GENETIC STRUCTURE OF THE *MACRHYBOPSIS AESTIVALIS* COMPLEX (TELEOSTEI: CYPRINIDAE) WITH EMPHASIS ON POPULATIONS IN THE ARKANSAS AND RED RIVER BASINS

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Abstract

I used protein electrophoresis of the allozyme products of 21 gene loci to examine the genetic structure and relationships of the three species of the *Macrhybopsis aestivalis* complex in the Arkansas and Red river basins. The monophyly of both *M. australis*, an endemic of the Red River Basin, and *M. tetranema*, an endemic of the Arkansas River Basin, was supported, although weakly because of a high level of genetic similarity between these two species and *M. hyostoma*. Across all samples, only 14% of total diversity was attributable to differences among species. Within the Arkansas and Red river basins separately, only 2% and 5%, respectively, of total diversity was attributable to differences between the endemic species and *M. hyostoma*. Monophyly of the endemic species and the small, but statistically significant genetic diversity explained by the taxonomy are consistent with allopatric speciation and secondary contact between *M. hyostoma* and each of the two regionally endemic species. There was little evidence of geographic partitioning of genetic variation within either *M. australis* or *M. tetranema*.

Introduction

In this study I used protein electrophoresis to examine genetic variation of the speckled chub complex in the Arkansas and Red river basins. Until recently, the complex was treated as a single, wide-ranging, morphologically plastic species, *Macrhybopsis aestivalis*. It had been suggested, however, that the complex may include more than one species (Miller and Robison, 1973; Page and Burr, 1991). Correspondingly, a recent morphological analysis of populations from the Mississippi River Drainage westward to the Rio Grande Drainage recognized five species in the complex (Eisenhour, 1999). The

species of primary concern in this study are *M. tetranema* and *M. australis*, which are endemics of, respectively, the Arkansas and Red river basins, and the wide-ranging *M. hyostoma*, which occurs in both of those basins, in other parts of the Mississippi River drainage, and south and west into the Sabine and Brazos rivers of Texas.

Members of the speckled chub complex in the Red and Arkansas river basins are in decline. In the Arkansas River Basin, the ranges of *M. hyostoma* and the endemic species, *M. tetranema*, have declined by about 55% and 90%, respectively (Luttrell et al., 1999). *Macrhybopsis tetranema* now is restricted to two small, widely disjunct areas, the Ninnescah and lower Arkansas rivers in Kansas and the South Canadian River between Ute Reservoir in New Mexico and Meredith Reservoir in the Texas Panhandle. The status of the two species in the Red River Basin is not well understood. Winston et al. (1991) reported extirpation of *M. australis* in the North Fork of the Red River following completion of Lake Altus. Species of the speckled chub complex are small, flood-spawning minnows (Bottrell, 1962). Decline of species with this type of life history often is attributable to effects of dam construction and surface-water diversion for irrigation (Cross and Moss, 1987; Winston et al., 1991; Luttrell et al., 1999).

In both the Red and Arkansas rivers, the wideranging form, *M. hyostoma*, is morphologically intermediate between the endemic species and the *M. hyostoma* morphotype seen in other basins (Eisenhour, 1997, 1999). This might be explained as a result of genetic introgression resulting from past or ongoing hybridization, or it might represent non-genetic (ecophenotypic) or genetic (ecotypic) morphological convergence in the absence of genetic introgression. My purpose was to use genetic data to evaluate these hypotheses. Specifically, I asked the following questions: 1) Does the pattern of

geographic variation indicate genetic introgression? 2) Is there evidence of genetic isolation in areas of contact between endemic species and *M. hyostoma*? 3) And lastly, do the various species represent separate, monophyletic groups as expected if they have had separate evolutionary histories?

Materials and Methods

Samples of all five western species of the speckled chub complex (Eisenhour, 1997) were taken from 28 sites (Fig. 1, Appendix A) distributed as follows (parentheses = site numbers in Fig. 1): *M. tetranema* from the Ninnescah (7) and South Canadian (14 and 15) rivers in the Arkansas River Basin, *M. australis* from the upper Red River Basin (17-21, 22b), and *M. hyostoma* from the Arkansas (8-13) and Red (16, 22a, 23) river basins and from widely separated localities outside those basins (1-3, 4a, 5-6, 24-26). For insight into the phylogeny of populations in the Arkansas and Red river basins, I also examined one sample of each of the two remaining western species of the speckled chub complex (Eisenhour, 1997): *M. aestivalis* from the Pecos River (28) and *M. marconis* from the San Marcos River (27). *Macrhybopsis gelida* (4b) was used as an outgroup for the phylogenetic analysis; this species is either sister to the speckled chub complex (Coburn and Cavender, 1992) or is one of two species forming the sister clade to the complex (Dimmick, 1993). The samples (n = 10-35) were collected by seining, frozen immediately in liquid nitrogen or on dry ice, transported to the laboratory, and stored at -76 C. From each fish, a sample of epaxial muscle and a mixture of eye and brain were homogenized separately in distilled water, centrifuged (4000 X gravity) for 15 sec, and stored at -76 C prior to protein electrophoresis. Standard methods of starch-gel protein

electrophoresis (Murphy et al., 1996) were used to examine 21 presumptive gene loci (Table 1). Alleles were designated with numbers reflecting percentage mobility relative to that of the most common allele, which was assigned a value of 100.

I used BIOSYS-1 (Swofford and Selander, 1981) to obtain average heterozygosity per individual per locus (H, estimated from allele frequencies for each sample), within-sample polymorphism (P = proportion of loci with > 1 allele), tests of conformance to Hardy-Weinberg expectations for genotypic frequencies (exact significance test with Levene's [1949] correction for small sample size), and heterogeneity in allele frequencies across samples. Total genetic diversity (H_T) was computed from the sum of total limiting variance across all loci divided by the number of loci. To visualize overall genetic divergence among samples, I used a principal components analysis (PCA) of the variance/covariance matrix of arcsine-transformed allele frequencies. I used Arlequin 1.1 (Schneider et al., 1997) to perform an analysis of linkage disequilibrium at the one site (22) where *M. hyostoma* occurred in sympatry with one of the two endemic species and to perform hierarchical analyses (AMOVA) of the distribution of genic diversity in the Red and Arkansas river basins. Significance of the variance components in the AMOVA were obtained by the non-parametric permutation method described by Excoffier et al. (1992).

I used the allele frequency parsimony approach (FREQPARS; Swofford and Berlocher, 1987) for phylogenetic analysis. As recommended by Berlocher and Swofford (1997), the BIOSYS-1 datafile was converted to the format for FREQPARS and imported into PAUP* 4.04a; (D. Swofford, 2000). PAUP produced a matrix of pairwise Manhattan distances (MANOB metric) and the associated distance-based stepmatrix. This stepmatrix was then subjected to the heuristic search, generalized parsimony algorithm in PAUP, with

M. gelida as the outgroup. I saved the 30 shortest trees derived with the simple-addition-sequence option and used FREQPARS to test each one for allele frequency parsimony. In these tests, tree length is the sum of branch lengths expressed in units of a Manhattan distance metric (MANAD) similar to MANOB, but constrained such that allele frequencies of hypothetical ancestors sum to 1.0. All 29 samples were kept in the analysis of relationships with PAUP. Because of limitations imposed by the FREQPARS program, the number of samples was reduced to 20 in the tests of the 30 shortest PAUP trees. For these tests, I eliminated the outgroup, *M. gelida*, and the relatively small samples of *M. hyostoma* from the Des Moines River ($n = 12$) and the Angelina River ($n = 15$), and, based on geographic proximity and the strict consensus of the 30 shortest trees from PAUP, I combined several sets of two to four samples into single samples. The designated outgroup for the FREQPARS test was *M. marconis*, the basal member of the ingroup in the 30 shortest trees from PAUP.

Results

Two or more alleles occurred at 18 of the 21 loci examined (Table 1; Appendix B). One polymorphic locus (CBP-B) was eliminated from the analysis because it was difficult to score consistently. This locus is of interest, however, because all samples from the Red River Basin (both *M. australis* and *M. hyostoma*) had, at moderately high frequencies (>0.50), an allele (CBP-B ^{65}) that appeared absent elsewhere. None of the 291 chi-square tests indicated significant deviations from Hardy-Weinberg expectation after the Bonferroni correction for a Type I error rate of 0.05.

Genetic variability was highest in *M. australis* ($H = 0.13$; $P = 0.76$) and *M.*

hyostoma ($H = 0.14$; $P = 0.86$) from an area where both species were taken together (site 22). High levels of variability also occurred in all other samples of *M. australis* and *M. hyostoma* from the Red River Basin ($H = 0.11$ to 0.13; $P = 0.33$ to 0.57), and in samples of *M. hyostoma* from drainages south of the Red River: the Sabine, Angelina, and Brazos rivers in Texas ($H = 0.09$ to 0.11; $P = 0.33$ to 0.48). Samples from other areas generally had lower variability. In *M. tetranema*, variability was highest in the samples from the Ninnescah River ($H = 0.08$; $P = 0.43$) and the South Canadian River in New Mexico ($H = 0.07$; $P = 0.43$) and was somewhat lower in the sample from the South Canadian River in the Texas Panhandle ($H = 0.05$; $P = 0.38$). Genetic variability in samples of *M. hyostoma* from the Arkansas River Basin ($H = 0.07$ to 0.08; $P = 0.33$ to 0.48) was similar to that in samples from the upper Mississippi River System ($H = 0.07$ to 0.11; $P = 0.33$ to 0.67). Variability was lowest in *M. aestivalis* from the Pecos River ($H = 0.04$; $P = 0.24$) and *M. marconis* from the San Marcos River ($H = 0.06$; $P = 0.24$).

There were no fixed or nearly fixed allele frequency differences among samples of *M. hyostoma*, *M. tetranema*, and *M. australis*, but such differences did occur in comparisons of these three with the other two members of the speckled chub complex, *M. aestivalis* and *M. marconis*, and the outgroup, *M. gelida*. *Macrhybopsis aestivalis* had a high frequency (0.98) of an allele, PGD-A^{83}, which was shared at low frequency (≤ 0.08) with other populations and *M. marconis* was fixed for a unique allele, LDH-B^{640}. In addition, *M. marconis* was fixed for m-IDH-A^{97}, which otherwise occurred only at a frequency of ≤ 0.025 in two other samples (Appendix A). *Macrhybopsis gelida* was fixed for a unique allele at LDH-B^{579}. At two other loci, *M. gelida* was fixed for alleles that were extremely rare among the ingroup species: s-IDH-A^{125}, which occurred only in two

other samples (frequency ≤0.03) and s-MDH-A^{87} , which occurred only in one other sample (frequency = 0.05).

The samples of *M. gelida, M. aestivalis, M. marconis*, and *M. hyostoma* from the Brazos River were omitted from the PCA analysis of allele frequencies because these samples were so divergent that plots of sample scores provided no resolution of pattern among the remaining samples. PCA I and II for the reduced dataset explained, respectively, 14.9% and 9.9% of the variance in allele frequencies among samples. The plot of sample scores on these axes grouped samples from the Red and Arkansas river basins according to basin of occurrence rather than according to species membership (Fig. 2). Thus, *M. hyostoma* from the Red and Arkansas river basins grouped with, respectively, *M. australis* and *M. tetranema*, the endemic species in those basins.

In the phylogenetic analysis, samples of the speckled chub complex from the Arkansas and Red river basins formed two separate clades, and, as in the PCA analysis, the samples grouped by river basin, rather than by species (Fig. 3). In both of these clades, samples of *M. hyostoma* formed a basal group that was paraphyletic with respect to a terminal clade containing the endemic species (*M. tetranema* in the Arkansas River; *M. australis* in the Red River). The FREQPARS output indicated that no unique alleles occurred as synapomorphies for the clade comprising the samples from the Red and Arkansas river basins. The Red River clade had four synapomorphic alleles (Ldh-A^{77} s-Mdh-A^{110}, Mpi-A^{93}, Pgm-A^{104}, and Pgm-A^{76} at frequencies of, respectively, 0.020 - 0.250, 0.000 - 0.036, 0.000 - 0.225, 0.007 - 0.050, 0.025 - 0.036) and the Arkansas River clade had two (s-Idh-A^{86} and Pep-A^{73}; at frequencies of 0.021 - 0.026 and 0.010 - 0.040).

The hierarchical analysis of genic diversity across all samples from the Arkansas

and Red river basins indicated that 82.2% of the total diversity was contained within the average sample (Table 2). Only 17.9% was associated with differences among samples; 13.7% reflected differences among the three species and 4.2% reflected differences among samples within species. Excluding Arkansas and Red river populations of *M. hyostoma* from the analysis produced a slight increase in total diversity. Correspondingly, the among-species component increased slightly (15.0%), and the portion attributable to differences among samples within species declined to 1.3%.

In both basins, most of the genic diversity, 93.3% and 97.0% in, respectively, the Red and Arkansas river basins was attributable to within-sample variation. For the samples of *M. tetranema* and *M. hyostoma* from the Arkansas River Basin, a small (2.2%) but statistically significant portion of the diversity reflected differences between species and 0.8% was attributable to differences among samples within species. The corresponding numbers for the samples of *M. australis* and *M. hyostoma* in the Red River Basin were 4.7% and 2.1%.

After the within-species Bonferroni correction, neither *M. tetranema* nor *M. australis* showed significant geographic variation in allele frequencies at individual loci. On average, 98.9% of total genic diversity in *M. tetranema* occurred within a single sample; only 1.1% was attributable to differences among samples. The corresponding values for *M. australis* were 99.4% and 0.6%.

For the one site of syntopy between sympatric forms (*M. hyostoma* n = 20 and *M. australis* n = 19), locus-by-locus tests of Hardy-Weinberg expectations in the combined sample revealed no significant deviations and there was no evidence of linkage disequilibrium ($\chi^2 = 8.7$; P = 1.0).

In agreement with Eisenhour's (1997) morphological analysis, *M. hyostoma* from the Brazos River in Texas is allozymically the most divergent member of its species. The population appears basal to the clade comprising *M. hyostoma*, *M. australis*, and *M. tetranema* (Fig. 3). Also in agreement with Eisenhour's (1997) results, *M. aestivalis* and *M. marconis* appear phylogenetically distinct from other members of the speckled chub complex.

Discussion

The results from allozyme variation are consistent with the hypothesis that genetic introgression explains Eisenhour's (1997, 1999) conclusion that the morphotype of *M. hyostoma* in the Red and Arkansas river basins converges toward that of, respectively, *M. australis* and *M. tetranema*. Whereas Eisenhour (1997, 1999) found greater morphological intergradation in *M. hyostoma* from more upstream areas of the two basins, my results indicate that genetic introgression involving genes encoding allozymes may have occurred throughout the distribution of both species in each basin. This would explain the extremely low levels of genetic divergence among the three species and the near absence of allozymically detectable genetic divergence among samples of the species pairs in the two basins. The hierarchical analyses did, however, demonstrate small, but statistically significant divergence attributable to differences among species.

There were limited opportunities to examine the question of whether *M. hyostoma* is genetically isolated from the other two species. Instances of co-occurrence in my samples occurred only between *M. hyostoma* and *M. australis* at locality 23 in the Red River. Combining these into a single sample revealed no evidence of the heterozygote

deficiency (Wahlund effect) expected in combined samples of two reproductively isolated species. This suggests that either reproductive isolation is very weak or that, as a result of genetic introgression, the Red River populations of these two species are so similar in allele frequencies that larger sample sizes would be required to demonstrate the Wahlund effect.

Extremely high levels of genetic similarity typical of those seen among samples of the same population have been reported in other instances of morphologically well-defined fish species occurring in sympatry. Phelps and Allendorf (1983) found two morphologically distinct species of sturgeon (*Scaphirhynchus platorhynchus* and *S. albus*) to be fixed for identical alleles at 34 allozyme-encoding loci and the two species were indistinguishable in allele frequencies at three other allozyme-encoding loci. Similar results were obtained for a group of four syntopic species of pupfishes (*Cyprinodon*) in Lake Chichancanab, Mexico (Humphries, 1984). Thus, we cannot discount the conclusion from morphology that the speckled chub complex in the Red and Arkansas river basins is divisible into three species. Indeed, the phylogenetic analysis of allozyme variation supported, albeit rather weakly, the monophyly of the endemic species, *M. australis* and *M. tetranema*, indicating they may retain remnants of past allozyme divergence from *M. hyostoma*.

One other point bears on the question of how many species are represented by the three morphotypes in the Red and Arkansas basins. The morphotypes representing *M. tetranema* and *M. hyostoma* once occurred sympatrically in the Cimarron River, where the former was much more common and widespread than the latter (Eisenhour, 1999). By the late 1970s, both forms had been extirpated from the basin, possibly because of drought

(Luttrell et al., 1999). Subsequently, and despite heavy collecting efforts, neither species was collected from the Cimarron River Basin until 1992 when *M. hyostoma* was taken from a downstream locality as a result of either human transport or natural dispersal from the Arkansas Rivers arm of Keystone Reservoir, an intervening area of poor speckled chub habitat (Luttrell et al., 1999). By 1997, *M. hyostoma* had spread approximately 200 km upstream, but the *M. tetranema* morphotype had not reappeared (Luttrell et al., 1999). This suggests that the morphotypes are different species and not ecophenotypes of the same population, unless the stream environment has changed such that one ecophenotype is no longer expressed.

The tendency for Red and Arkansas river populations of *M. hyostoma* to cluster with, respectively, *M. australis* and *M. tetranema*, is explainable as a result of evolution in geographic isolation followed by secondary contact and genetic introgression. Eisenhour's (1997) phylogenetic analysis of morphology indicated a sister relationship between *M. tetranema* and *M. australis* and he suggested that they evolved from a common ancestor in a south-flowing stream in western Kansas and Oklahoma that may or may not have been part of Metcalf's (1966) Ancestral Plains Stream. By Early Pleistocene this stream extended southward from the Dakotas and may have emptied into the Gulf of Mexico independently of the Mississippi River (Cross et al., 1986). Divergence of *M. tetranema* and *M. australis* might have begun during Mid-Pleistocene when the headward eroding Arkansas River breached the Ozark-Ouachita Highlands area and captured a large part of the Ancestral Plains Stream, forming the upper Arkansas River Basin (Eisenhour, 1997). Contact and resultant introgressive hybridization with *M. hyostoma* presumably occurred as a result of dispersal of that species from elsewhere in the Ancestral Plains

Steam system, and this might have occurred either before or after the geologic event separating populations in the Arkansas and Red river basins (Eisenhour, 1997).

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Table 1. Protein designations, presumptive loci, tissues and buffer systems used to assay genetic variation in the speckled chub complex. Locus abbreviations follow Buth (1984); protein names and numbers follow International Union of Biochemistry (1992).

Protein (EC number)	Locus	Tissue	Analytical system [1]
Adenylate kinase (EC 2.7.4.3)	Ak-A	Muscle	TC-III
Calcium binding protein (non-specific)	Cbp-1	Muscle	TC-8
Creatine kinase (EC 2.7.3.2)	Ck-A	Eye-Brain	TC-III
	Ck-B	Muscle	TC-III
Glyceraldehyde-3-phosphate dehydrogenase (EC 1.2.1.12)	Gapdh-A	Eye-Brain	TC-III
	Gapdh-B	Muscle	TC-III
Glucose-6-phosphate isomerase (EC 5.3.1.9)	Gpi-A	Muscle	TC-6
	Gpi-B	Muscle	LiOH,TC-6
Isocitrate dehydrogenase (EC 1.1.1.42)	m-Idh-A	Eye-Brain	TC-8
	s-Idh-A	Eye-Brain	TC-8
L-Lactate dehydrogenase (EC 1.1.1.27)	Ldh-A	Eye-Brain	T-EDTA
	Ldh-B	Eye-Brain	T-EDTA
Malate dehydrogenase (EC 1.1.1.37)	s-Mdh-A	Muscle	TC-8
	s-Mdh-B	Muscle	TC-8
	m-Mdh-A	Muscle	TC-8
Malate dehydrogenase (NADP+) (EC 1.1.1.40)	m-Mdhp-A	Eye-Brain	TC-8
Manose-6-phosphate isomerase (EC 5.3.1.8)	Mpi-A	Muscle	T-EDTA
Peptidase-A (EC 3.4.-.-)	Pep-A	Muscle	TC-8
Peptidase-B (EC 3.4.-.-)	Pep-B	Eye-Brain	T-EDTA
Phosphogluconate dehydrogenase (EC 1.1.1.44)	Pgd-A	Muscle	TC-III
Phosphoglucomutase (EC 2.7.5.1)	Pgm-A	Muscle	TC-8

[1] Analytical systems are as follows: TC-III: Stock solution = 0.75 M Tris-hydroxymethylaminomethane (= "Tris"), 0.25 M citric acid, pH 7.0; anodal electrode

buffer = 1 volume stock, 6 volumes water; cathodal electrode buffer = 1 volume stock, 4 volumes water; gel buffer: 1 volume stock, 19 volumes water. TC-6: electrode buffer and stock solution = 0.223 M Tris, 0.86 M citric acid, pH 6.0; gel buffer = 1 volume stock, 28 volumes water. LiOH: Stock solution A = 0.19 M boric acid,0.03 lithium hydroxide, pH 8.1. Stock solution B = 0.05 M Tris, 0.008 M citric acid, pH 8.4. Electrode solution = undiluted stock solution A; gel buffer = 1 volume stock solution A, 9 volumes stock solution B, pH 8.3. TC-8: electrode buffer and stock solution = 0.69 M Tris, 0.16 M citric acid, pH 8.0; gel buffer = 1 volume stock, 28 volumes water. T-EDTA: Stock solution = 0.90 M Tris, 0.50 M boric acid, 0.1 M disodium EDTA, pH 8.6; electrode solution = 1 volume stock, 6.9 volumes water; gel buffer = 1 volume stock, 24 volumes water. All pH adjustments were made with 10 N NaOH.

Table 2. Hierarchical analyses of genic diversity in speckled chubs of the Red and Arkansas river basins. Asterisks signify significance of the associated variance component at the 0.05 level.

		Percentage attributable to:		
Analysis	H_T	Within sample variation	Differences among samples within species	Differences among species
1. Both basins (all three species)	0.108	82.2	4.2*	13.7*
2. Both basins (*M. hyostoma* excluded)	0.112	83.7	1.3*	15.0*
3. Arkansas River Basin (*M. tetranema* and *M. hyostoma*)	0.127	97.0	0.8*	2.2*
4. Red River Basin (*M. australis* and *M. hyostoma*)	0.118	93.3	2.1*	4.7*
5. *M. tetranema*	0.108	98.9	1.1	--
6. *M. australis*	0.112	99.4	0.6	--

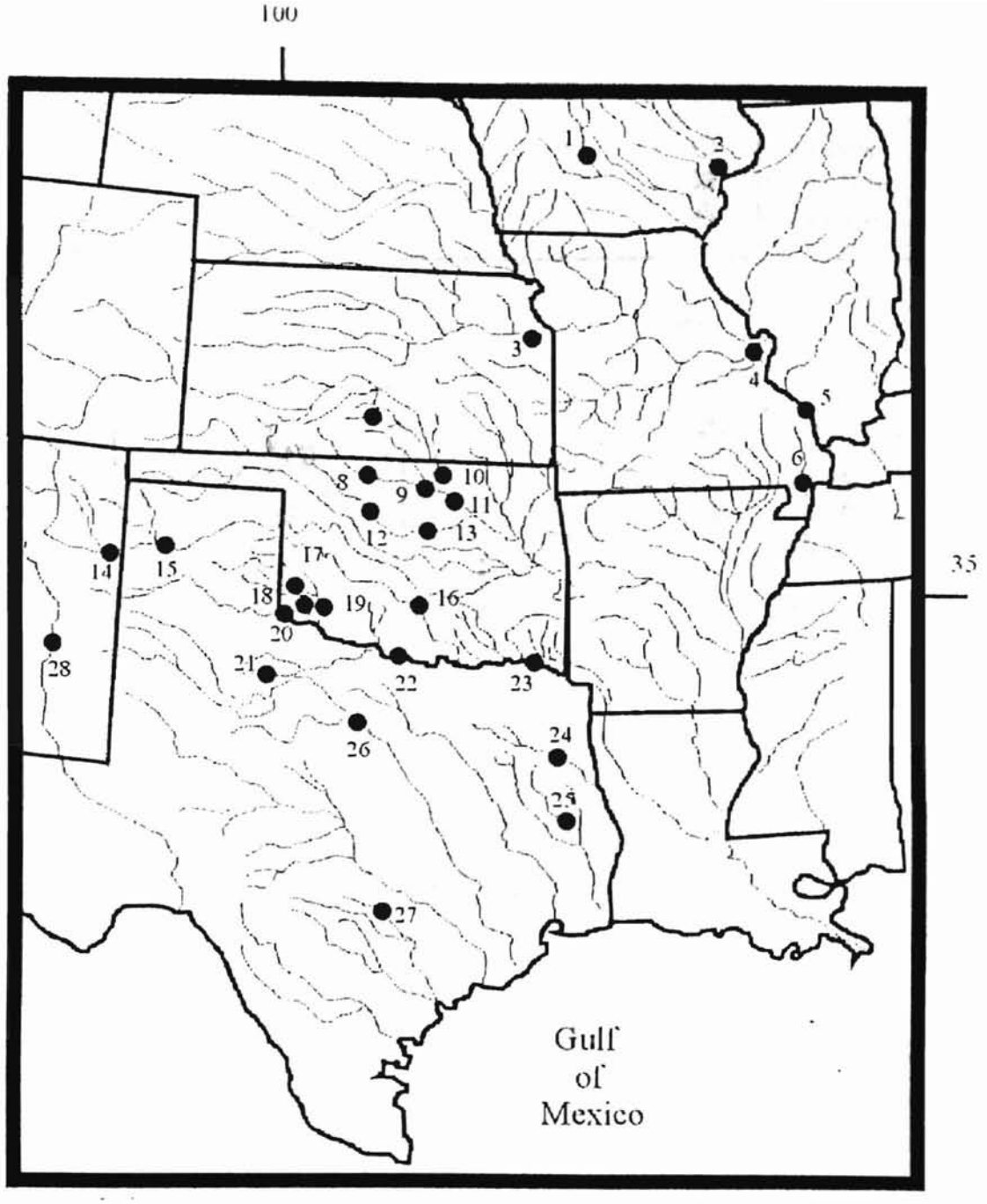

Figure 1 Sample sites for collections used in the genetic analysis of the speckled chub complex. Collection numbers correspond to those in appendix A.

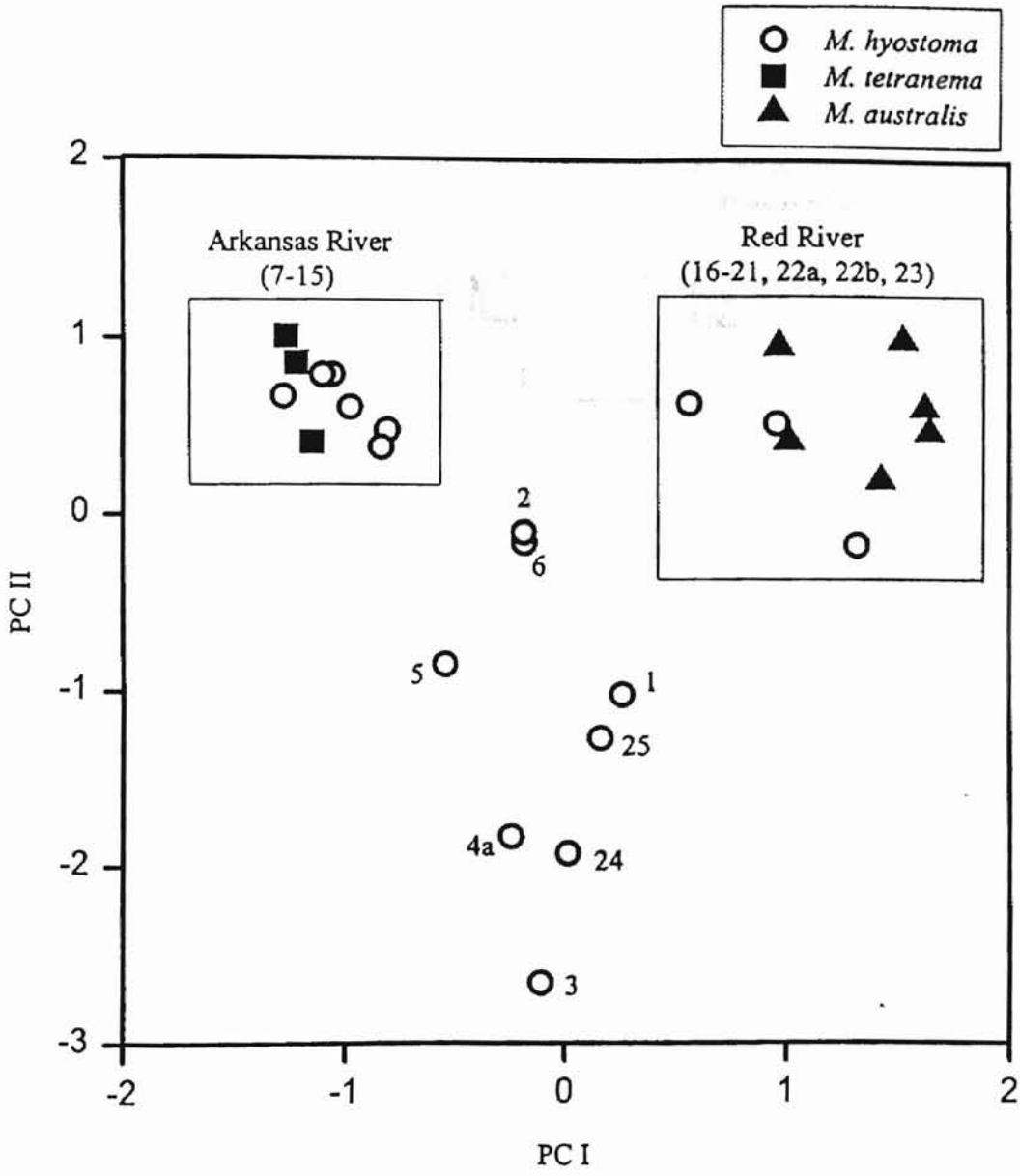

Figure 2. Principal components analysis of allele frequency variation. Numbers correspond with those in Figure 1.

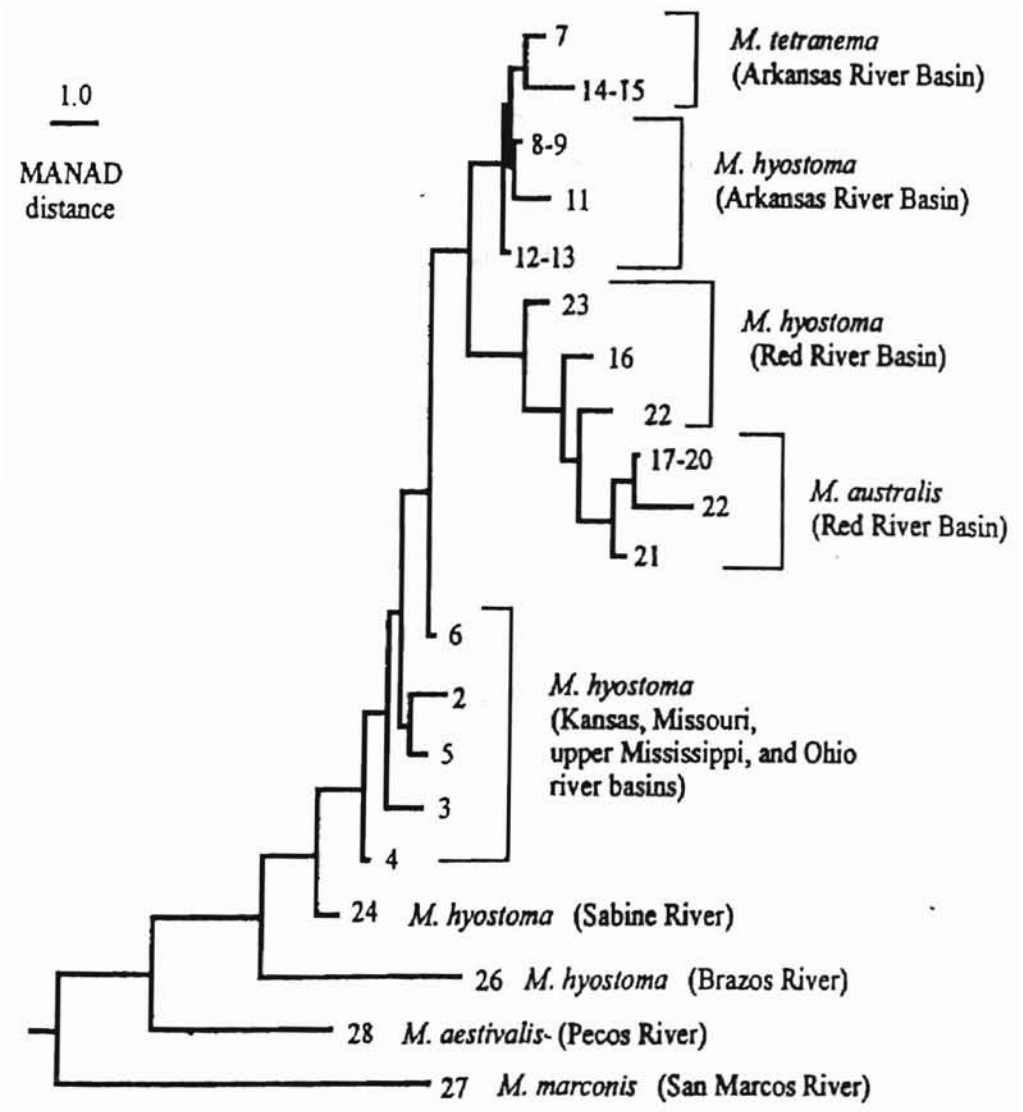

Figure 3. The shortest FREQPARS tree for members of the speckled chub complex. The outgroup was *M. marconis*, the basal member of the ingroup in the 30 shortest PAUP trees.

Appendix A. Museum voucher numbers, locality data and collection dates for samples used in the genetic analysis. Sample numbers correspond to site numbers in Figure 1.

Species	Site number	Voucher numbers, locality and collection date
M. hyostoma	1	(SIUC 26568) IA: Boone County. Des Moines River at lowhead dam, 0.3 km W of Fraser. 30 June 1996.
	2	(SIUC 26581) IA: Muscatine County. Cedar River at state highway 22 bridge. 30 July 1996.
	3	(KU 24655) KS: Douglas County. Kansas River in Lawrence at lowhead dam. 6 October 1995.
	4	(OSUS 27518) MO: St. Charles County. Missouri River at upstream end of Cora Island. 26 May 1997.
	5	(SIUC 27519) MO: Scott County. Mississippi River at Gray's Point, 1.1 km N of Thebes. 7 June 1997.
	6	(SIUC 24448) MO: New Madrid County. Ditch #290 at State Highway B crossing, 1.8 km S of Tallapoosa. 10 June 1995.
	8	(OSUS 27504) OK: Grant County. Salt Fork of the Arkansas River, N of Salt Fork at State Highway 74 bridge. 16 October 1995.
	9	(OSUS 27505) OK: Kay County. Salt Fork of the Arkansas River at the mouth of the Chikaskia River. October 1995
	10	(OSUS 27511) OK: Osage County. Arkansas River at Kaw Dam. 12 May 1998.
	11	(OSUS 27512) OK: Osage County. Arkansas River at State Highway 20 bridge, at Ralston. 15 October 1997.
	12	(OSUS 27506) OK: Major County. Cimarron River 2.4 km W and 1.2 km S of Ames. 17 October 1995.
	13	(OSUS 27507) OK: Logan County. Cimarron River at State Highway 77 bridge, north of Guthrie. October 1995
	16	(OSUS 27513) OK: Garvin County. Washita River at State Highway 29 bridge. 27 June 1998.
	22a	(SIUC 26042) TX: Clay County. Red River at State Highway 79 bridge, 4.2 km NE of Byers. 29 June 1996.

Species	Site number	Voucher numbers, locality and collection date
M. hyostoma	23	(SIUC 24664) OK: McCurtain County. Red River at U.S. Highway 259 bridge. 30 June 1996.
	24	(SIUC 26485) TX: Panola County. Sabine River at Watt Shoals on unnamed road opposite county road 291, 6.0 km NNE of Carthage. 26 June 1996.
	25	(SIUC 26035) TX: Nacodoches County. Angelina River at State Highway 7 bridge. 26 June 1996.
	26	(SIUC 26469) TX: Young County. Brazos River at State Highway 7 bridge, 4.8 km S of Graham. 29 June 1996.
M.tetranema	7	(OSUS 27508) KS: Kingman County. Ninnescah River at Kingman city park. 26 October 1995.
	14	(OSUS 27509) NM: Quay County. South Canadian River 3.2 km E of Logan. 1 September 1996.
	15	(OSUS 27510) TX: Oldham County. South Canadian River at State Highway 385 bridge, S of Boy's Ranch. 1-2 September 1996.
M. australis	17	(OSUS 27514) OK: Greer County. Elm Fork of the Red River at State Highway 34 bridge. 14 July 1997.
	18	(OSUS 27522) OK: Greer County. Salt Fork of the Red River at State Highway 34 bridge. 14 July 1997.
	19	(OSUS 27515) OK: Jackson County. North Fork of the Red River at State Highway 62 bridge. 2 August 1997.
	20	(OSUS 27516) OK: Jackson County. Prairie Dog Town Fork of the Red River at State Highway 6 bridge, SW of El Dorado. 2 August 1997
	21	(OSUS 27517) TX: Knox County. South Fork of the Wichita River, 2.4 km N of Vera. 15 June 1998
	22b	(OSUS 27523) TX: Clay County. Red River at State Highway 79 bridge, 4.2 km NE of Byers. 29 June 1996.
M. aestivalis	28	(OSUS 27521) NM: Chaves County. Pecos River at Sallie Ranch. T11S, R25E,S36. 28 October 1997.

Species	Site number	Voucher numbers, locality and collection date
M. marconis	27	(SIUC 26492) TX: Caldwell County. San Marcos River at U.S. 90 bridge, SW of Luling. 27 June 1996.
M. gelida	4b	(OSUS 27520) MO: St. Charles County. Missouri River at upstream end of Cora Island. 26 May 1997.

Appendix B. Genotypic frequencies, polymorphism (*P*), and heterozygosity (*H*) at 18 polymorphic loci across 29 populations of the *Macrhybopsis aestivalis* complex and one population of *M. gelida*. Collection numbers correspond with those in Appendix A.

Locus	*M. hyostoma*			
	1	2	3	4
Ak-A	100:100(12)	100:100(20) 100:67(1)	100:100(18)	100:100(19) 100:67(1)
Ck-A	100:100(12)	100:100(21)	100:100(18)	100:100(20)
Ck-B	100:100(12)	114:100(1) 100:100(20)	100:100(18)	100:100(20)
Gpi-A	100:100(12)	108:100(1) 108:89(1) 100:100(16) 100:89(3)	108:100(2) 100:100(15) 100:89(1)	108:108(1) 108:100(1) 105:100(1) 100:100(15) 100:89(2)
Gpi-B	114:-100(1) -100:-100(8) -100:-293(2) -293:-456(1)	114:114(1) 114:-100(3) -100:-100(11) -100:-293(6)	114:114(2) 114:-100(5) -100:-100(8) -100:-293(3)	114:114(1) 114:-100(3) -100:-100(16)
m-Idh-A	100:100(12)	100:100(20) 100:91(1)	111:100(1) 100:100(17)	100:100(20)

Locus	*M. hyostoma*			
	1	2	3	4
s-Idh-A	100:100(12)	100:100(21)	125:100(1) 100:100(17)	100:100(20)
Ldh-A	100:100(12)	100:100(21)	100:100(18)	100:100(20)
Ldh-B	558:558(4) 558:100(6) 100:100(2)	640:558(1) 558:558(8) 558:100(10) 100:100(2)	640:558(2) 558:558(8) 558:100(4) 100:100(4)	640:558(1) 558:558(10) 558:100(7) 100:100(2)
s-Mdh-A	100:100(12)	100:100(20) 100:93(1)	100:100(18)	100:100(20)
s-Mdh-B	100:100(12)	100:100(21)	123:100(1) 100:100(17)	100:100(20)
m-Mdh-A	100:100(12)	138:138(2) 138:100(5) 100:100(14)	138:100(1) 100:100(17)	138:100(1) 100:100(15) 100:62(3) 100:40(1)
m-Mdhp-A	100:100(12)	100:100(21)	100:100(17) 100:94(1)	100:100(20)

Locus	*M. hyostoma*			
	1	2	3	4
Mpi-A	100:100(12)	100:100(21)	100:100(18)	100:100(12)
Pep-A	109:109(5) 109:100(4) 100:100(2)	119:119(1) 119:100(3) 109:109(5) 109:100(8) 100:100(4)	109:109(1) 109:100(9) 100:100(8)	119:109(1) 109:109(1) 109:100(7) 100:100(11)
Pep-B	100:100(12)	100:100(21)	100:100(18)	100:100(20)
Pgd-A	100:100(12)	100:100(21)	100:100(18)	100:100(18) 100:92(1) 100:83(1)
Pgm-A	100:100(12)	100:100(21)	100:100(18)	100:100(20)
P	0.143	0.381	0.429	0.429
H	0.065	0.111	0.091	0.083

Locus	*M. hyostoma*				
	5	6	8	9	10
Ak-A	100:100(18) 100:67(1)	100:100(20)	100:100(24) 100:67(1)	138:100(1) 100:100(23) 100:67(1)	100:100(10)
Ck-A	100:100(19)	100:100(20)	100:100(25)	100:100(24)	100:100(7) 100:95(2) 100:65(1)
Ck-B	100:100(19)	100:100(20)	100:100(25)	100:100(25)	100:100(10)
Gpi-A	108:100(2) 100:100(16) 100:89(1)	100:100(19) 100:89(1)	108:100(1) 100:100(23) 100:78(1)	108:100(1) 108:93(1) 108:78(1) 100:100(20) 100:93(1) 100:78(1)	100:100(10)
Gpi-B	114:-100(5) -100:-100(7) -100:-293(6) -100:-456(1)	114:-100(1) -100:-100(14) -100:-293(3) -100:-456(1) -293:-293(1)	133:-100(9) 133:-293(1) 116:-100(1) 114:-100(1) -100:-100(12) -100:-293(1)	133:133(2) 133:-100(5) -100:-100(18)	133:-100(2) 114:-100(1) -100:-100(7)
m-Idh-A	100:100(19)	100:100(20)	100:100(24) 100:86(1)	100:100(24) 100:86(1)	100:100(10)
s-Idh-A	100:100(19)	100:100(20)	100:100(25)	100:100(25)	100:100(10)

Locus	*M. hyostoma*				
	5	6	8	9	10
Ldh-A	100:100(19)	100:100(20)	100:100(25)	100:100(25)	100:100(10)
Ldh-B	640:100(1) 558:558(10) 558:100(7) 100:100(1)	558:558(6) 558:100(11) 100:100(3)	558:558(1) 558:100(7) 100:100(17)	558:100(7) 100:100(18)	558:100(2) 100:100(8)
s-Mdh-A	100:100(19)	100:100(19) 100:84(1)	100:100(25)	100:100(25)	100:100(10)
s-Mdh-B	100:100(19)	100:100(20)	100:100(25)	100:100(25)	100:100(10)
m-Mdh-A	138:100(1) 100:100(16) 100:62(2)	100:100(20)	100:100(25)	138:100(2) 100:100(23)	100:100(10)
m-Mdhp-A	108:100(1) 100:100(18)	100:100(20)	100:100(25)	100:100(25)	108:100(1) 100:100(9)
Mpi-A	108:100(1) 100:100(18)	100:100(20)	100:100(25)	100:100(25)	108:100(2) 100:100(8)
Pep-A	109:109(4) 109:100(7) 100:100(7) 100:88(1)	109:109(7) 109:100(7) 100:100(6)	109:100(8) 109:88(1) 109:73(1) 100:100(13) 100:88(2)	109:109(1) 109:100(8) 109:88(1) 100:100(13) 100:88(1) 88:88(1)	119:100(1) 109:100(3) 100:100(5) 88:73(1)

Locus	*M. hyostoma*				
	5	6	8	9	10
Pep-B	100:100(19)	100:100(20)	100:100(25)	119:100(1) 100:100(24)	100:100(9) 100:90(1)
Pgd-A	100:100(19)	100:100(19) 100:92(1)	100:100(22) 100:92(2) 100:71(1)	100:100(22) 100:92(1)	100:100(10)
Pgm-A	100:100(19)	100:100(18) 100:88(2)	110:100(1) 100:100(23) 100:88(1)	100:100(23) 100:88(2)	100:100(10)
P	0.667	0.381	0.476	0.476	0.333
H	0.092	0.075	0.074	0.074	0.078

Locus	*M. hyostoma*				
	11	12	13	16	22a
Ak-A	100:100(19)	138:100(1) 100:100(23) 100:67(1)	138:100(1) 100:100(24)	100:100(20)	100:100(24) 100:67(1)
Ck-A	100:100(19)	100:100(25)	100:100(20)	100:100(19) 100:95(1)	100:100(23) 100:95(2)
Ck-B	100:100(19)	100:100(25)	100:100(25)	100:100(20)	100:100(25)
Gpi-A	108:100(2) 100:100(15) 100:78(2)	100:100(22) 100:93(2) 100:78(1)	108:100(5) 100:100(20)	108:100(3) 108:89(1) 100:100(16)	108:100(5) 108:89(1) 100:100(18) 100:89(1)
Gpi-B	133:133(1) 133:-100(4) 133:-293(1) -100:-100(12) -456:-456(1)	133:133(1) 133:-100(3) 114:-100(1) 114:-293(1) -100:-100(19)	133:-100(3) -100:-100(20) -100:-293(2)	114:-100(1) 114:-293(1) -100:-100(12) -100:-293(2) -100:-456(4)	114:114(1) 114:-100(6) -100:-100(14) -100:-93(3) -93:-93(1)
m-Idh-A	100:100(18) 100:86(1)	100:100(25)	100:100(25)	100:100(20)	111:100(1) 100:100(24)
s-Idh-A	100:100(19)	100:100(25)	100:100(25)	100:100(20)	125:100(1) 100:100(24)

Locus	*M. hyostoma*				
	11	12	13	16	22a
Ldh-A	100:100(19)	100:100(25)	100:100(25)	100:100(18) 100:77(2)	103:100(1) 100:100(23) 100:77(1)
Ldh-B	558:100(1) 100:100(18)	558:558(1) 558:100(8) 100:100(16)	558:100(10) 100:100(14) 100:50(1)	558:100(1) 100:100(19)	558:100(5) 100:100(20)
s-Mdh-A	100:100(19)	100:100(25)	100:100(24) 100:93(1)	100:100(20)	100:100(25)
s-Mdh-B	100:100(19)	115:100(2) 100:100(23)	100:100(25)	100:100(20)	115:100(1) 100:100(24)
m-Mdh-A	100:100(18) 100:62(1)	100:100(25)	138:100(1) 100:100(24)	100:100(20)	100:100(25)
m-Mdhp-A	100:100(19)	100:100(25)	108:100(1) 100:100(24)	100:100(20)	100:100(23) 100:94(2)
Mpi-A	108:100(1) 100:100(18)	108:100(4) 100:100(18)	100:100(25)	100:100(15) 100:93(4) 93:93(1)	100:100(18) 100:93(5) 93:93(2)
Pep-A	109:100(5) 109:88(2) 100:100(7) 100:88(4) 88:88(1)	109:109(1) 109:100(8) 109:88(1) 100:100(14) 100:88(1)	109:109(2) 109:100(6) 109:73(1) 100:100(16)	109:109(10) 109:100(6) 109:88(1) 100:100(3)	119:109(1) 109:109(9) 109:100(11) 100:100(4)

Locus	*M. hyostoma*				
	11	12	13	16	22a
Pep-B	119:100(1) 100:100(18)	100:100(25)	100:100(25)	100:100(16) 100:90(3) 90:90(1)	100:100(21) 100:90(4)
Pgd-A	100:100(15) 100:92(2) 100:83(2)	113:100(1) 100:100(22) 100:83(1)	100:100(21) 100:92(2) 100:83(2)	123:100(1) 100:100(16) 100:92(1) 100:83(2)	123:100(1) 100:100(24)
Pgm-A	100:100(19)	110:100(1) 100:100(24)	100:100(21) 100:88(4)	110:100(3) 100:100(9) 100:88(5) 88:88(1)	110:100(1) 110:88(1) 100:100(9) 100:88(10) 88:88(4)
P	0.429	0.429	0.476	0.476	0.857
H	0.079	0.076	0.075	0.115	0.137

Locus	*M. hyostoma*				*M. tetranema*
	23	24	25	26	7
Ak-A	100:100(20)	100:100(20)	100:100(15)	138:100(2) 100:100(15)	100:100(21)
Ck-A	100:100(18) 100:95(2)	100:100(20)	100:100(15)	100:100(16) 100:95(1)	100:100(19) 100:95(2)
Ck-B	100:100(20)	100:100(20)	100:100(15)	100:100(17)	100:100(21)
Gpi-A	108:100(2) 100:100(14) 100:93(2) 100:89(2)	113:89(1) 108:89(1) 100:100(15) 100:89(3)	108:100(1) 100:100(9) 100:96(1) 100:89(4)	108:108(14) 108:100(3)	100:100(19) 100:93(2)
Gpi-B	114:-100(2) -100:-100(14) -100:-293(1) -100:-456(3)	114:-100(2) -100:-100(18)	114:-100(4) -100:-100(11)	114:-100(2) -100:-100(13) -100:-293(2)	133:-100(3) 100:-293(1) 114:-100(1) -100:-100(13) -100:-293(2) -100:-456(1)
m-Idh-A	100:100(20)	111:100(1) 100:100(18) 100:97(1)	100:100(15)	100:100(17)	111:100(1) 100:100(20)
s-Idh-A	100:100(20)	100:100(20)	100:100(15)	100:100(17)	100:100(21)
Ldh-A	100:100(17) 100:77(3)	100:100(20)	100:100(15)	100:100(17)	100:100(21)

Locus	*M. hyostoma*				*M. tetranema*
	23	24	25	26	7
Ldh-B	558:558(1) 558:100(1) 100:100(18)	100:100(20)	558:558(15)	558:558(15) 558:100(2)	558:100(6) 100:100(15)
s-Mdh-A	100:100(20)	100:100(20)	100:100(15)	100:100(17)	100:100(21)
s-Mdh-B	100:100(20)	123:100(1) 100:100(18)	100:100(15)	100:100(17)	100:100(21)
m-Mdh-A	100:100(20)	138:100(1) 100:100(19)	100:100(15)	100:100(16) 100:25(1)	100:100(19) 100:73(1) 100:62(1)
m-Mdhp-A	108:100(1) 100:100(19)	100:100(20)	100:100(15)	100:100(17)	100:100(21)
Mpi-A	100:100(12) 100:93(7) 93:93(1)	108:100(3) 100:100(17)	108:108(1) 108:100(4) 100:100(10)	100:100(17)	108:100(2) 100:100(19)
Pep-A	119:100(1) 109:109(3) 109:100(10) 109:93(1) 100:100(5)	109:109(2) 109:100(6) 100:100(11) 100:88(1)	119:109(2) 109:109(1) 109:100(7) 109:88(1) 100:100(4)	119:109(1) 119:100(1) 109:109(12) 109:100(3)	109:109(1) 109:100(2) 109:88(1) 100:100(12) 100:88(5)
Pep-B	100:100(19) 100:90(1)	100:100(18) 100:90(1) 100:70(1)	100:100(14) 100:90(1)	100:100(13) 100:90(4)	100:100(21)

Locus	*M. hyostoma*				*M. tetranema*
	23	24	25	26	7
Pgd-A	100:100(20)	123:123(1) 123:100(2) 100:100(12) 100:92(1) 100:83(3)	123:100(4) 100:100(7) 100:83(2) 83:83(2)	113:113(2) 113:100(2) 113:71(1) 100:100(9) 100:71(3)	100:100(16) 100:83(4) 83:83(1)
Pgm-A	100:100(13) 100:88(7)	110:100(1) 100:100(17) 100:88(2)	110:100(1) 100:100(12) 100:88(2)	100:100(13) 100:88(4)	100:100(16) 100:88(8)
P	0.476	0.476	0.333	0.476	0.333
H	0.107	0.085	0.109	0.097	0.093

Locus	*M. tetranema*		*M. australis*		
	14	15	17	18	19
Ak-A	138:100(1) 100:100(24)	138:100(2) 100:100(23)	100:100(21)	100:100(10)	100:100(20)
Ck-A	100:100(25)	100:100(24)	100:100(21)	100:100(10)	100:100(20)
Ck-B	100:100(25)	100:100(25)	100:100(21)	100:100(10)	100:100(20)
Gpi-A	108:100(1) 100:100(23) 100:78(1)	100:100(22) 100:93(1) 100:78(2)	108:100(1) 105:100(1) 100:100(19)	100:100(10)	108:100(3) 100:100(15) 100:89(1) 100:78(1)
Gpi-B	114:-100(1) -100:-100(20) -100:-293(1) -100:-456(2) -456:-456(1)	-100:-100(25)	133:-100(1) 114:114(1) 114:-100(1) -100:-100(12) -100:-293(1) -100:-456(4) -293:-293(1)	114:-100(1) -100:-100(8) -100:-293(1)	-100:-100(17) -100:-293(2) -100:-456(1)
m-Idh-A	100:100(25)	100:100(25)	100:100(21)	100:100(10)	111:100(2) 100:100(17) 100:97(1)
s-Idh-A	100:100(25)	100:100(25)	100:100(21)	100:100(10)	100:100(20)
Ldh-A	100:100(25)	100:100(25)	100:100(17) 100:77(4)	100:100(5) 100:77(5)	100:100(14) 100:77(6)

Locus	*M. tetranema*		*M. australis*		
	14	15	17	18	19
Ldh-B	558:100(5) 100:100(20)	558:100(1) 100:100(24)	558:100(4) 100:100(17)	558:100(2) 100:100(8)	558:100(1) 100:100(19)
s-Mdh-A	100:100(25)	100:100(25)	100:100(20) 100:93(1)	100:100(10)	110:100(1) 100:100(19)
s-Mdh-B	115:100(1) 100:100(24)	100:100(25)	115:100(1) 100:100(20)	100:100(10)	100:100(20)
m-Mdh-A	100:100(25)	138:100(1) 100:100(24)	138:100(1) 100:100(19) 100:62(1)	100:100(10)	100:100(20)
m-Mdhp-A	108:100(1) 100:100(24)	100:100(25)	100:100(21)	100:100(10)	100:100(20)
Mpi-A	108:108(1) 108:100(4) 100:100(20)	108:100(3) 100:100(21)	100:100(18) 100:93(3)	100:100(5) 100:93(2)	100:100(15) 100:93(4) 93:93(1)
Pep-A	109:100(2) 100:100(15) 100:88(5) 100:73(2) 88:88(1)	109:100(1) 100:100(15) 100:88(7) 100:73(2)	119:109(1) 109:109(10) 109:100(8) 100:100(2)	109:109(6) 109:100(1) 100:100(3)	119:109(2) 109:109(8) 109:100(9) 100:100(1)
Pep-B	100:100(25)	119:100(1) 100:100(24)	100:100(19) 100:90(2)	100:100(10)	100:100(20)

Locus	*M. tetranema*		*M. australis*		
	14	15	17	18	19
Pgd-A	100:100(25)	100:100(25)	113:100(1) 100:100(20)	113:100(2) 100:100(7) 100:92(1)	100:100(18) 100:83(1) 83:83(1)
Pgm-A	110:100(5) 100:100(16) 100:88(4)	110:100(2) 110:88(1) 100:100(20) 100:88(2)	104:100(1) 100:100(6) 100:88(7) 88:88(7)	100:88(6) 88:88(4)	100:100(2) 100:88(8) 88:88(10)
P	0.429	0.381	0.571	0.333	0.476
H	0.072	0.048	0.112	0.107	0.105

Locus	*M. australis*			*M. aestivalis*	*M. marconis*	*M. gelida*
	20	21	22b	28	27	4b
Ak-A	100:100(20)	100:100(20)	100:100(11) 100:67(2)	100:100(24) 100:67(1)	100:100(34)	100:100(20)
CK-A	100:100(20)	100:100(20)	100:100(14)	100:100(25)	100:100(32) 100:90(2)	100:100(20)
CK-B	100:100(20)	100:100(20)	100:100(14)	88:88(25)	88:88(34)	88:88(19) 88:65(1)
Gpi-A	108:108(1) 108:100(4) 100:100(13) 100:89(1) 100:78(1)	108:100(1) 100:100(18) 100:89(1)	105:100(1) 100:100(9) 100:93(1) 100:89(2) 100:78(1)	100:100(25)	100:89(6) 89:89(28)	113:113(6) 113:100(9) 100:100(5)
Gpi-B	114:-100(3) -100:-100(11) -100:-293(1) -100:-456(4) -293:-456(1)	114:-100(1) -100:-100(16) -100:-456(2) -456:-456(1)	114:-100(1) 100:100(11) -100:-293(1) -100:-456(1)	114:-100(3) 114:-293(1) -100:-100(14) -100:-293(4) -100:-456(2) -293:-293(1)	114:114(22) 114:-100(10) -100:-100(1)	114:114(20)
m-Idh-A	100:100(20)	100:100(20)	100:100(14)	100:100(20) 100:91(5)	97:97(34)	111:111(4) 111:100(12) 100:100(4)
s-Idh-A	100:100(20)	100:100(20)	100:100(14)	100:100(25)	100:100(34)	125:125(20)

Locus	*M. australis*			*M. aestivalis*	*M. marconis*	*M. gelida*
	20	21	22b	28	27	4b
Ldh-A	100:100(12) 100:77(6) 77:77(2)	100:100(11) 100:77(8) 77:77(1)	100:100(8) 100:77(6)	100:100(25)	100:100(34)	100:100(20)
Ldh-B	558:100(2) 100:100(18)	558:100(1) 100:100(19)	558:558(1) 100:100(13)	558:558(25)	640:640(34)	579:579(20)
s-Mdh-A	100:100(20)	100:100(19) 100:84(1)	110:100(1) 100:100(13)	100:100(25)	100:100(34)	87:87(20)
s-Mdh-B	100:100(20)	100:100(20)	100:100(14)	100:100(25)	100:100(34)	100:100(20)
m-Mdh-A	100:100(20)	100:100(20)	138:100(1) 100:100(13)	100:100(25)	100:100(34)	62:62(20)
m-Mdhp-A	100:100(20)	100:100(20)	138:100(1) 100:100(13)	100:100(20)	100:100(34)	100:100(20)
Mpi-A	100:100(14) 100:93(4) 100:85(1) 93:93(1)	100:100(13) 100:93(3)	100:100(5)	100:100(25)	85:85(30)	108:100(1) 100:100(2) 100:90(5) 90:90(2)
Pep-A	119:100(1) 109:109(9) 109:100(7) 100:100(3)	119:109(1) 109:109(11) 109:100(5) 100:100(3)	119:109(1) 109:109(6) 109:100(5) 100:100(1)	109:109(25)	109:109(28) 109:100(5)	100:100(1) 100:88(13) 88:88(6)

Locus	*M. australis*			*M. aestivalis*	*M. marconis*	*M. gelida*
	20	21	22b	28	27	4b
Pep-B	100:100(20)	100:100(19) 100:90(1)	100:100(12) 100:90(2)	119:100(1) 100:100(24)	70:70(33)	100:100(20)
Pgd-A	123:100(1) 100:100(17) 100:92(1) 100:83(1)	100:100(19) 100:83(1)	100:100(12) 100:83(2)	92:83(1) 83:83(24)	123:123(8) 123:100(15) 100:100(10)	100:100(20)
Pgm-A	100:100(3) 100:88(12) 88:88(5)	110:104(1) 110:88(1) 104:88(1) 100:100(4) 100:88(8) 88:88(4) 100:76(1)	100:100(2) 100:88(4) 88:88(7) 88:76(1)	100:100(25)	100:100(34)	110:110(4) 110:100(13) 100:100(3)
P	0.381	0.476	0.762	0.238	0.238	0.286
H	0.129	0.103	0.125	0.035	0.056	0.126

VITA

David Mason Underwood

Candidate for the Degree of

Master of Science

Thesis: GENETIC STRUCTURE OF THE *MACRHYBOPSIS AESTIVALIS* COMPLEX (TELEOSTEI: CYPRINIDAE) WITH EMPHASIS ON POPULATIONS IN THE ARKANSAS AND RED RIVER BASINS

Major Field: Zoology

Biographical:

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Experience: Worked as a volunteer in the Oklahoma State University Collection of Vertebrates from May 1995 to present.
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