mean value of the interpair phase shift was 92.1° ± 6.5°.

In some cases (Fig. 3, A and C), the phase shift across an extended range of the spatial frequency spectrum remained close to 90°. This finding indicates that the axes of the receptive field centers must be the same and thus rules out the possibility that the two receptive field profiles are identical but simply shifted with respect to one another. In fact, if cells have the same spatial tuning curve (Fig. 1) and a 90° phase shift independent of frequency (Fig. 3A), their receptive fields must be conjugate pairs—that is, one field with even symmetry and one with odd symmetry around the same axis.

Moreover, in the last two pairs studied, we used stationary flashed stimuli to categorize the receptive field type of each pair member separately with the aid of the spike amplitude discriminator and audio amplifier. In both cases, one pair member had an approximately even-symmetric receptive field and the other an odd-symmetric profile. Marčelja (*8*) has shown that the even-symmetric and odd-symmetric receptive field profiles of simple cells can be fitted to the product of a Gaussian and either a cosine or sine function, respectively. Marčelja realized that these functions represent the elementary signals described by Gabor (*9*). When paired, these functions permit simultaneous maximal localization of a signal in space and spatial frequency. Simple cells, like Gabor functions, can be considered to represent spatial frequency filters of medium bandwidth (full band width ~ 1 octave) that are reasonably well localized in space.

How might the sequence of simple cells with incremental 90° phase shifts and common spatial frequency and orientation preference be arrayed within the striate cortex? Hubel and Wiesel (*10*) have shown that "columns" subserving constant preferred orientations are actually parallel sheets or slabs running perpendicular to the cortical surface. Kronauer (*11*) has suggested that the 90° phase increments may define the orthogonal processing function along each sheet. The simple cell pairs may constitute subsets of a much longer contiguous cortical sequence. For example, progressive shifts of phase of 90° would imply a uniform stepwise translation of receptive fields over the retina that could be extended in a long sequence across the cortex.

The finding that the negative components of the response of a simple cell to a drifting sine-wave grating are so often markedly or completely truncated (*4, 7*) requires consideration. In principle, the "information" lost by truncation could be preserved if there exists, perhaps elsewhere in the orientation column, another pair of simple cells similarly tuned to orientation, direction, and spatial frequency, but with receptive fields of reversed polarity to those of the observed pair. The members of the second pair would selectively respond when the responses of the first pair were truncated. Between these four cells, the available information would specify sine and cosine components and thereby suffice to specify the amplitude and phase information at one spatial frequency, orientation, and direction over the receptive field region. A single pair would have sufficed (*12*) had it not been for the truncation problem.

When Pollen *et al.* (*13*) first proposed that striate neurons carry out a two-dimensional spatial frequency analysis over "a restricted region of visual space," they assumed that this analysis began at the complex cell stage. Recent research has established that both simple and complex cells participate in this analysis (*3, 14*).

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All-Female Fish: A Cryptic Species of *Menidia* (Atherinidae)

Abstract. *Electrophoretic evidence revealed the common occurrence of an all-female species of* Menidia *(Pisces: Atherinidae) at two localities separated by 280 kilometers on the Gulf Coast of Texas. This finding adds significantly to the known taxonomic spectrum of unisexuality in fishes and demonstrates that unisexuality may be more common among fishes that do not bear live young than is generally suspected.*

Electrophoresis of proteins in 18 widely scattered Texas populations of the genus *Menidia* (Pisces: Atherinidae) revealed an undescribed species consisting entirely of females. The new form is found with two bisexual species, *Menidia beryllina* and *M. peninsulae*, in brackish waters at two widely separated areas on the Texas Gulf Coast. Because of high morphological similarity to the two bisexual species (Fig. 1), which are themselves difficult to separate (*1, 2*), the unisexual form has gone undetected despite its abundant occurrence in Nine Mile Point Pond, a site of intensive ichthyological activity (*3*), including one study (*4*) on *Menidia* taxonomy.

Most of the few well-studied unisexual animal species apparently arose ancestrally as hybrids between closely related bisexual species (*5–7*). Thus unisexual forms represent a potentially major source of undetected species, especially when, as in the present example, the apparent parental forms are highly similar. Since discovery (*8*) of the Amazon mollie, *Poecilia formosa*, the first known unisexual vertebrate, only about 40 natu-

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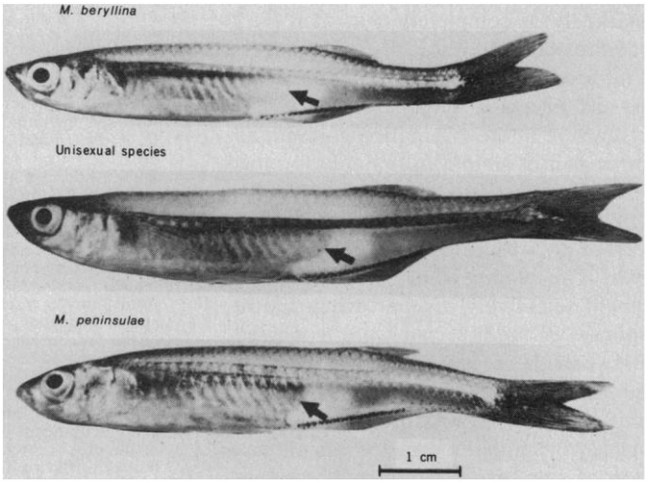

Fig. 1. Appearance of the gasbladder in three species of *Menidia* from the Texas Gulf Coast. Photographs were made with reflected light from above and with light transmitted through the specimens. Arrows point to the extension of the gasbladder to the caudal muscle mass. The gasbladder extension is long and transparent in *M. beryllina*, long and opaque in the unisexual species, and short and opaque in *M. peninsulae*.

rally occurring, unisexual vertebrate species have been well documented. Except for various Asian and Japanese populations of silver carp and goldfish (Cyprinidae), which may be man-induced (*6*), the ten or so known species of unisexual fishes are of the family Poeciliidae and bear live young. This discovery of unisexuality in *Menidia* suggests that unisexuality may be more common among fishes that do not bear live young than is usually recognized. The apparent rarity of unisexuality may reflect the difficulty of detection.

Electrophoretic gel slices stained for phosphoglucomutase (PGM) had two zones of stain activity, but only one, PGM-B, was intense enough for consistent results (*9*). Only three electromorphs were sufficiently abundant for consideration; these are encoded by different alleles designated PGM-B^c, PGM-B^g, and PGM-B^i. The PGM-B^c and PGM-B^g forms correspond, respectively, to the alleles considered diagnostic (*1*) between *M. beryllina* and *M. peninsulae*. During a 3-year period, PGM-B^i has occurred consistently in 9 to 31 percent of the specimens obtained from two sample sites on the Gulf Coast. The two sites, Nine Mile Point Pond, near Copano Bay, and a pool on Galveston Island (*10*), are separated by 280 km. Although sometimes abundant (*11*), PGM-B^i occurred only in the heterozygous state with the typical *M. beryllina* allele, PGM-B^c. To date we have found 248 specimens with PGM-B^i, and all except four had the heterozygous PGM-$B^{c/i}$ genotype. The exceptions were three possibly triploid individuals with the PGM-$B^{c/g/i}$ genotype, and a fourth which was homozygous for PGM-B^i; all four were from Nine Mile Point Pond.

We determined sex for 141 specimens with PGM-B^i, and all were females. Samples of specimens with the PGM-B genotypes of *M. peninsulae* and *M. beryllina* included 33 percent or more of both males and females (*12*). Of five specimens with high probability of being first-generation hybrids of *M. peninsulae* and *M. beryllina* (*13*), three were males. Thus, the PGM-B^i allele represents a genetic marker for a unisexual form of *Menidia*.

Gels stained for glucose phosphate isomerase (GPI) had three zones of stain activity resulting from dimeric enzymes encoded by two presumptive gene loci, GPI-A and GPI-B. *Menidia* populations on the Texas coast were essentially fixed for a single electromorph at GPI-B. For GPI-A, *M. beryllina* and *M. peninsulae* were segregating randomly for two common alleles, GPI-A^d and GPI-A^e, and, depending on the species, one or two less common alleles (*14*). We assayed GPI-A genotypes for 247 specimens (203 from Nine Mile Point Pond and 44 from Galveston Island) showing the PGM-B^i allele and all were heterozygotes for the two common alleles in the bisexual species. Thus, the unisexual form is a fixed heterozygote for single pairs of alleles at both PGM-B and GPI-A.

Analysis of 29 total genetic loci in 29 specimens of the unisexual form from Nine Mile Point Pond and 21 from Galveston Island further revealed that such individuals are fixed heterozygotes for a single pair of alleles at each of six loci, and that, except for three variant specimens at single loci, there is a paucity of genetic variation (*15*). In contrast, *M. beryllina* and *M. peninsulae* from both Nine Mile Point Pond and Galveston Island are segregating randomly for two or more alleles at 12 to 16 loci (*15*). In addition to PGM-B^i, the unisexual form has a second unique allele, IDH-A^b, at an isocitrate dehydrogenase locus. Neither PGM-B^i nor IDH-A^b were found in a survey of several populations of *M. beryllina* and *M. peninsulae* (*1*), and we have not found either of the two alleles except in association with the fixed genotype of the unisexual form.

The unisexual form differs from the two bisexual species in two morphological characteristics. *Menidia* from the Texas coast show three fairly distinct gasbladder types (Fig. 1). In collections from Nine Mile Point Pond and Galveston Island, 97 to 99 percent of specimens with the genotype of the unisexual form had long, opaque gasbladders, whereas 93 to 98 percent of those with *M. peninsulae* genotypes had short, opaque gasbladders, and 90 to 91 percent of those with *M. beryllina* genotypes had long, transparent gasbladders (*16*). Counts of rays in the second dorsal fin show that 91 percent of the unisexual form have eight rays, whereas 77 and 75 percent, respectively, of *M. beryllina* and *M. peninsulae* have nine or more (*16*).

There are several possible explanations for the observed rigid association between all-femaleness, fixed genotype at 29 genetic loci, long opaque gasbladders, and eight soft dorsal fin rays. We can eliminate the possibility that the unisexual form is an abnormal component of one of the bisexual species; this would require a level of genetic disequilibrium far greater than any yet demonstrated for a sexual population. The hypothesis that the unisexual form is the result of ongoing hybridization between *M. beryllina* and *M. peninsulae* is untenable for the following reasons. (i) Texas populations of the two bisexual species are almost fixed for different alleles at the creatine kinase A locus (*1, 16*); yet the unisexual form is homozygous for the *M. beryllina* allele (*14, 15*). (ii) The unisexual form is fixed for two unique alleles that have not been found in extensive surveys of *M. beryllina* and *M. peninsulae*. Repression of maternal or paternal genes may occur in hybrids (*17*), but we know of no examples of hybrid phenotypes with altered mobilities of electromorphs. (iii) Five probable first-generation hybrids of *M. peninsulae* and *M. beryllina* (*13*) included three males. (iv) The unisexual form shows very little variation, whereas hybrids should be highly variable; of the five first-generation hybrids detected, no two had the same genotype and individuals differed at one to five of the 29 loci examined. (v) Both bisexual species have a modal number of nine soft dorsal fin rays, and as expected of a hybrid population, the five hybrids mentioned above have the same mode (three had

nine rays); however, the unisexual form has a very strong mode of eight rays.

We conclude that the unisexual *Menidia* is a separate, self-perpetuating species that reproduces without the genetic segregation and recombination expected of sexual populations (*18*). The abundance and consistent occurrence of the unisexual species at two locations over a geographic range of 390 km show that it is a persistent part of the fauna on the Gulf Coast of Texas.

Except for the fixed presence of unique alleles at PGM-B and IDH-A, the genetic structure of the all-female species of *Menidia* is readily explained as a product of past hybridization between *M. beryllina* and *M. peninsulae* (*15*). In another all-female fish, *Poecilia formosa*, Turner *et al.* (*7*) offered several alternative explanations for two "orphan alleles" that were absent in samples of both proposed parental species. Similar arguments apply to the unisexual *Menidia*. Orphan alleles aside, the unisexual *Menidia* species apparently arose by hybridization between two forms similar to *M. beryllina* and *M. peninsulae* (*15*).

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11. In samples representative of relative abundance of the three forms of *Menidia*, the unisexual form represented 10 percent of 86 specimens in the one such sample from Galveston Island and 9 to 31 percent (mean, 19.4 percent) of 67 to 125 specimens in five such samples from Nine Mile Point Pond. In the past 3 years, the unisexual and both bisexual species were taken in all samples from Galveston Island (four samples) and Nine Mile Point Pond (eight samples).
12. No samples show statistically significant deviation from the expected 1:1 sex ratio (chi-square, $P > .05$).
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Memory Performance of Chemical Workers Exposed to Polybrominated Biphenyls

Abstract. *Twenty-five chemical workers who manufactured polybrominated biphenyls (PBB's) were given objective tests of learning and memory. Although this group had high concentrations of PBB's in adipose tissue, mean scores on all memory tests were normal. The PBB concentration was not correlated with memory performance; the most contaminated workers showed no evidence of memory dysfunction.*

Polybrominated biphenyls (PBB's) were inadvertently mixed into an animal feed supplement and sent to some Michigan farms in 1973 (*1*). The PBB's entered the food chain and were widely dispersed throughout the state's lower peninsula, contaminating urban as well as farm residents (*2*).

After exposure to PBB's, some Michigan residents complained of memory loss (*3*). In one study, 30 of 46 Michigan residents from both quarantined and unquarantined farms complained of memory problems (*4*). We have reported on the memory functioning of 21 Michigan farm residents who had persistent medical complaints after contact with PBB (*5*). The farm group had more difficulty than an urban group on tests of memory for prose and short-term retention of words. Poor memory on both verbal memory tasks was correlated with measures of anxiety and depression on the Minnesota Multiphasic Personality Inventory (MMPI) but was not correlated with the PBB concentration in adipose tissue. These findings suggest that memory dysfunction in some Michigan residents exposed to PBB's was related to psychological dysfunction and not PBB body burden.

Three aspects of our earlier study (*5*) limited the degree to which we would generalize its findings to other Michigan residents who had contact with PBB's. (i) The sample size was small. (ii) Most people studied had relatively low PBB contamination. (iii) There was a clear self-selection bias in our sample; most of the farm residents were studied because they had persistent medical complaints that had resisted diagnosis. Because depression and anxiety are often associated with multiple somatic complaints that are difficult to explain by a diagnosis of physical disease, this admission criterion may have selected for farm residents with psychological disorders (*6*).

To determine whether high PBB body burden would correlate with memory deficits, we studied a group of chemical workers with high PBB contamination who were selected in a way to avoid the selection bias of the sample of farm residents. These chemical workers demonstrated normal memory functioning, and their scores on memory tests were unrelated to the concentration of PBB in adipose tissue.

The Michigan Department of Public Health identified 25 PBB chemical workers on the basis of their proximity to PBB contact. Fifteen of the chemical workers directly handled PBB's or performed maintenance work in the area where PBB's were manufactured. The rest worked in a different department at the same plant. The chemical workers did not differ significantly in age, education, IQ, or predicted IQ from the farm residents whom we studied previously. The predicted IQ is an estimate based on a subject's educational, occupational, and cultural background (*7*). There were no significant differences between the chemical workers' observed full scale IQ and the predicted IQ; this suggests that as a group their intellectual functioning was typical of people of their educational, occupational, and cultural backgrounds (see Table 1).

The mean ($\bar{X}$) PBB concentration in fat for the chemical workers was 9.33 parts per million (ppm) with a standard deviation (S.D.) of 15.26 ppm. In the farm residents studied earlier, $\bar{X}$ was 3.94 ppm (S.D. = 9.96 ppm). Because distributions of PBB values have a strong posi-

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