the same phase at all stations, while the peaks of all other modes cancel each other because their phase is more or less randomly divided between 0 and π. If properly excited, ${}_5S_{26}$ should dominate the summed spectrum, and if the stations are uniformly distributed over the earth the frequency thus determined will be the average frequency corresponding to the degenerate eigenfrequency of an ideal unperturbed spherically symmetric earth model (*4*).

The excitation criterion was successfully applied to identify spectral peaks of oscillations excited by the deep shock which occurred on 31 July 1970 in southern Colombia, at a depth of 651 km. This event was not followed by aftershocks that would complicate the radiation pattern. The close agreement between the theoretical and observed spectra at single stations for the fundamental spheroidal modes between 170 and 600 seconds supports the assumption that the source mechanism derived from *P* waves is valid for long-period oscillations.

Spectra from 83 stations were used in this case. In order to increase the signal-to-noise ratio, I did not use spectra from stations where the theoretical amplitude of the peak to be identified was less than half the average amplitude over all the stations, since adding these spectra merely increases the noise in the summed spectrum. Some of the peaks that have been identified are shown in Fig. 1. These new data will impose strong constraints on earth models in the future.

The excitation criterion not only identifies unambiguously the spectral peaks but also enhances the signal-to-noise ratio. It is successful even for modes with low values of the parameter *Q* (high attenuation) and at frequencies where the spectral peaks are very close to each other. The resulting identifications are not biased by personal judgment, and the method is not critically dependent on the earth model used to compute the theoretical amplitudes. An extension of this technique would be to sum the spectra of many earthquakes after applying the proper correction to the phase.

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Unisexual Fish: Laboratory Synthesis of a "Species"

Abstract. *By hybridizing bisexual (gonochoristic) fishes, all-female clones have been produced that are comparable to those of a wild unisexual "species,"* Poeciliopsis monacha-lucida, *living in northwestern Mexico. The laboratory unisexuals have consistently given birth only to female progeny for six generations.*

Unisexual "species" are known from no fewer than nine genera of cold-blooded vertebrates. Morphological, cytological, and biochemical studies have demonstrated that most of these are of hybrid origin (*1, 2*). Although parental precursors have been identified for several all-female vertebrates, until now none have been synthesized in the laboratory. Among the lizards, where the greatest number of all-female "species" occurs, rearing difficulties limit the amount of experimental manipulation possible. The same is true of *Ambystoma*, the only genus of amphibians with unisexual representatives.

In fishes, however, only three genera contain unisexuals; all are readily cultured. Hubbs and Hubbs (*3*) experimented for 15 years with *Poecilia formosa*, the first all-female "species" to be discovered. Although its parental origin was determined, they were unable to synthesize it. Apparently, no attempts have been made to trace the origin or to synthesize the unisexual goldfish, *Carassius auratus*, that occurs in Russia and Japan (*4*).

The third genus with all-female representatives is *Poeciliopsis*, which, like *Poecilia formosa*, is a live-bearer (family Poeciliidae). Included in this genus are three diploid and three triploid unisexual forms, all from northwestern Mexico (*2*). This report concerns one of the diploids, *Poeciliopsis monacha-lucida*, which is postulated to be an evolutionary stepping-stone to the other five (*5*). Morphological, experimental, and ecological evidence gathered for 17 years indicates that this fish arose as a *P. monacha* × *P. lucida* hybrid in the Río Fuerte of Sinaloa, Mexico.

The evolutionary events that produced and now sustain this unique all-female "species" are as follows. In one of the narrow zones where the ranges of the parental species overlap, *P. monacha* females crossed with *P. lucida* males, giving rise to the morphologically intermediate form *P. monacha-lucida*. Because the sex-determining mechanism of *P. monacha* is "stronger" than that of *P. lucida*, such hybrids are exclusively females. Within the hybrid, random segregation of maternal and paternal chromosomes does not occur. Although the possibility exists for an occasional *P. lucida* chromosome to be transmitted to the egg (*6*), genetic evidence indicates that only those of *P. monacha* survive oogenesis (*7*). In this manner the "strength" of the maternal genome is held intact through successive generations, and unisexuality is preserved in each union with the "weaker" *P. lucida* sperm. Elimination of paternal chromosomes occurs in the mitotic divisions preceding meiosis. A single set of chromosomes, presumably *P. monacha*, becomes associated with a unipolar spindle. The other set, presumably the paternal complement, remains scattered in the cytoplasm. At anaphase, the maternal (*P. monacha*) chromosomes are clustered at the single pole, where they become surrounded by the reconstituted nuclear membrane; whereas the paternal (*P. lucida*) chromosomes are either absorbed or expelled in the fashion of a polar body (*6*). Meiosis apparently consists of a single equational division, which eliminates crossing-over or random segregation as a path for introgression of paternal elements. After 27 generations, laboratory strains of *P. monacha-lucida*, originally collected from the Río Fuerte in 1961, still produce only female offspring by their *P. lucida* mates. This unique mode of reproduction has been termed "hybridogenesis" (*5*).

More than 67 matings of *P. monacha* with *P. lucida* have been attempted since 1957; five were successful in the sense of providing fertile offspring that survived to maturity. Difficulties with this cross derive mainly from a disparity in size between the hybrid embryo and

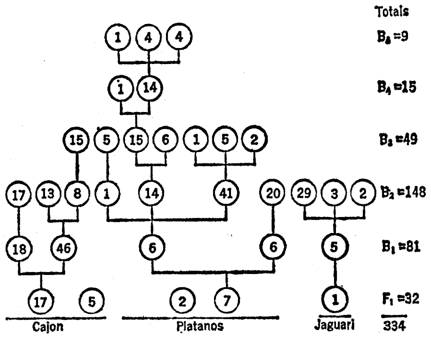

Fig. 1. Lineages of the unisexual "species" *P. monacha-lucida*, synthesized from parental stocks that originated from three different tributaries of the Río Fuerte in Sinaloa, Mexico. Each circle represents a female. Those at the bottom are *P. monacha* founding mothers. The number within the circle indicates the number of young each female produced that were reared to sexual maturity. All offspring were females.

the *P. monacha* yolk; *P. monacha* has large embryos, nourished by eggs 2.2 mm in diameter, whereas *P. lucida* has small embryos in 1.4-mm eggs (*5*). At birth, the medium-sized hybrid young has not used all the yolk; thus, its heart is still outside on the anterior ventral surface of the yolk sac. The survival rate of newborn hybrids is reduced as a result of (i) yolk-sac rupture and heart damage during the birth process, (ii) closure of abdominal walls before the yolk is absorbed and the heart retracted, and (iii) predation on clumsy, yolk-laden young. Subsequent generations do not have surplus yolk, because they develop in medium-sized hybrid eggs (1.8 mm). Offspring from both wild unisexuals and synthesized unisexuals of the second and later generations are hardy in the laboratory; their mortality rates from birth to maturity are less than 2 percent. Large broods from synthesized unisexuals contain 10 to 19 young, which is comparable to those of wild strains.

Transmission of lactate dehydrogenase marker genes was traced through oogenesis to determine whether or not synthesized unisexuals are hybridogenic as is the wild *P. monacha-lucida*. At the *LDH-E* locus, *P. monacha* has two alleles, medium (*E*) and a fast mutant (*E′*); *P. lucida* has the medium (*E*) and a slow mutant (*E″*) (*8*). When a synthesized *P. monacha-lucida*, heterozygous for *E′* and *E″*, was mated to an *EE* male of *P. lucida*, all eight offspring produced were *E′E* and none were *E″E*, a result indicating that the paternal genome marked with the *E″* allele is not transmitted to the egg. Furthermore, after five generations of backcrossing synthesized clones to *P. lucida*, no more *P. lucida* traits were detectable in the backcross progeny than in the F_1 generation.

Unisexual *P. monacha-lucida* females were synthesized independently five times, by using *P. monacha* females from three separate localities of the Río Fuerte and *P. lucida* males from four different sites. Laboratory lines (Fig. 1) were established from each of the three female localities by backcrossing to males of *P. lucida* in the same manner as the wild lines are maintained. One line was studied, then terminated after four generations because of space problems; two lines died out before their numbers could be built up to safe levels. Of the two lines remaining, one is now in its third generation; the other, its sixth.

A total of 334 F_1 to F_6 synthesized *P. monacha-lucida* offspring were reared to maturity. All were females, indistinguishable from wild *P. monacha-lucida*. Such characters as the shape of the lips, jaws, inner teeth, outer teeth, and genitalia are all intermediate to those of *P. monacha* and *P. lucida*. Quantitative values such as inner and outer tooth numbers and tooth dimensions are also intermediate to those of the parental species (*5*). A few quantitative values are presented for comparison of wild populations with synthesized clones (Table 1).

Each upper and lower jaw in *Poeciliopsis* contains a single row of large spatula-shaped outer teeth, following the curvature of the lips; behind them are 1 to 15 rows of fine inner teeth, less than one-third the size of the outer teeth and either tricuspid or unicuspid in form. Dental characters of *P. monacha* and *P. lucida* are highly contrasting; *P. monacha* has few outer teeth (20.3) and a high number of inner teeth (157.5), whereas *P. lucida* has a high outer number (27.8) and a low inner number (29.1). Mean values for clones of *P. monacha-lucida* vary about a median of the parental values. Two wild clones differed from each other in both outer ($P < .01$) and inner tooth numbers, as did two synthesized clones ($P < .01$, $P < .02$) (*9*). One synthesized line (clone B) had the same number of inner teeth as did a wild line (clone A), and both synthesized lines had the same number of outer teeth as did one of the wild stocks.

Table 1. Inner and outer tooth numbers of synthesized and wild strains of *Poeciliopsis monacha-lucida* unisexuals and their parental precursors, *P. lucida* and *P. monacha*. Abbreviations: *luc.*, *lucida*; *mon.*, *monacha*; Syn., synthesized; S.D., standard deviation.

Strain	Jaws examined (No.)	Inner teeth (mean ± S.D.)	Outer teeth (mean ± S.D.)
		Parental species	
P. luc.	14	27.8 ± 27.8	29.1 ± 2.9
P. mon.	15	157.5 ± 38.3	20.3 ± 1.7
		Unisexual lines	
Syn. A	13	94.5 ± 17.8	22.0 ± 1.6
Syn. B	13	67.4 ± 10.0	24.2 ± 2.5
Wild A	13	71.8 ± 8.4	22.6 ± 1.5
Wild B	12	54.5 ± 11.9	24.4 ± 1.9

Genetic variation within clones of *P. monacha-lucida* derives mainly from the *P. lucida* father, since the *P. monacha* genome essentially remains intact from one generation to the next. Differences between clones come from an additional source, namely, differences between *P. monacha* genomes that originated each clone. Several clones of wild unisexuals have been identified from the Río Fuerte by both morphological and electrophoretic analyses (*7*, *8*); how many actually exist has not been established. Theoretically, there should be few wild clones, because zones of contact between *P. monacha* and *P. lucida* are limited and the cross itself does not go well. However, the most important consideration lies in the capacity of founding *P. monacha* genomes to coadapt to any *P. lucida* genome encountered. Such coadaptation requires not only the appropriate interspecific gene interactions for production of viable zygotes; but also requires that a new clone, if it is to become established, have the necessary endowments to compete successfully with the parental species and previously established clones of unisexuals.

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