

Factors Affecting Clonal Diversity and Coexistence

ROBERT C. VRIJENHOEK

Department of Zoology and Bureau of Biological Research, Rutgers University, New Brunswick, New Jersey 08903

SYNOPSIS. Recent genetic studies of asexually reproducing fishes in the genus *Poeciliopsis* (Poeciliidae) revealed abundant variation in the form of multiple sympatric clones. Recurrent hybridizations between sexual species provides the principal source of clonal variation. The hybrids are spontaneously endowed with a clonal reproductive mechanism that perpetuates a high level of heterozygosity. Migration within and between river systems, and mutations, also contribute to clonal diversity in these fish. Coexistence among different clones and with the sexual ancestors depends in part upon specializations characteristic of individual clones. Clonal reproduction is an efficient mechanism for freezing a portion of the niche-width variation contained in the gene pool of the more broadly adapted, sexual ancestors. Multiclonal populations achieve significantly higher densities relative to the sexual forms than do monoclonal populations. This relationship is a function of the clonal variability upon which natural selection can act and upon the capacity of a multiclonal population to better exploit a heterogeneous environment through niche diversification. In all-female organisms such as *Poeciliopsis*, which are dependent upon sexual species for insemination, competitive abilities probably are at a premium in the densely populated pools and arroyos of the Sonoran Desert. Competitive abilities are probably less important for truly parthenogenetic clones which rely on colonization abilities to escape from their sexual ancestors and from other clones.

INTRODUCTION

Most theoretical studies advocating the adaptive benefits of sexual reproduction generally assume that asexual populations lack genetic variation. The absence of recombinational variability in asexual populations is commonly thought to: 1) decrease the rate of adaptive evolution; 2) decrease the rate of speciation; and 3) increase the rate of extinction (Fisher, 1930; Muller, 1932; Crow and Kimura, 1965; Stanley, 1975; Williams, 1975; White, 1978). However, when the possibility of extensive clonal variation is considered, sexuality confers no clear advantage (Maynard Smith, 1968; Eshel and Feldman, 1970; Roughgarden, 1972). Many recent discoveries of substantial clonal variation in natural pop-

ulations of asexually reproducing animals raise some doubts, therefore, about the conclusion that asexuality is an evolutionary dead end. Nevertheless, one cannot avoid the obvious fact that asexuality is rare among animal species (White, 1978). Perhaps better explanations for the predominance of sexuality will develop from ecological and genetic studies of these rare exceptions, and the peculiar conditions under which they arise and sometimes thrive.

Field and laboratory studies of fishes in the genus *Poeciliopsis* (Poeciliidae) provide one of the rare opportunities to compare the possible advantages and disadvantages of distinct sexual and asexual breeding systems that occur together in a highly heterogeneous environment. All-female forms of *Poeciliopsis* inhabit the rivers of northwestern Mexico (Fig. 1). For a detailed description of their hybrid origins, breeding systems, biogeography and ecology see the recent review by Schultz (1977). The names of the hybrid, all-female forms reflect their genomic compositions and dosages (Table 1). Triploid gynogenetic forms require insemination by males of a coexisting sexual

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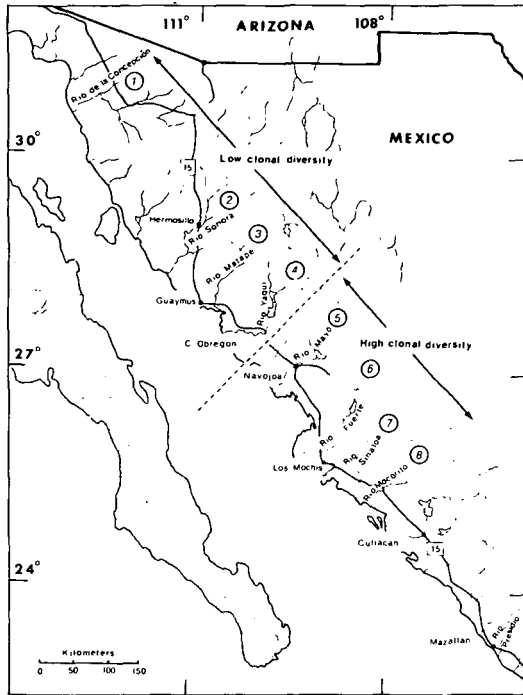


FIG. 1. The rivers of northwestern Mexico. The diagonal line separates river systems with high clonal diversity from those with low clonal diversity.

species, but the sperm contribute nothing genotypically or phenotypically to the offspring, which are triploid females identical with their mothers. Premeiotic doubling of the chromosomes, followed by sister chromosome pairing, preserves the maternal genotype during oogenesis (Cimino, 1972*a*). The cytological model is consistent with their clonal pattern of inheritance based upon morphological, electrophoretic, and tissue grafting criteria (Schultz, 1967; Vrijenhoek, 1972; Moore, 1977).

The diploid hybridogenetic forms also rely upon males of a sexual host species for insemination. During hybridogenetic oogenesis only the haploid *monacha* genome is transmitted to the ova; the paternal genome is expelled from oögonia thereby preventing synapsis and recombination (Cimino, 1972b). The haploid *monacha* ova produced by these hybrids are fertilized by sperm from the host species, reestablishing diploid hybrids that express morphological and electrophoretic traits encoded by both

parental genomes (Schultz, 1966; Vrijenhoek, 1972). Hybridogenetic unisexuals are not clones in the strict sense because their paternal genomes are substituted in each generation and therefore have access to all of the allelic variation in the gene pool of the sexual host (Vrijenhoek *et al.*, 1977). Nevertheless, the *monacha* genome is inherited clonally, therefore discussions of clonal variation in these fish refer only to genotypic and phenotypic differences among the haploid *monacha* genomes in the hybridogenetic populations.

Unlike truly parthenogenetic species, hybridogenetic and gynogenetic *Poeciliopsis* can never escape from their sexual hosts to invade new habitats, nor can they competitively exclude their hosts, for in doing so they lose their sperm source and ensure their own extinction. Theoretically, a unisexual individual produces two female offspring for each one produced by a sexual individual. This reproductive advantage is offset by the significantly lower mating success of unisexual females (Moore and McKay, 1971; Moore, 1976). The sexual males strongly prefer conspecific sexual females as mates (McKay, 1971). When the density of sexual individuals is high, dominance hierarchies develop among the males. The subordinates, which are denied access to conspecific females, apparently are responsible for unisexual inseminations. However, when sexual density is low, solitary males mate with conspecific females and the unisexuals are mostly uniseminated (Moore and McKay, 1971). Consideration of these factors led Moore (1976) to propose the following major components of fitness in the unisexual and sexual forms: 1) the probability of producing female offspring; 2) mating success; and 3) primary fitness, a residual component including survivorship, fecundity and other factors affected by the local environment. Moore proposed that as long as the primary fitness of the unisexuals exceeds that of the sexual host, unisexuals can achieve a maximum frequency of about 80% of female population. Increase beyond this point is limited by low unisexual mating success resulting from low male densities.

The preceding scenario for coexistence

TABLE 1. The distribution and reproductive modes of diploid and triploid unisexual forms of *Poeciliopsis*.

Unisexual form	Ploidy	Sexual host	Reproductive mode	Distribution*
<i>P. monacha-occidentalis</i>	2n	<i>P. occidentalis</i>	hybridogenetic	1,2,3,4,5
<i>P. monacha-lucida</i>	2n	<i>P. lucida</i>	hybridogenetic	6,7,8
<i>P. monacha-latidens</i>	2n	<i>P. latidens</i>	hybridogenetic	6,7,8
<i>P. 2 monacha-lucida</i>	3n	<i>P. monacha</i>	gynogenetic	5,6,7
<i>P. monacha-2 lucida</i>	3n	<i>P. lucida</i>	gynogenetic	6
<i>P. monacha-lucida-viriosa</i>	3n	<i>P. viriosa</i>	gynogenetic	8

* River systems are assigned numbers as appear in Figure 1.

between the unisexuals and their sexual hosts treats both forms as if they were only a pair of alternative phenotypes competing for the same limiting resources. The present paper attempts to integrate these ideas with our current understanding of genotypic and phenotypic variation in the unisexual and sexual forms of *Poeciliopsis*. Also, I hope to demonstrate that the rate of adaptive evolution in an asexual population is proportional to the genetic variance of that population.

CLONAL VARIATION IN UNISEXUAL *POECILIOPSIS*

Protein electrophoresis, tissue grafting, and crossing experiments all revealed considerable genetic variation in unisexual populations of *Poeciliopsis*. An electrophoretic analysis of 37 laboratory strains of *P. monacha-lucida* from the Rio Fuerte identified eight distinct haploid *monacha* genotypes, or haplotypes (Vrijenhoek *et al.*, 1978). The 37 strains had all been bred with the same inbred strain of *P. lucida*, a procedure that standardized their paternal genomes and ensured that genetic differences among strains were encoded by the clonal *monacha* genome. Tissue grafting experiments with these standard bred strains revealed additional variation and extended the number of distinct clones in the Rio Fuerte to at least 18 (Angus and Schultz, 1979). More recent electrophoretic studies have identified five *monacha* haplotypes in the Rio Sinaloa. Limited population samples from the Rio Mocorito have revealed only one electromorph haplotype, but earlier crossing experiments with several laboratory strains indicated that clonal variation occurs in this river (Vrijenhoek and Schultz, 1974).

A parallel study with *P. monacha-occidentalis* identified only four electromorph haplotypes (Vrijenhoek *et al.*, 1977). At least 17 immunologically distinct clones masquerade under three of these haplotypes in the Rio Mayo (Angus, 1979). The high clonal diversity in this river probably results from recurrent hybridizations between *P. monacha* and *P. occidentalis*. Because *P. monacha* exhibits very low levels of electrophoretic polymorphism in this river (Vrijenhoek, 1979), it is likely that recurrent hybridizations will produce electrophoretically identical haplotypes but immunologically distinct clones. The Rios Yaqui, Matape, and Sonora all contain the same electromorph haplotype; however, these fish represent at least four histocompatibility clones, two in the Rio Matape, and one each in the Rios Yaqui and Sonora (Angus, 1979). The Rio Concepcion contains a unique electromorph haplotype that differs from that found in more southern rivers by what appears to be two mutant alleles (Vrijenhoek *et al.*, 1977). The absence of *P. monacha* from these northern rivers, hence the absence of recurrent hybridizations, clearly has an effect on clonal diversity in hybridogenetic unisexuals.

Electrophoretic studies of the triploid gynogen, *P. 2 monacha-lucida* identified three clones. One occurs alone in the Rio Mayo and two coexist in the Rio Fuerte. Tissue grafting studies with the Rio Fuerte clones corroborated the electromorph distinctions and found additional minor variations in one of the two electromorph types (W. S. Moore, personal communication). The two Rio Fuerte electromorph clones exhibit consistent differences in dentition patterns and feeding behaviors (Vrijenhoek, 1978).

Electrophoretic studies of clonal variation in the hybridogenetic form *P. monacha-latidens* and in the gynogenetic forms *P. monacha-2 lucida* and *P. monacha-lucida-viriosa* are underway. At least three clones of *P. monacha-2 lucida* occur in the Rio Fuerte. Only one clone of the trihybrid triploid, *P. monacha-lucida-viriosa*, was found in a small sample from the Rio Mocorito. *P. monacha-latidens* has two haplotypes, one in the Rio Fuerte and another in the Rios Sinaloa and Mocorito. Tissue grafting studies have not been performed with these unisexual forms.

The genetic studies clearly implicate polyphyletic hybrid origins as the predominant source of clonal variation in hybridogenetic fishes. Each hybrid event freezes a *monacha* genotype along with whatever morphological, behavioral, and ecological characteristics it encodes. Laboratory syntheses of hybridogenetic unisexuals have been accomplished by matings between *P. monacha* and *P. lucida* (Schultz, 1973) and between *P. monacha* and *P. occidentalis* (Vrijenhoek, unpublished data). Thus the potential for generating new hybridogenetic clones is high in the upstream tributaries of the southern rivers: the Rio Mayo, where *P. monacha* and *P. occidentalis* occur, and the Rios Fuerte and Sinaloa, where *P. monacha* and *P. lucida* occur. It is not surprising that the highest clonal diversity is found in these rivers. The northern rivers (Fig. 1) lacking *P. monacha*, and therefore lacking a potential for endemic hybridizations, are essentially monoclonal. The events leading to triploidy and gynogenesis are not known; these forms only occur in the southern rivers (Table 1).

Migration also contributes to unisexual variation. Immunologically and electrophoretically identical individuals of the same clone of *P. monacha-lucida* were captured in distant localities in isolated tributaries of the Rio Fuerte (Vrijenhoek *et al.*, 1978). The presence of unisexuals in the northern rivers, which do not contain *P. monacha*, was interpreted as evidence for migration between separate drainage systems (Moore *et al.*, 1970; Vrijenhoek *et al.*, 1977). Schultz (1971) proposed that the acquisition of locally adapted paternal ge-

nomes in the progeny of a migrant facilitates the establishment of hybridogenetic clones in a novel environment. This source of local adaptability is not available to gynogenetic triploids and might explain their limited distribution compared to the hybridogens.

The extensive surveys of protein variation in the hybridogenetic unisexuals and their sexual progenitors suggest that mutations contribute to clonal variation. A silent allele encoding a non-functional esterase (*Es-5^o*) and a unique muscle protein allele (*Mp-3^c*) mark the haplotype of an isolated *P. monacha-occidentalis* clone inhabiting the Rio Concepcion (Vrijenhoek *et al.*, 1977). A silent lactate dehydrogenase (*Ldh-1^o*) and a unique esterase (*Es-5^o*) mark two *P. monacha-lucida* clones inhabiting the Rio Sinaloa. A unique malate dehydrogenase (*Mdh-1^b*) marks one clone in the Rio Fuerte. Recessive mutations are expected to accumulate in the sheltered clonal genomes because they are permanently maintained in the heterozygous condition. Crossing experiments with *P. monacha-lucida* were designed to test this hypothesis (Leslie and Vrijenhoek, 1978). Two laboratory strains marked with distinct electromorph and immunological haplotypes (IIb and Va) were mated with males of an inbred strain of *P. monacha* (M/M). Since hybridogenetic females transmit only the clonal genome to their eggs (IIb and Va, respectively), the resulting progeny contained one clonal and one wild-type *monacha* genome (IIb/M and Va/M, respectively). Backcrosses of hybrid (IIb/M and Va/M) males to their maternal hybridogenetic strain provides a test for hidden deleterious genes. Clone Va contains a minimum of two lethal equivalents and IIb contains a minimum of four. Considerations of the population structure of *P. monacha* (Vrijenhoek, 1979) and inbreeding experiments with this species (work in progress) suggest that the lethal gene loads in the clonal genomes were not simply "frozen" from the *P. monacha* gene pool but have accumulated as a result of mutation.

Matings between hybridogenetic females and males of *P. monacha*, as in the preceding experiment, produce fertile "clonal/*monacha*" hybrids which resemble normal *P.*

monacha. Backcrosses of these hybrids with *P. monacha* in nature would permit the introgression of unique clonal mutations or migrant clonal genomes into the local *P. monacha* gene pool (Vrijenhoek, 1979). Once in the *P. monacha* gene pool, clonal alleles can recombine and if involved in interspecific hybridizations, can be "frozen" into new hybridogenetic combinations. The clonal breakdown and reformation process provides the potential for recombination between clonal genomes and thereby supplements variation obtainable by polyphyletic hybridizations alone. The breakdown-reformation process has contributed to clonal variation in *P. monacha-lucida* inhabiting the Rio Mocorito, but it involves *P. viriosa*, a species closely related to *P. monacha* (Vrijenhoek and Schultz, 1974).

The electrophoretic studies also reveal that unisexual *Poeciliopsis* contain substantially higher levels of heterozygosity than their sexual progenitors (Table 2). Whether this level of heterozygosity at 38.5–52% of the gene loci examined contributes to unisexual fitness or simply reflects their hybrid ancestry is presently under investigation. The "enforced" heterozygosity of unisexual *Poeciliopsis* results in a multiplicity of proteins shared by all the individuals of a clone, but does not exact the potential costs that sexual species would pay in terms of segregational load. Studies of thermal tolerance in *P. monacha-lucida* strains support the hypothesis that some of these unisexu-

als are heterotic with respect to their more homozygous sexual progenitors (Bulger and Schultz, 1979); however, studies of *P. monacha-occidentalis* and its progenitors did not support this hypothesis (Bulger, 1978). Even though some unisexual *Poeciliopsis* may be heterotic for certain characteristics, heterosis does not serve as a general explanation for their success relative to the less heterozygous sexual species (see Moore, 1977; Schultz, 1977; and Bulger and Schultz, 1979, for discussions of this issue).

NICHE WIDTH AND COEXISTENCE AMONG CLONES

The habitats occupied by unisexual *Poeciliopsis* are distributed discontinuously both within and between river systems. During the long dry season in northwestern Mexico, December to June, these fish are often crowded into isolated residual pools and small streams fed by natural springs. Movement between these habitats is possible during the rainy season unless hampered by man-made impoundments or natural barriers (see Vrijenhoek, 1979). In some years drought conditions are severe and local extinctions occur. The diversity of clones at a particular locality reflects the balance between forces that generate new clones and those that cause their extinction.

Local catastrophes such as severe droughts might occasionally reduce unisexual populations to the point where random drift is the primary regulator of clonal

TABLE 2. Heterozygosity in sexual and unisexual *Poeciliopsis*.^a

Species of <i>Poeciliopsis</i>	Number of populations	Number of gene loci	Percent loci heterozygous
Sexual (2N)			
<i>P. monacha</i>	8	25	4.7 ± 2.5
<i>P. lucida</i>	5	25	2.1 ± 1.6*
<i>P. occidentalis</i>	5	25	1.8 ± 2.7
<i>P. latidens</i>	2	25	0.6 ± 0.5*
Hybridogenetic (2N)			
<i>P. monacha-lucida</i>	5	23	42.6 ± 3.9
<i>P. monacha-occidentalis</i>	5	25	42.5 ± 1.1
<i>P. monacha-latidens</i>	2	26	38.5 ± 0*
Gynogenetic (3N)			
<i>P. 2 monacha-lucida</i>	7	25	50.7 ± 1.9
<i>P. monacha-2 lucida</i>	8	25	54.4 ± 2.0
<i>P. monacha-lucida-viriosa</i>	1	25	52.0 ± 0*

^a Based upon electrophoretic studies of Vrijenhoek *et al.* 1977, 1978 and unpublished preliminary data (asterisk).

composition. If true, one would expect large and relatively permanent rivers with large fish populations to sustain higher clonal diversity than small rivers, where clonal drift should reduce diversity. No such relationship exists. Some of the smallest populations in ephemeral pools and arroyos maintain considerable clonal diversity despite the potential for its random loss; large populations such as those in the Rios Yaqui and Sonora can be monoclonal (Vrijenhoek *et al.*, 1977, 1978; Angus, 1979). It is more likely that the clonal composition at any locality depends primarily upon the rate of origin of new clones through hybridization, migration, and mutation; upon the competitive regime encountered by new clones; and also upon the capacity of the environment to provide multiple niches.

The success of individual clones, competing for limiting resources with one another and with their sexual ancestors, may benefit from the absence of recombination. Recombinational variability in sexual populations can significantly retard the rate of adaptive evolution at gene loci involved in epistatic interactions (Eshel and Feldman, 1970). Roughgarden (1972) extended this line of reasoning in his treatment of niche width. He described two components of niche width: 1) the within-phenotype component, due to the variety of resources used by each phenotype; and 2) the between-phenotype component, due to differences among phenotypes. Roughgarden concluded that "the between-phenotype component of niche width in asexual populations is more malleable to the force of natural selection than in sexual populations," providing that the asexual population has sufficient genetic variability.

Where polyphyletic origins are possible, the asexual population size can increase through exploitation of the between-phenotype component of niche width contained in the ancestral sexual populations. Clonal reproduction could freeze adaptive complexes of genes which decrease niche overlap among clones and also provide high efficiency within specific subniches. The fundamental niches of the different clones could be completely included within

those of the sexual ancestors, as long as the clones are more efficient within specific subniches. A broad panel of efficient specialist clones could competitively exclude the sexual host, unless limited by sperm dependence as in the case of hybridogens and gynogens.

Coexistence between a pair of gynogenetic *P. 2 monacha-lucida* clones apparently follows this model (Vrijenhoek, 1978). During the dry season both clones are densely crowded into small residual pools and streams in the Rio Fuerte drainage. Clone I individuals primarily engage in scraping algae from rocky surfaces. They have a dense "sandpaper-like" patch of small tricuspid teeth on the dentary bone and these teeth often show patterns of wear consistent with their scraping behavior (Fig. 2B). Clone II individuals browse through detritus and floating mats of *Hydrodictyon* algae. They have significantly fewer of the small dentary teeth, which are arranged in four orderly rows and are typically unworn (Fig. 2D). The absence of strong competitive interference between these two clones is indicated by their numerical independence over time and space. The frequencies of both clones were determined relative to females of *P. monacha*, their sexual host (Fig. 3). Clone I frequencies are statistically independent of Clone II frequencies. The scraping clone (I) generally comprises about 10% of the population, except in one case (29%) where it inhabited a scoured bedrock pool. Frequencies of the browsing clone (II) clearly relate to resource abundance. In sunny, productive habitats, characterized by floating algae and accumulated detritus, clone II achieves its highest frequencies relative to *P. monacha*. Its frequencies are low in the less productive habitats. A preliminary examination of gut contents in these fish indicated that the sexual species, *P. monacha*, is significantly more generalized in its food preferences than either clone. A very similar relationship occurs with the geometrid moth *Alsophila pometaria* (Mitter *et al.*, 1979). Different gynogenetic clones associate with specific host plants upon which they feed. Also, the hatching time of specific clones coincides with host tree foliation (J. Schneider, per-

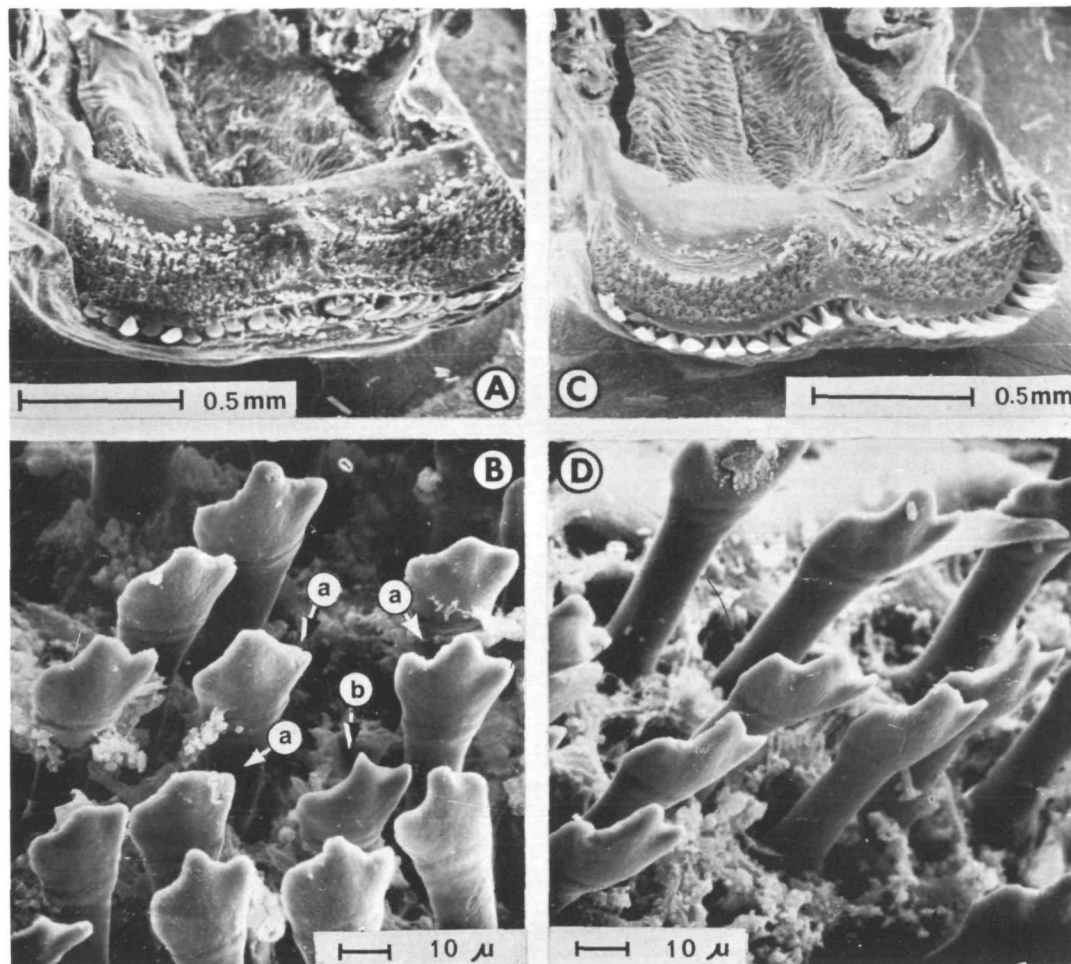


FIG. 2. Inner view of the dentary bone in *P. 2 monacha-lucida*. A. Clone I. B. Patterns of dental wear (a) on the small tricuspid teeth of clone I as opposed to new teeth (b) not emerged above the gum-line. C.

Clone II. D. Typically unworn teeth of clone II. Scanning electron microscopy was performed by T. Mariano, Jr. and Dr. V. Greenhut of Rutgers University.

sonal communication). The sexual individuals apparently are generalists.

Temporal heterogeneity in the environment may further increase the number of clones that can coexist. Bulger and Schultz (1979) recently described differences between two triploid clones of *Poeciliopsis monacha-2 lucida*. One clone is better at surviving heat stresses and the other better at surviving cold stresses. Perhaps these two clones are favored differentially during different parts of the annual summer and winter cycles. Coexisting clones might employ different fertility and survivorship schedules which follow annual climatic cy-

cles (Angus, 1979). An "r-selected" clone might achieve high frequencies under non-competitive conditions during the rainy season. A "K-selected" clone might have higher survivorship when densely crowded during the dry season. Clones of dandelions, *Taraxacum officinale*, apparently exploit different portions of the "r and K continuum" (Solbrig, 1971). The combined effects of temporal and spatial heterogeneity in the environment provide a great variety of subniches that could maintain numerous distinct clones.

Although clonal specialization might benefit the short-term success of unisexual

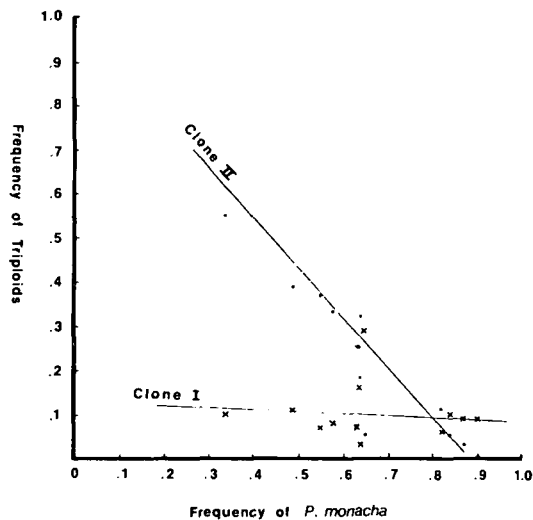


FIG. 3. Frequencies of *P. 2 monacha-lucida* triploid, clones I and II relative to that of *P. monacha* females. Clone I frequencies are independent of clone II and *P. monacha*. The latter two are negatively correlated ($r = -.999$; $P < .001$).

Poeciliopsis, long-term survival in an unpredictable environment is more complex. Persistence might depend upon continuous recruitment of new clones from a generalist ancestor. Thus, the ability to keep up with a changing environment would depend upon: 1) the between-phenotype variation in niche-width of the sexual ancestor; 2) the clonal recruitment rate; and 3) the persistence of the sexual ancestor. This process should give rise to considerable endemism, and locally adapted clones. An alternative solution for long-term survival might depend upon variation in the sexual ancestor for the within-phenotype component of niche width. If the sexual ancestors produce a range of genotypes varying from narrow specialists to broad generalists, selection in a highly unpredictable environment should favor broadly tolerant clones (Parker *et al.*, 1977). Such generalists could achieve widespread distributions through migration, and thus avoid extinction. It is fascinating that the most widely distributed clone of *P. monacha-lucida* (1e) is also the most broadly tolerant of heat and cold stresses (Bulger and Schultz, 1979). Many of the other *P. monacha-lucida* clones are endemics. Two endemic clones (VIIa and VIIb) occurring near a thermal spring are

intolerant of cold stresses (Bulger and Schultz, 1979).

Low clonal variation is associated with some extremely wide-spread parthenogenetic organisms. The wide geographical distributions of certain parthenogenetic cockroach clones (*Pycnoscelus surinamensis*) and a pair of earthworm clones (*Octolasion tyrtaeum*) were interpreted as evidence that they were broadly adapted "general purpose genotypes" (Parker *et al.*, 1977; Jaenike *et al.*, 1979). A single clone of the mealybug *Ferrisia virgata* (Pseudococcidae) is widespread geographically and also with regard to host plants it feeds upon; five related sexual species are quite restricted, both geographically and with regard to host plants (U. Nur, personal communication). It is possible that substantial clonal variation was overlooked in these studies since they were based on electrophoretic techniques; however, another reasonable explanation exists. In these organisms, the major advantage of parthenogenetic reproduction may lie in the high intrinsic rate of increase and colonization ability it imparts (Baker, 1965). One would expect low clonal diversity in such organisms because of founder effects during colonizations and because there is no premium on competitive abilities in such "weedy" species (Wright and Lowe, 1968). Quite different forces impinge upon hybridogenetic and gynogenetic unisexuals, such as *Poeciliopsis* and *Alsophila pometaria*. Because of their sperm dependence they are forced to coexist with their sexual hosts: thus, colonization abilities are not a premium, but competitive abilities are (Schultz 1971). Also, generalism *versus* specialism are not necessarily clear-cut alternatives for asexual organisms. Many parameters contribute to a multidimensional niche (Hutchinson, 1957); broad ecological tolerance on one resource axis, such as thermal tolerance in *P. monacha-lucida*, does not necessarily imply the same for all axes, such as food resources. Attempts to attribute the adaptive success of asexual organisms to single factors, such as "general purpose genotypes," heterosis, and "weedy" tendencies overlook the complexity of interactions between a group of organisms and its physical and biotic environment.

ADAPTIVE EVOLUTION AND VARIATION IN
UNISEXUAL POPULATIONS

Prior to our knowledge of the extensive clonal variation in unisexual *Poeciliopsis*, Moore (1976) developed models that related the frequencies of unisexual females and females of the sexual host species to their "primary fitness" in any particular locality. However, if different clones are ecologically and genetically distinct lineages, it makes little sense to speak of unisexual "primary fitness" in the collective sense (R. K. Selander, personal communication). Nevertheless, it is reasonable to consider the frequency of unisexual females as a measure of the relative success of different unisexual populations.

A clear relationship exists between unisexual success and clonal diversity (Fig. 4). Estimates of clonal diversity in each river system are based on electrophoresis, crossing experiments, and tissue grafting studies of *P. monacha-occidentalis* and *P. monacha-lucida* (Vrijenhoek and Schultz, 1974; Vrijenhoek *et al.*, 1977, 1978; Angus, 1979; Angus and Schultz, 1979; Vrijenhoek, unpublished data). Electrophoresis allows large sample sizes but tends to underestimate the number of clones; tissue grafting and crossing experiments are difficult techniques resulting in a limited sample size. Because of these limitations, the proportions of each clone at each locality in a river are not fully ascertainable. For the present, one can at best only treat clonal diversity according to the mean number of identified clones per collection locality for each river system. These means were calculated from three localities in the Rio Mayo, two localities from the Rios Fuerte and Sinaloa, and one locality each for the remaining rivers. Estimates of unisexual frequencies were obtained independently of the electrophoretic and tissue grafting samples: from a previous study by Moore *et al.* (1970) and from preserved collections by Vrijenhoek. Unisexual success is expressed as mean unisexual frequency per river system. The correlation between mean clonal diversity and mean unisexual frequency is high ($r = 0.93$; $P < .01$). Its numerical value should not be taken too seriously because of

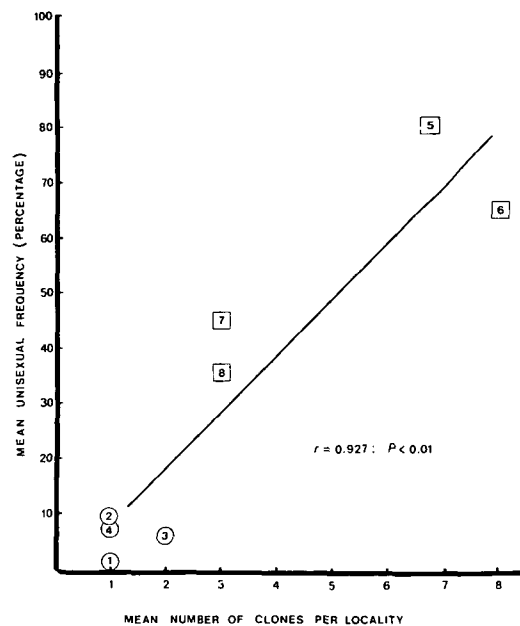


FIG. 4. Unisexual frequency as related to clonal diversity. Unisexual frequency is based upon the frequencies of *P. monacha-lucida* and *P. monacha-occidentalis* females relative to the females of their sexual host species *P. lucida* and *P. occidentalis*, respectively. The numbers inside the circles and squares correspond to river designations in Figure 1.

the difficulties in ascertaining clonal diversity. Nevertheless, if the mean number of clones per site in the Rios Sinaloa (7) and Mocorito (8) were doubled with the future application of tissue grafting experiments, this robust relationship is not substantially altered in its level of significance ($r = 0.92$, $P < .01$). Also this correlation is not a sampling artifact; the sample sizes used to estimate clonal diversity are independent of the sample sizes used to estimate unisexual frequency. The relationship is striking; high unisexual diversity is associated with high unisexual frequency.

Clonal drift in rivers where the unisexuals are at low frequency could cause this relationship, yet no obvious relationship between clonal diversity and population size is apparent. For example, the Rio Sonora contains millions of *Poeciliopsis*, even in some of the worst drought years in which we have sampled (Schultz, 1977; Vrijenhoek, personal observations). Even though unisexual females comprise less than 10%

of the population they still have a large population size. Conversely, in the Rios Fuerte and Sinaloa, clonal diversity is maintained in numerous isolated localities containing no more than a few thousand unisexuals. Often these clones are endemics; therefore it is not reasonable to invoke migration among tributaries as the force that maintains this variation.

One clear distinction does separate rivers with high unisexual frequencies from those with low unisexual frequencies. The squares in Figure 4 represent rivers where *P. monacha* or its relative *P. viriosa* is present, and therefore in which polyphyletic hybrid origins are possible. The circles represent rivers where polyphyletic origins are not possible, and therefore mutations and migration are the only sources of clonal variation. The unisexual populations achieve their highest numerical success where continuous recruitment of sexual genomes is possible.

The numerical success of unisexual *Poeciliopsis* relative to females of the sexual host species apparently depends upon the recruitment of new clonal genomes from the sexual ancestors. Thus, for these unisexual populations the rate of adaptive evolution is a function of the variability contained in the gene pool of the sexual ancestors, a curious offshoot of Fisher's (1930) Fundamental Theorem of Natural Selection. Each new clonal genome "freezes" a unique genotype along with its peculiar temporal, spatial, and trophic niche requirements. A multiclonal population, which exploits the between-phenotype components of niche width, can achieve significantly higher numbers of individuals than a monoclonal population. It will be of interest to see if these proposed relationships between clonal diversity and overall numerical success occur in other sperm dependent unisexual populations.

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