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GEOGRAPHIC VARIATION IN MORPHOLOGY OF SPIKEDACE, *MEDA FULGIDA*, IN ARIZONA AND NEW MEXICO

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ABSTRACT—*Meda fulgida* (Pisces: Cyprinidae) is a species endemic to the Gila River basin of Arizona, Mexico, and New Mexico. The extent of geographic variation in morphology within this species has not been explored although evidence indicates that subpopulations have long been isolated. We examined samples from the four restricted areas within the Gila River basin where subpopulations persist, and used principal components analysis, regression against PC1 (to eliminate variation due to size), and ANOVA to demonstrate that individuals from the Verde River (Arizona) have smaller mouths in proportion to body length as compared to individuals from Aravaipa Creek (Arizona). Subpopulations from New Mexico and Eagle Creek in Arizona have intermediate measurements. Additional analyses confirm that females have shorter pre-pectoral measurements, greater mid-body size, and shorter pectoral fins than do males.

RESUMEN—*Meda fulgida* (Pisces: Cyprinidae) es una especie endémica del Rio Gila en Arizona, México, y Nuevo México. Lo amplio de la variación geográphica de la morfología de esta especie no ha sido explorada, aunque pruebas indican que subpoblaciones han sido largamente aisladas. Nosotros examinamos muestras provenientes de las cuatro áreas restringidas dentro del Rio Gila donde persisten subpoblaciones, y usamos análisis de componentes principales, regresión encontra del PC1 (para eliminar la variación debida al tamaño), y ANOVA para demonstrar que individuos provenientes Rio Verde (Arizona) tienen la boca más pequeña en proporción a la longitud del cuerpo en comparación con individuos provenientes del Arroyo Aravaipa (Arizona). Subpoblaciones de Nuevo México y Arroyo Eagle (Arizona) tienen una medida intermedia. Análisis adicionales confirman que las hembras tienen medidas prepectorales más cortas, mayor tamaño en la mitad del cuerpo, y aletas pectorales más cortas que los machos.

Meda fulgida is a small cyprinid that historically ranged throughout most of the Gila River's major tributaries in Arizona, New Mexico, and Sonora, and the mainstem Gila River above Phoenix (Fig. 1; Gilbert and Scofield, 1898; Miller and Winn, 1951). *Meda fulgida* has been extirpated from the San Francisco River in New Mexico and the Agua Fria River and most of the San Pedro River in Arizona (Barber and Minckley, 1966; Minckley, 1973; Rhode, 1980). Currently, remnant subpopulations in the upper Verde River, Eagle Creek, and Aravaipa Creek in Arizona, and the Gila River in New Mexico occupy six percent of the species' former range (Barber and Minckley, 1966; Minckley, 1973; Rhode, 1980; Abarca-Gonzalez, 1989). This decline coupled with new threats led to listing of the species as threatened in 1986 (United States Department of the Interior, 1986).

Although many workers suspected the presence of geographic morphological variation in *M. fulgida* (D. Hendrickson, pers. obser.) previous studies have only described biology and abundance. Researchers focused on Aravaipa Creek in Arizona and the Gila River system in New Mexico, both areas where the species remains comparatively abundant (Barber and Minckley, 1966; Barber et al., 1970; Anderson, 1978; Rinne, 1991). *Meda fulgida* was shown to be extirpated in the San Francisco River (Anderson, 1978). Marsh et al. (1991) reported that collectors did not find *M. fulgida* in Eagle Creek until 1985 despite considerable earlier collecting efforts there.

There may have been some pre-historic degree

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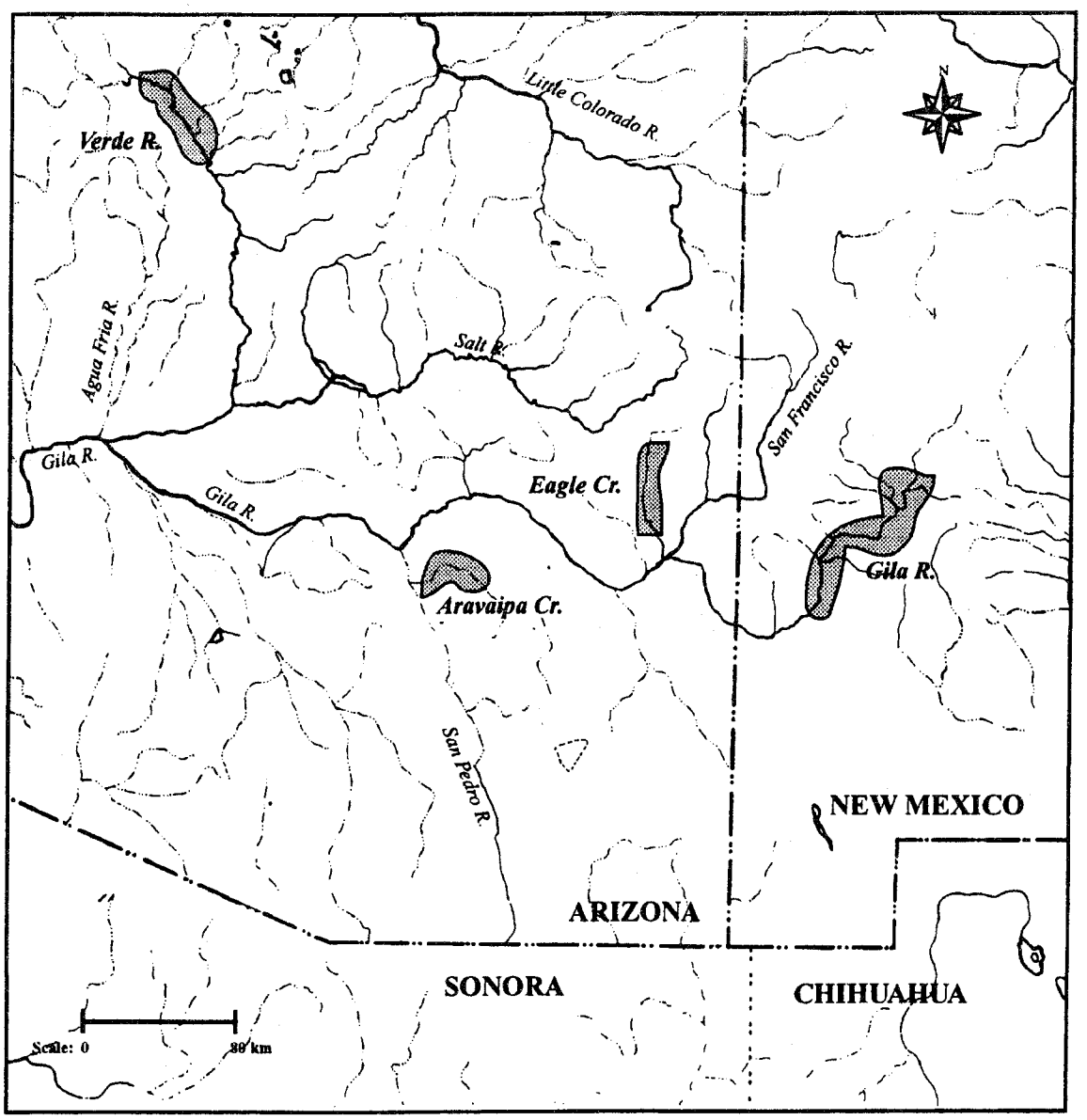

FIG. 1—Map of the Gila River basin. *Meda fulgida* for this study came from the upper Verde River (4 localities), Aravaipa Creek (3 localities), Eagle Creek (3 localities), and New Mexico portion of the Gila River (5 localities).

of isolation among areas where extant subpopulations remain. Habitat preferences might have limited gene flow among subpopulations, but recent extensive habitat fragmentation has almost surely eliminated gene exchange among remnant subpopulations (Minckley, 1973; Hendrickson and Minckley, 1984). Before Europeans settled the Gila River Basin, the Gila and San Pedro Rivers were essentially permanent, with abundant vegetation, marshes, and cienegas (Miller, 1961; Hendrickson and Minckley, 1984). Continuous, unaltered river reaches that yielded historic collections of *M. fulgida* (Minckley, 1973) once characterized the species' range (Hendrickson and Minckley, 1984). In this century, water extraction and stream impoundment have exacerbated habitat fragmentation (Miller, 1961; Hendrickson and Minckley, 1984), to the point that long reaches of highly altered or dry streams now isolate subpopulations. The purpose of this

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TABLE 1—Character loadings on H2, H3, and H4. Only values greater than absolute 0.200 are presented; remaining values are represented only by their signs. Acronyms are described in Appendix 2.

Character	H2	H3	H4
ANALL	−	0.264	+
BODWID	0.267	−0.453	0.026
CPDEP	−	+	0.214
CPWID	−0.842	−0.444	−
DORS-PELV	0.200	−0.250	+
INTRORB	+	−	0.209
MAX-PECT	−	0.226	+
MOUTWID	+	−0.254	0.344
OP-DORS	+	+	−0.289
OP-PELV	+	−	−0.245
PECT-DORS	+	−	−0.260
PECT-PELV	+	−	−0.394
PECTL	−	0.234	+
PELVL	−	0.238	+
SN-MAX	+	+	0.311
Eigenvalue	0.145	0.048	0.026
Proportion of total variance	0.926	0.048	0.026

study was to explore the extent of morphological variation among isolated subpopulations and between sexes.

METHODS AND MATERIALS—We measured a total of 147 specimens (7 to 10 preserved specimens from each locality) from the four remaining subpopulations where the species occurs: Verde River, Aravaipa Creek, Eagle Creek, and Gila River (Appendix 1). Samples represented all seasons.

Following Hubbs and Lagler (1964) and using digital calipers accurate to 0.01 mm, we measured 35 morphometric variables (Appendix 2) that included variables which composed a box truss between physical landmarks (Humphries et al., 1981; Bookstein et al., 1985). We obtained dorsal, anal, pectoral, pelvic, and caudal fin ray counts from 10 individuals from each subpopulation, and dissected 25 specimens from each of three subpopulations to determine sex (scarcity of specimens from Eagle Creek precluded their dissection).

We $\log_{10}$-transformed linear morphometric data for all analyses (see Bookstein et al., 1985), and did not omit any variables or cases. We performed multivariate analyses using SAS version 6.06 (SAS Institute Inc., 1989) and univariate analyses and graphs with SYSTAT version 5.0 (SYSTAT Inc., 1990).

Because of complex problems associated with size in morphometric data and significant differences in specimen size among samples, we chose to use sheared principal components analysis to explore the nature of variation among subpopulations (Bookstein et al., 1985). Using a SAS routine modified from one published in Bookstein et al. (1985), we extracted sheared principal components from the pooled, within group covariance matrix of $\log_{10}$-transformed morphometric variables using subpopulation (Verde River, Gila River, Eagle Creek, and Aravaipa Creek) as the grouping variable.

To confirm our findings from the sheared principal components analysis, we performed univariate analyses on the data after first removing the effect of specimen size, which varied among samples. We did this by linear regressions of the $\log_{10}$-transformed raw data against individuals' scores on PC1 (Bookstein et al., 1985), the general size component from the previously described sheared PCA. We then performed ANOVA and post hoc Tukey HSD (Wilkinson et al., 1992) tests separately for subpopulations and sexes on the size-free residuals from these regressions.

RESULTS AND DISCUSSION—Sheared principal component two (H2) described 92.6% of the total variance remaining after variation attributable to size was removed in PC1. This component was very strongly influenced by CPWID, as well as BODWID and DORS-PELV (Table 1; abbreviations are in Appendix 2). The same variables had heavy loadings on H3 as well, which described an additional 4.8% of total size-free variance (Table 1). A lack of geographic, sexual, or other obvious patterns in scatterplots of scores for H2 and H3 indicates that these components describe variance associated with general ecological condition, seasonality, and reproductive condition. This is supported by the fact that variances about the means of size-free residuals (Table 2) of variables important in H2 and H3 were consistently among the highest of all variables. In particular, variances of CPWID were far greater (0.004 to 0.010) in all subpopulations than were variances of any other variable (all <0.002).

Component four (H4) contained 2.6% of variance remaining in the data after removal of size, and scores on it showed a geographic trend. A frequency distribution of scores on H4 by subpopulation showed that the Aravaipa and Verde subpopulations overlapped little, but the Gila and Eagle subpopulations were intermediate (but more like Aravaipa than Verde; Fig. 2A). A similar distribution for all subpopulations combined showed a distinctly bimodal curve (Fig. 2B).

Both variable loadings in Table 1 and regression residuals in Table 2 revealed that specimens scoring high on H4, such as those from Aravaipa

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TABLE 2—Mean values of residuals from regression against PC1 (see Bookstein et al., 1985) for both sexes and all four subpopulations. Because PC1 is a general size factor, residuals express size-free variation in shape. Values between −0.001 and +0.001 are represented by their signs only.

Variable	Males	Females	Verde	Aravaipa	Eagle	Gila
ANAL-HYP	0.004	−0.007	0.020	−0.013	−0.008	−0.002
ANALBASE	0.008	−0.009	0.025	−0.010	−0.009	−0.007
ANALL	0.002	−0.019	−0.008	0.002	−0.012	0.012
BODWID	−0.019	0.029	−0.019	0.005	0.028	−0.006
CPDEP	0.008	−0.012	−0.017	0.009	+	0.007
CPWID	0.014	−0.005	0.023	0.002	0.023	−0.032
DORS-ANAL	−0.002	0.009	−0.003	0.017	−0.004	−0.006
DORS-PELV	−0.013	0.012	−0.019	0.004	0.021	−0.001
DORSBASE	0.006	−0.005	0.005	0.006	−0.016	0.002
DORSL	0.003	−0.007	0.003	0.001	−0.001	−0.002
EYE	0.003	0.007	−0.006	0.023	−0.008	−0.005
FL	0.001	−0.001	0.010	−0.005	−0.006	−
HDEP	0.002	0.005	−0.015	0.017	0.002	−
HEADL	0.004	−0.003	−0.009	0.009	−0.005	0.004
HWID	0.004	−0.001	−0.014	0.008	0.013	−0.003
IDORS-ANAL	−0.004	0.002	−0.016	0.006	0.007	0.004
IDORS-HYP	0.005	0.005	0.022	−0.002	−0.013	−0.006
IDORS-PELV	−0.011	0.003	−0.002	−0.013	0.014	0.001
INTRORB	0.002	0.001	−0.013	0.007	−0.005	0.008
MAX-OP	0.005	−0.005	−0.004	0.004	−0.006	0.004
MAX-PECT	0.011	−0.011	−0.008	0.002	−0.010	0.011
MOUTWID	0.002	0.002	−0.025	0.015	0.023	−0.005
OP-DORS	−0.012	0.007	0.016	−0.030	0.002	0.006
OP-PECT	−0.001	0.007	−0.002	0.017	−0.005	−0.005
OP-PELV	−0.004	0.013	0.013	−0.013	+	−0.002
PECT-DORS	−0.014	0.009	0.011	−0.028	0.010	0.002
PECT-PELV	−0.011	0.018	0.023	−0.029	0.002	−0.002
PECTL	0.013	−0.017	0.001	+	−0.014	0.008
PELV-ANAL	−0.004	0.005	0.012	−0.006	−0.005	−0.002
PELVL	0.004	−0.012	0.001	−0.005	−0.011	0.009
SL	+	+	0.012	−0.008	−0.007	−
SN-MAX	−0.005	0.002	−0.031	0.023	−0.007	0.013
SN-OP	0.001	−0.004	−0.008	0.010	−0.006	0.004
SN-PECT	0.007	−0.009	−0.014	0.010	−0.004	0.007
TL	0.002	−0.001	0.012	−0.006	−0.008	−0.001

Creek ($\bar{X} = -0.595$), had greater head and mouth dimensions (MOUTWID, INTRORB, and SN-MAX), and shorter pre-pelvic length (especially PECT-PELV, OP-DORS, PECT-DORS, and OP-PELV) compared to low-scoring Verde River specimens ($\bar{X} = -0.741$). These same variable-by-variable comparisons between the Verde and Aravaipa subpopulations were all (except INTRORB) found to be highly significant when tested with the Tukey HSD multiple comparison test (Table 3). Differences between the Eagle and Gila subpopulations were far less pronounced (Table 3), as would be expected since their mean scores on H4 scarcely differ (−0.659 and −0.652 respectively).

Tables 2 and 3 also reveal differences between subpopulations that were not expressed in H4, but which presumably would have been contained in components subsequent to it that we did not extract. Post-pelvic lengths (ANAL-HYP, ANALBASE, IDORS-HYP, and PELV-ANAL), like the pre-pelvic lengths from H4, were all significantly greater in specimens from the Verde River than in Aravaipa specimens (Table 3). Differences between the same two groups in size-free regression residuals for FL, SL and TL

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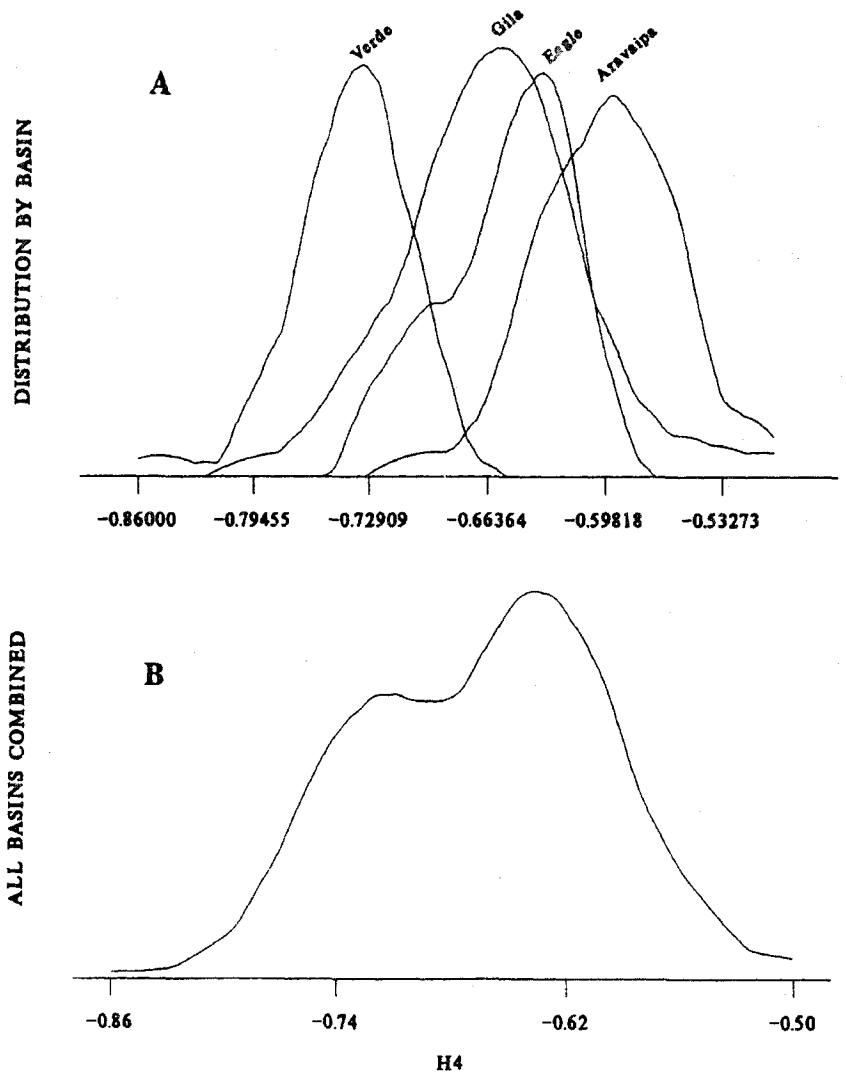

FIG. 2—Relative distributions of scores for H4, separated into scores per subpopulation (A) and all subpopulations combined (B). Smoothed histograms use the kernel density estimate method (Silverman, 1986).

(Table 2), each of which contains these separate lengths as well as the previously mentioned prepelvic lengths, appear to be correlates of the differences in their component lengths. Some body depths also differed between Verde and Aravaipa subpopulations, but not as much as body lengths (Table 2). Thus, individuals from the Verde subpopulation show separation from the Aravaipa subpopulation on the basis of overall body length in comparison to body depth, but no one particular measurement stands out for use as a diagnostic tool. We also found the Eagle and Gila subpopulations to have generally intermediate body lengths.

Our subsample of meristic data did not reveal any significant trend in variation. Dorsal fin ray counts were invariant, and pectoral fin ray counts varied only in three specimens. Pectoral, caudal and anal counts varied somewhat, but showed no geographic pattern. Environmental elements, such as temperature, are known to affect meristic characters (Hubbs, 1922; Strawn, 1957) and we could not control for such factors.

Dissection of 25 specimens selected at random from each subpopulation among specimens used in the previous analyses revealed roughly equal proportions of the sexes (40 males, 35 females). The subpopulations had the following proportions: Verde, 11 females and 14 males; Gila, 12 females and 13 males; Aravaipa, 12 females and 13 males.

We tested for differences between sexes by us-

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TABLE 3—Tukey HSD multiple comparison probabilities. Pairwise probabilities are for between sexes, and between each subpopulation pair (V = Verde, A = Aravaipa, G = Gila, E = Eagle). Using Sidak's multiplicative comparison inequality for an original significance level of 0.05 (Sokal and Rohlf, 1981) only values of $P \leq 0.008$ are presented; a blank indicates a nonsignificant value ($P > 0.008$).

Variable	Sex	V-A	V-E	V-G	A-E	A-G	G-E
ANAL-HYP		<0.001	<0.001	<0.001			
ANALBASE		<0.001	<0.001	<0.001			
ANALL							
BODWID	<0.001		<0.001				0.003
CPDEP	<0.001	<0.001	0.002	<0.001			
CPWID				0.007			
DORS-ANAL		<0.001			<0.001	<0.001	
DORS-PELV	0.001	0.006	<0.001				0.006
DORSBASE			0.005		0.007		
DORSL							
EYE		<0.001			<0.001	<0.001	
FL		<0.001	<0.001	<0.001			0.007
HDEP		<0.001	<0.001	<0.001	0.003	<0.001	
HEADL		<0.001		<0.001	<0.001		
HWID		<0.001	<0.001				0.003
IDORS-ANAL		<0.001	<0.001	<0.001			
IDORS-HYP		<0.001	<0.001	<0.001			
IDORS-PELV					<0.001		
INTRORB				0.001			
MAX-OP							
MAX-PECT	<0.001			0.001			0.001
MOUTWID		<0.001	<0.001				
OP-DORS	0.003	<0.001			<0.001	<0.001	
OP-PECT							
OP-PELV	0.005	<0.001					
PECT-DORS	<0.001	<0.001			<0.001	<0.001	
PECT-PELV	0.001	<0.001		0.001	<0.001	<0.001	
PECTL	<0.001						<0.001
PELV-ANAL		0.004	0.008				
PELVL							0.008
SL		<0.001	<0.001	<0.001		<0.001	0.002
SN-MAX		<0.001	<0.001	<0.001	<0.001		0.001
SN-OP		<0.001		0.004	0.002		
SN-PECT	<0.001	<0.001		<0.001	0.002		
TL		<0.001	<0.001	<0.001			0.002

ing ANOVA and post hoc Tukey HSD multiple comparison tests on size-free regression residuals. Nearly all pairwise probabilities of similarity for measurements dealing with the pectoral fin were highly significant except for OP-PECT (Table 3). Also significantly different between sexes were measurements related to body width (BODWID, DORS-PELV, and OP-PELV), which is understandable in regard to spawning (CPDEP was smaller for females). Analysis of the mean values for each sex (Table 2) confirmed that pectoral fins are longer in males, and further indicated that females have wider bodies, as well as greater pectoral to pelvic fin distances. Barber et al. (1970) also observed (but did not quantify) a slightly longer pectoral fin in relation to head length, and that this fin is wider and more fan-shaped in males. Because most characters displaying geographic variation are not sexually dimorphic (except perhaps origin of pectoral fin to origin of pelvic fin) and each sample contained roughly equal numbers of each size, geographic variation among subpopulations is essentially unlinked to sexual dimorphism.

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In conclusion, small, but statistically significant variation in morphology exists among the four remnant subpopulations of *M. fulgida*. The Verde River subpopulation can be differentiated on the basis of its smaller mouth and longer body in proportion to body depth. Verde River fish can be discriminated morphologically from Aravaipa Creek fish, but specimens from the Gila River in New Mexico and Eagle Creek in Arizona are intermediate and partially overlap the other two subpopulations. Geographically variable characters do not appear related to seasonal factors nor to sexual dimorphism. Future research on the morphology of this species might examine historic material from extirpated subpopulations. Such studies may reveal that remnant subpopulations represent discrete intervals of a former broad continuum of morphological variation throughout the Gila River basin.

Future investigations could also determine whether the species should be managed as a single taxon or a complex of differentiated forms. Gene flow among areas where remnant subpopulations persist, while perhaps once possible, has been precluded by recent anthropogenic habitat alteration. The next step is to look at genetic variation directly. Managing subpopulations without understanding their adaptive genetics can lead to loss of the population as a whole (Altukhov and Salmenkova, 1987), and management of taxa without regard to intra- and inter-population structure of overall geographic variation can have similarly catastrophic results (Allendorf et al., 1987). Phenotypic variation is sometimes controlled by environmental factors to the extent that misinterpretations of morphological variation can result in taxonomic over-splitting (Allendorf et al., 1987).

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APPENDIX 1

Specimens examined came from the fish collections at Arizona State University (ASU) and the Museum of Southwestern Biology, University of New Mexico (MSB). Locality data are given as found on specimen jar labels, with additional information in brackets.

ASU 7098—Arizona, Pinal Co., Aravaipa Creek at Woods Ranch, 11 Aug. 1973 [n = 10]; ASU 10603—Arizona, Greenlee Co., Eagle Creek above dam, 8 Mar. 1986 [n = 10]; ASU 10628—Arizona, Yavapai Co., Verde River, E. of Paulden, off F.S. road 638 [T17N R1W S4], 21 May 1986 [n = 10]; ASU 11696—Arizona, Graham Co., Aravaipa Creek, 16 Apr. 1983 [n = 10]; ASU 11975—Arizona, Greenlee Co., Eagle Creek, ½ mi. above S Sheep Wash [T2S R28E S5], 14 Jul. 1987 [n = 10]; ASU 12016—Arizona, Greenlee Co., Eagle Creek below P-Bar Ranch, 17 Jul. 1987 [n = 10]; ASU 12815—Arizona, Yavapai Co., Verde River, 1.2 mi. below RR bridge below Perkinsville area, T17N R2E S5, 6 Sept. 1989 [n = 10]; ASU 12816—Arizona, Yavapai Co., Verde River, 1.6 mi. below Perkinsville bridge, T18N R2E NE ¼ of SE ¼ of S31, 13 Jan. 1987 [n = 10]; ASU 12818—Arizona, Yavapai Co., Verde River, 0.2 mi. above RR bridge, T18N R2E S31, 19 Mar. 1990 [n = 7]; ASU 63049—Arizona, Graham Co., Aravaipa Creek, T6S R19E SE ¼ of the NW ¼ of S20, Nov. 1974 [n = 10]; MSB 1241—New Mexico, Grant Co., Gila River, ca. 11 mi. below Cliff, 26 Aug 1949 [n = 10]; MSB 1249—New Mexico, Catron Co., Taylor Creek near Wall Lake [T11S R12W S10], 4 Sept. 1951 [n = 10]; MSB 2568—New Mexico, Grant Co., Gila River, ⅛ mi. above conjunction with West Fork [T12S R14W S25], 9 Nov. 1966 [n = 10]; MSB 2763—New Mexico, Grant Co., Gila River in the vicinity of Lyon Lodge (E. Fork) [T13S R13W], 6 Feb. 1967 [n = 10]; MSB 4690—New Mexico, Grant Co., Gila River, at Riverside Street bridge, 15 Jul. 1987 [n = 10].

APPENDIX 2

Character acronyms used in the text and their descriptions.

ANAL-HYP, origin of anal fin to terminus of hypural plate; ANALBASE, anal fin base length; ANALL, anal fin length; BODWID, maximum body width; CPDEP, least depth of caudal peduncle; CPWID, least width of caudal peduncle; DORS-ANAL, origin of dorsal fin to origin of anal fin; DORS-PELV, origin of dorsal fin to origin of pelvic fin; DORSBASE, dorsal fin base length; DORSL, dorsal fin length (depressed); EYE, eye diameter; FL, fork length; HDEP, maximum head depth; HEADL, head length; HWID, maximum head width; IDORS-ANAL, insertion of dorsal fin to origin of anal fin; IDORS-HYP, insertion of dorsal fin to terminus of hypural plate; IDORS-PELV, insertion of dorsal fin to origin of pelvic fin; INTRORB, interorbital distance; MAX-OP, terminus of maxillary to top of opercular aperture; MAX-PECT, terminus of maxillary to origin of pectoral fin; MOUTWID, maximum mouth width; OP-DORS, top of opercular aperture to origin of dorsal fin; OP-PECT, top of opercular aperture to origin of pectoral fin; OP-PELV, top of opercular aperture to origin of pelvic fin; PECT-DORS, origin of pectoral fin to origin of dorsal fin; PECT-PELV, origin of pectoral fin to origin of pelvic fin; PECTL, pelvic fin length; PELV-ANAL, origin of pelvic fin to origin of anal fin; PELVL, pelvic fin length; SL, standard length; SN-MAX, snout to terminus of maxillary; SN-OP, snout to top of opercular aperture; SN-PECT, snout to origin of pectoral fin; TL, total length.

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