end. The unisexual lineage that gave rise to this new sexual species was itself drawn from the recombinant variation in a sexual gene pool. When that unisexual lineage gave rise to something new, it did so because clonal reproduction broke down. The new sexual species is a product of recombination, not cloning. Although mutational changes have occurred in the hemiclinal genomes that gave rise to this new species (Spinella and Vrijenhoek, 1982), the critical transitions in this unusual speciation pathway involved recombination.

SUMMARY AND CONCLUSIONS

In general, the origin of new unisexual vertebrates depends on a delicate balance between meiotic disruption and developmental coordination in interspecific hybrids (Wetherington et al., 1987; Moritz et al., this volume). Once formed, a new unisexual lineage must either invade a sexual population or become established in habitats that are ecologically suboptimal for its sexual ancestors. Some parthenogenetic lizards are thought adept at colonization and occupation of marginal habitats, but others coexist with one or more of their sexual relatives. Sperm-dependent unisexual fishes and amphibians must live with a sexual relative. Furthermore, the conditions necessary for a stable sperm-dependent relationship may be highly restrictive (Stenseth et al., 1985). Studies of ecological interactions between unisexual hybrids and their sexual ancestors can offer many new insights on factors that promote coexistence between closely related taxa that are morphologically and behaviorally very similar.

Discoveries of abundant clonal diversity in many unisexual populations should alert us to the danger of erecting simple ecological hypotheses that assume the existence of only one "kind" of bisexual form and one "kind" of unisexual form in stable complexes. Evidence for niche partitioning between coexisting clones and their sexual ancestors is accumulating from careful field studies (Schenck and Vrijenhoek, 1986, this volume). Most of the clonal diversity observed in unisexual vertebrates stems from multiple hybridization events. Experimental studies are showing that new clones are likely to differ substantially in many traits that could affect resource use in spatially and temporally heterogeneous environments (Wetherington, 1988). Over the long term, individual clones probably are evolutionary dead ends, but the unisexual population might persist because of recurrent clonal origins. This hypothesis needs to be tested. Application of molecular approaches will help us learn more about the relative ages of individual clones. The limited data currently available suggest that extant unisexual vertebrates represent relatively recent evolutionary events (Avisé and Vrijenhoek, 1987; Goddard et al., this volume; Lowcock, this volume; Moritz et al., this volume).

Despite the ecological success of clonally diverse populations of unisexual fishes, amphibians, and lizards, we lack evidence that strictly asexual lineages are cladogenetic, that they can split into diversified descendent clonal lineages. Although the

apparent example of speciation reported here does involve a unisexual ancestor, the product of this event was a new sexual species, not a new clone. Furthermore, the origin of this morphologically and ecologically distinct species involved genetic recombination, the essence of sexuality. Cladogenetic speciation and sexual recombination may be closely intertwined (Stanley, 1975). The phylogenetic rarity of asexual "species" would not appear, therefore, to require any special explanations. A low rate of origin of novel unisexual forms might simply be balanced by a high rate of extinction, keeping the overall frequency of unisexual "species" low. To draw an analogy with events at the genic level, we could imagine all unisexual "species" as mutants and all the bisexual species as wild-type alleles at a hypothetical locus controlling meiosis. As such, unisexuality is not even a valid polymorphism. The taxonomic rarity of unisexual "species" could be determined by a higher level process comparable to mutation-selection balance at the genic level.

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LITERATURE CITED

- ALLENDORF, F. W., AND G. H. THORGAARD. 1984. Thraploidy and the evolution of salmonid fishes, pp. 1-53. *In*: Evolutionary Genetics of Fishes. B. J. Turner (ed.). Plenum Press, New York.
- ANGUS, R. A. 1980. Geographical dispersal and clonal diversity in unisexual fish populations. *Amer. Natur.* 115:531-550.
- ASTAUROV, B. L. 1969. Experimental polyploidy in animals. *Ann. Rev. Genet.* 3:99-126.
- AVISE, J. C., AND R. C. VRIJENHOEK. 1987. Mode of inheritance and variation of mitochondrial DNA in hybridogenetic fishes of the genus *Poeciliopsis*. *Mol. Biol. Evol.* 4:514-525.
- AVISE, J. C., J. C. PATTON, AND C. F. AQUADRO. 1980. Evolutionary genetics of birds. I. Relationships among North American thrushes and allies. *The Auk* 97:135-147.
- BAKER, H. G. 1965. Characteristics and modes of origin of weeds, pp. 147-172. *In*: Genetics of Colonizing Species. H. G. Baker and G. L. Stebbins (eds.). Academic Press, New York.
- BELL, G. 1982. The Masterpiece of Nature: The Evolution and Genetics of Sexuality. Univ. Calif. Press, Berkeley.
- BERGER, L. 1971. Viability, sex and morphology of F2 generation within forms of *Rana esculenta-complex*. *Zool. Poloniae* 21:373-393.
- BULGER, A. J., AND R. J. SCHULTZ. 1979. Heterosis and interclonal variation in thermal tolerance in unisexual fish. *Evolution* 33:848-859.
- BULGER, A. J., AND R. J. SCHULTZ. 1982. Origins of thermal adaptation in northern vs. southern populations of a unisexual hybrid fish. *Evolution* 36:1041-1050.
- CASE, M. L., AND T. J. TAPER. 1986. On the coexistence and coevolution of asexual and sexual competitors. *Evolution* 40:366-387.

- CIMINO, M. C. 1972a. Meiosis in triploid all-female fish (Poeciliopsis, **Poeciliidae**). *Science* 175:1484-1486.
- CIMINO, M. C. 1972b. Egg production, polyploidization and evolution in a diploid all-female fish of the genus *Poeciliopsis*. *Evolution* 26:294-306.
- CLANTON, W. 1934. An unusual situation in the salamander *Ambystoma jeffersonianum* (Green). *Occ. Pap. Mus. Zool. (Univ. Michigan)* 290:1-15.
- COLE, C. J. 1975. Evolution of parthenogenetic species of reptiles, pp. 340-355. In: *Intersexuality in the Animal Kingdom*. R. Reinboth (ed.), Springer-Verlag, Berlin-Heidelberg-New York.
- COLLARES-PEREIRA, M. J. 1985. The "Rutilus alburnoides (**Steindacher**, 1866) complex" (Pisces, Cyprinidae). II. First data on the karyology of a well-established diploid-triploid group. *Arquivos do Museu Bocage (Serie A)* 3:69-89.
- COLLARES-PEREIRA, M. J. This volume. Hybridization in European cyprinids: Evolutionary potential of unisexual populations.
- CUELLAR, O. 1971. Reproduction and the mechanism of meiotic restitution in the parthenogenetic lizard *Cnemidophorus uniparens*. *J. Morphol.* 133:139-166.
- CUELLAR, O. 1974. On the origin of parthenogenesis in vertebrates: The cytogenetic factors. *Amer. Natur.* 108:625-648.
- CUELLAR, O. 1977a. Animal parthenogenesis. *Science* 197:837-843.
- CUELLAR, O. 1977b. Genetic homogeneity and speciation in the parthenogenetic lizards *Cnemidophorus velox* and *C. mexicanus*, evidence from interspecific histocompatibility. *Evolution* 31:24-31.
- DARLINGTON, C. D. 1939. *The Evolution of Genetic Systems*. Cambridge Univ. Press, Cambridge, U.K.
- DAWLEY, R. M. 1987. Hybridization and polyploidy in a community of three sunfish species (Pisces: Centrarchidae). *Copeia* 1987:326-335.
- ECHELLE, A. A., A. F. ECHELLE, AND C. D. CROZIER. 1983. Evolution of an all-female fish, *Menidia clarkhubbsi* (Atherinidae). *Evolution* 37:772-784.
- FELSENSTEIN, J. 1974. The evolutionary advantage of recombination. *Genetics* 78:737-756.
- FERRIS, S. D. 1984. **Tetraploidy** and the evolution of catostomid fishes, pp. 55-93. In: *Evolutionary Genetics of Fishes*. B. J. Turner (ed.). Plenum Press, New York.
- GODDARD, K. A., R. M. DAWLEY, AND T. E. DOWLING. This volume. Origin and genetic relationships of diploid, triploid, and diploid-triploid mosaic biotypes in the *Phoxinus eos-neogaeus* unisexual complex.
- GRAF, J.-D., AND M. POLLS PELAZ. This volume. Evolutionary genetics of the *Rana esculenta* complex.
- HIGHTON, R., AND A. LARSON. 1979. The genetic relationships of the salamanders of the genus *Plethodon*. *Syst. Zool.* 28:579-599.
- HOTZ, H. 1983. Genic diversity among water frog genomes inherited with and without recombination. Ph.D. thesis, University of Zurich, Switzerland.
- HOTZ, H., G. MANCINO, S. BUCCIINOCENTI, M. RAGGHIANI, L. BERGER, AND T. M. UZZELL. 1985. *Rana rid ibunda* varies geographically in inducing clonal gametogenesis in interspecies hybrids. *J. Exper. Zool.* 236:199-210.
- KEEGAN-ROGERS, V. 1984. Unfamiliar-female mating advantage among clones of unisexual fish (*Poeciliopsis*: **Poeciliidae**). *Copeia* 1984:169-174.
- KIDWELL, M. G., J. F. KIDWELL, AND J. A. SVED. 1977. Hybrid dysgenesis in *Drosophila melanogaster*: A syndrome of aberrant traits including mutation, sterility, and male recombination. *Genetics* 86:813-833.
- KIESTER, A. R., T. NAGYLAKI, AND B. SHAFFER. 1981. Population dynamics of species with gynogenetic sibling species. *Theor. Pop. Biol.* 19:358-369.
- KIRKENDALL, L. R., AND N. C. STENSETH. 1988. Ecological and evolutionary stability of pseudogamy: Effects of partial niche overlap between **sexual** and asexual females. *Evolution*, in press.
- LESLIE, J. F., AND R. C. VRIJENHOEK. 1978. Genetic dissection of clonally inherited genomes of *Poeciliopsis*. I. Linkage analysis and preliminary assessment of deleterious gene loads. *Genetics* 90:801-811.
- LESLIE, J. F., AND R. C. VRIJENHOEK. 1980. Consideration of Muller's ratchet mechanism through studies of genetic linkage and genomic compatibilities in clonally reproducing *Poeciliopsis*. *Evolution* 34:1105-1115.
- LOWCOCK, L. A. This volume. Biogeography of hybrid complexes of *Ambystoma*: Interpreting unisexual-bisexual data through space and time.
- LYNCH, M. 1984. Destabilizing hybridization, general-purpose genotypes and geographical parthenogenesis. *Quart. Rev. Biol.* 59:257-290.
- LYNCH, M., AND W. GABRIEL. 1983. Phenotypic evolution and parthenogenesis. *Amer. Natur.* 122:745-764.
- MACGREGOR, H. C., AND T. M. UZZELL. 1964. Gynogenesis in salamanders related to *Ambystoma jeffersonianum*. *Science* 143:1043-1045.
- MASLIN, T. P. 1971. Parthenogenesis in reptiles. *Amer. Zool.* 11:361-380.
- MAYNARD SMITH, J. 1978. *The Evolution of Sex*. Cambridge Univ. Press, Cambridge, UK.
- MAYNARD SMITH, J. 1986. Contemplating life without sex. *Nature* 324:300-301.
- MCKAY, F. E. 1971. Behavioral aspects of population dynamics in unisexual-bisexual *Poeciliopsis* (Pisces: **Poeciliidae**). *Ecology* 52:778-790.
- MONACO, P. J., E. M. RASCH, AND J. S. BALSANO. 1984. Aponictic reproduction in the Amazon mollie, *Poecilia formosa*, and its triploid hybrids, pp. 311-328. In: *Evolutionary Genetics of Fishes*. B. J. Turner (ed.). Plenum Press, New York.
- MOORE, W. S. 1976. Components of fitness in the unisexual fish *Poeciliopsis monacha-occidentalis*. *Evolution* 30:564-578.
- MOORE, W. S. 1984. Evolutionary ecology of unisexual fishes, pp. 329-398. In: *Evolutionary Genetics of Fishes*. B. J. Turner (ed.). Plenum Press, New York.
- MOORE, W. S., AND F. E. MCKAY. 1971. Coexistence in unisexual-bisexual species complexes of *Poeciliopsis* (Pisces: **Poeciliidae**). *Ecology* 52:791-799.
- MORITZ, C., W. M. BROWN, L. D. DENSMORE, J. W. WRIGHT, D. VYAS, S. DONNELLAN, M. ADAMS, AND P. BAVERSTOCK. This volume. Genetic diversity and the dynamics of hybrid parthenogenesis in *Cnemidophorus* (Thuidae) and *Heteronotia* (Gekkonidae).
- MULLER, H. J. 1964. The relation of mutation to mutational advance. *Mutat. Res.* 1:2-9.
- NEI, M. 1987. *Molecular Evolutionary Genetics*. Columbia Univ. Press, New York.
- PAMILO, R. M. NEI, AND W. LI. 1987. Accumulation of mutations in sexual and asexual populations. *Genet. Res. Camb.* 49:135-146.
- PARKER, E. D. 1979. Ecological implications of clonal diversity in parthenogenetic morphospecies. *Amer. Zool.* 19:753-762.
- PECCININI-SEALE, D. M. This volume. Genetic studies on bisexual and unisexual populations of Amazonian *Cnemidophorus*.

CONSTRAINTS ON UNISEXUAL VERTEBRATES

- SCHENCK, R. A., AND R. C. VRIJENHOEK. 1986. Spatial and temporal factors affecting coexistence among sexual and clonal of *Poeciliopsis*. *Evolution* 40:1060-1070.
- SCHENCK, R. A., AND R. C. VRIJENHOEK. This volume. Coexistence among sexual and asexual forms of *Poeciliopsis*: Foraging behavior and habitat selection.
- SCHULTZ, R. J. 1969. Hybridization, unisexuality, and polyploidy in the teleost *Poeciliopsis* (Poeciliidae) and other vertebrates. *Amer. Natur.* 103:605-619.
- SCHULTZ, R. J. 1971. Special adaptive problems associated with unisexual fishes. *Amer. Zool.* 11:351-360.
- SCHULTZ, R. J. 1973. Unisexual fish: Laboratory synthesis of a "species". *Science* 179:180-181.
- SCHULTZ, R. J. 1977. Evolution and ecology of unisexual fishes. *Evol. Biol.* 10:277-331.
- SCHULTZ, R. J. 1980. The role of polyploidy in the evolution of fishes, pp. 313-339. *In: Polyploidy: Biological Relevance.* W. H. Lewis (ed.). Plenum Publ. Co., New York.
- SCHULTZ, R. J. 1982. Competition and adaptation among diploid and polyploid clones of unisexual fishes, pp. 103-119. *In: Evolution and Genetics of Life Histories.* H. Dingle and J. P. Hegmann (eds.). Springer-Verlag, Berlin-Heidelberg-New York.
- SCHULTZ, R. J., AND E. FIELDING. This volume. Fixed genotypes in variable environments.
- SIMMONS, M. J., AND J. F. CROW. 1977. Mutations affecting fitness in *Drosophila* populations. *Ann. Rev. Genet.* 11:49-78.
- SPINELLA, D. G., AND R. C. VRIJENHOEK. 1982. Genetic dissection of clonally inherited genomes of *Poeciliopsis*: II. Investigation of a silent carboxylesterase allele. *Genetics* 100:279-286.
- STANLEY, S. M. 1975. Clades versus clones in evolution: Why we have sex. *Science* 190:382-383.
- STENSETH, N. C., L. R. KIRKENDALL, AND N. MORAN. 1985. On the evolution of pseudogamy. *Evolution* 39:294-307.
- SUOMALAINEN, E., A. SAURA, AND J. LOKKI. 1987. Cytology and evolution in parthenogenesis. CRC Press, Boca Raton, Florida.
- TEMPLETON, A. R. 1982. The prophecies of parthenogenesis, pp. 75-102. *In: Evolution and Genetics of Life Histories.* H. Dingle and J. P. Hegmann (eds.). Springer-Verlag, Berlin-Heidelberg-New York.
- TUNNER, H. G., AND H. NOPP. 1979. Heterosis in the common European water frog. *Naturwissenschaften* 66:268-269.
- TURNER, B. J., B. L. BREIT AND R. R. MILLER. 1980. Interspecific hybridization and the evolutionary origin of a gynogenetic fish, *Poecilia formosa*. *Evolution* 34:917-922.
- UZZELL, T. M. 1964. Relations of the diploid and triploid species of the *Ambystoma jeffersonianum* complex (Amphibia, Caudata). *Copeia* 1964:257-300.
- UZZELL, T. M. 1969. Notes on spermatophore production by salamanders of the *Ambystoma jeffersonianum* complex (Amphibia, Caudata). *Copeia* 1969:602-612.
- UZZELL, T. M. 1970. Meiotic mechanisms of naturally occurring unisexual vertebrates. *Amer. Natur.* 104:433-445.
- UZZELL, T. M., AND L. BERGER. 1975. Electrophoretic phenotypes of *Rana ridibunda*, *Rana lessonae*, and their hybridogenetic associate, *Rana esculenta*. *Proc. Acad. Sci. Phila.* 127:13-24.
- VASILEV, V. P., K. D. VASILEVA, AND A. G. OSINOV. This volume. Evolution of a diploid-triploid-tetraploid complex in fishes of the genus *Cobitis* (Pisces, Cobitidae).
- VRIJENHOEK, R. C. 1978. Coexistence of clones in a heterogeneous environment. *Science* 199:549-552.
- VRIJENHOEK, R. C. 1979. Factors affecting clonal diversity and coexistence. *Amer. Zool.* 19:787-797.
- VRIJENHOEK, R. C. 1984a. Ecological differentiation among clones: The frozen niche variation model, pp. 217-231. *In: Population Biology and Evolution.* K. Wohrmann and V. Loeschke (eds.). Springer-Verlag, Berlin-Heidelberg-New York.
- VRIJENHOEK, R. C. 1984b. The evolution of clonal diversity in *Poeciliopsis*, pp. 399-429. *In: Evolutionary Genetics of Fishes.* B. J. Turner (ed.). Plenum Press, New York.
- VRIJENHOEK, R. C. 1989. Genetic diversity and the ecology of asexual populations, *in press.* *In: Population Biology and Evolution.* K. Wohrmann and S. Jain (eds.). Springer-Verlag, Berlin-Heidelberg-New York.
- VRIJENHOEK, R. C., R. M. DAWLEY, C. J. COLE, AND J. P. BOGART. This volume. A list of the known unisexual vertebrates.
- VRIJENHOEK, R. C., AND S. LERMAN. 1982. Heterozygosity and developmental stability under sexual and asexual breeding systems. *Evolution* 36:768-776.
- VRIJENHOEK, R. C., AND R. J. SCHULTZ. 1974. Evolution of a tri-hybrid unisexual fish (*Poeciliopsis*, Poeciliidae). *Evolution* 28:767-781.
- VRIJENHOEK, R. C., R. A. ANGUS, AND R. J. SCHULTZ. 1977. Variation and heterozygosity in sexually vs. clonally reproducing populations of *Poeciliopsis*. *Evolution* 31:767-781.
- WETHERINGTON, J. D. 1988. Genetic variation among synthetic hemiclones of *Poeciliopsis*. Ph.D. thesis, Rutgers Univ., New Brunswick, New Jersey.
- WETHERINGTON, J. D., K. E. KOTORA, AND R. C. VRIJENHOEK. 1987. A test of the spontaneous heterosis hypothesis for unisexual vertebrates. *Evolution* 41:721-731.
- WHITE, M. J. D. 1978. Modes of Speciation. Freeman, San Francisco.
- WILLIAMS, G. C. 1975. Sex and Evolution. Princeton University Press, Princeton, New Jersey.
- WRIGHT, J. W. AND C. H. LOWE. 1968. Weeds, polyploids, parthenogenesis and the geographical and ecological distribution of all-female species of *Cnemidophorus*. *Copeia* 1968:128-138.