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Authors: Dowling, Thomas E., Tibbets, C. Alana, Minckley, W. L., and Smith, Gerald R.

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Evolutionary Relationships of the Plagopterin (Teleostei: Cyprinidae) from Cytochrome *b* Sequences

THOMAS E. DOWLING, C. ALANA TIBBETS, W. L. MINCKLEY, AND GERALD R. SMITH

Sequences of cytochrome *b* (*cytb*) were used to examine composition and phylogenetic relationships of cyprinid fishes of the tribe Plagopterini, endemic to the Great Basin and Lower Colorado River in southwestern North America. The plagopterin genera, *Lepidomeda*, *Meda*, *Plagopterus*, and *Snyderichthys*, were most closely affiliated with the chubs *Couesius* and *Margariscus* of northern and eastern North America. As indicated by previous morphologic, allozymic, and mtDNA studies, *Snyderichthys* is intimately related to *Lepidomeda*. The relationship is paraphyletic, however, according to our molecular data. *Snyderichthys* from the Snake and Bear River drainages are part of a clade that includes *Lepidomeda mollispinis* and *Lepidomeda albivallis* according to the *cytb* sequence, with *Snyderichthys* from the central and southern Bonneville basin more divergent. This paraphyly and the complex geographic relationships of mtDNA sequences indicate a complex history of the group and cast doubt on the validity of morphologically diagnosed *Snyderichthys*. Estimates of divergence time, based on a combination of fossil and molecular data, indicate that the plagopterins are an ancient clade, at least 17 million years old.

THE Cyprinidae or minnows are the most diverse freshwater fish family in North America, represented by more than 300 species in approximately 50 genera (Burr and Mayden, 1992). Although recent morphological studies provide hypotheses of relationships among genera, species groups, and species (Mayden, 1989; Cavender and Coburn, 1992; Coburn and Cavender, 1992), analysis of molecular characters sometimes produce conflicting results (e.g., Simons and Mayden, 1997, et seq.; Broughton and Gold, 2000) and a different perspective of evolutionary relationships.

The plagopterins are a monophyletic group of North American cyprinids diagnosed by spinelike ossification of the first two rays of the dorsal and pelvic fins. As defined by Miller and Hubbs (1960), the group consists of six species in three genera: *Lepidomeda vittata*, *Lepidomeda mollispinis*, *Lepidomeda albivallis*, and *Lepidomeda altivelis*, *Meda fulgida*, and *Plagopterus argentissimus*. These are (or were) endemic to the middle and lower Colorado River drainage. Relationships of this group to several other cyprinids of the region have been hypothesized, especially *Snyderichthys copei* (Miller, 1945) of the adjacent Bonneville basin and upper Snake River drainage. That species was placed in the monotypic genus *Snyderichthys* by Miller (1945) but considered a monotypic subgenus of the genus *Gila* by Uyeno (1960).

Coburn and Cavender (1992) completed an extensive analysis of phylogenetic relationships among North American cyprinids based on morphological and osteological characters.

They hypothesized existence of three major groups: “shiner,” “chub,” and “western” clades. Plagopterins fell within a *Gila* clade of western minnows, most closely related to a clade containing *Agosia*, *Moapa*, and *Rhinichthys*. As previously indicated by Uyeno (1960), *Gila copei* was considered distinct from the plagopterins.

Studies of molecular characters indicated different plagopterin relationships. DeMarais (1992) provided allozymic evidence that *G. copei* was closely affiliated with *Lepidomeda*, possibly rendering the plagopterins paraphyletic. Further taxonomic studies were deemed necessary to ensure proper phylogenetic placement of *G. copei*; however, its close affinities with *Lepidomeda* led DeMarais (1992) to recommend resurrection of *Snyderichthys*, a recommendation we follow.

Simons and Mayden (1997, et seq.) identified four major lineages (with sequences from 12S ribosomal DNA) that differed from those identified by Coburn and Cavender (1992). Both morphological and molecular data indicated a distinct western clade; however, there were major differences in composition and placement of taxa within the chubs and shiners. Creek chubs and relatives (*Couesius*, *Hemitremia*, *Margariscus*, *Semotilus*) were identified as a distinct lineage (“creek chub clade”) instead of being members of the chub clade as hypothesized by Coburn and Cavender (1992). Plagopterins (including *Snyderichthys*) were more closely related to this clade than to members of the genus *Gila*. Simons and Mayden (1997) included only two plagopterins (*L. vittata*, *M. fulgida*); therefore,

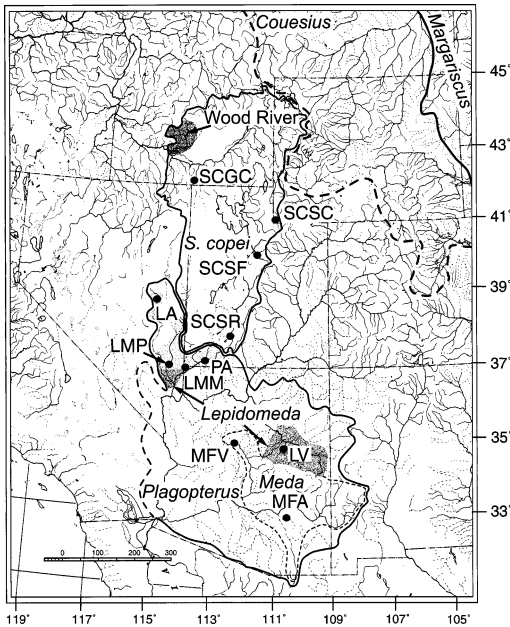


Fig. 1. Approximate distribution of species and samples (indicated by lines and shading). *Snyderichthys copei*, Goose Creek (SCGC), Sulphur Creek (SCSC), Spanish Fork River (SCSF), Sevier River (SCSR); *Lepidomeda albivallis* (LA), *Lepidomeda mollispinus mollispinus* (LMM), *Lepidomeda mollispinus pratensis* (LMP); *Lepidomeda vittata* (LV); *Plagopterus argentissimus* (PA); *Meda fulgida*, Verde River (MFV), Aravaipa Creek (MFA). The southwest range limits of the sister groups, *Couesius plumbeus* and *Margariscus margarita*, are shown in the upper right.

relationships within the group and effects of taxonomic sampling on placement of *Snyderichthys* could not be examined.

We use sequences from the cytochrome *b* (*cytb*) gene from all extant plagopterins to examine relationships among members of this group and to test the hypothesized placement of these fishes relative to other cyprinids [as proposed by Coburn and Cavender (1992) and Simons and Mayden (1997)]. Given the unique morphology and geography of these fishes, knowledge of their phylogenetic relationships to other minnow lineages provides important information for the evolution of morphological characters and the biogeography of several major drainages in western North America.

MATERIALS AND METHODS

Samples.—Most plagopterin taxa now occupy limited ranges (Fig. 1) in the lower Colorado River system. *Lepidomeda albivallis* and *Lepidomeda mollispinus mollispinus* are restricted to single localities and *L. m. mollispinus*, *L. vittata*, and *Pla-*

gopterus argentissimus are found only in single drainages. Previous studies of variation in *L. vittata* indicated limited divergence among localities (Tibbets, 1998; Tibbets et al., 2001); therefore, single individuals of *Lepidomeda mollispinus mollispinus*, *L. vittata*, and *Plagopterus argentissimus* were used to represent each. Previous studies of *Meda fulgida* (Anderson and Hendrickson, 1994; Tibbets and Dowling, 1996) identified divergent populations in the Gila and Verde Rivers; therefore each was represented. Because of the widespread distribution and potential paraphyly of *Snyderichthys* to the plagopterins, multiple samples were also examined (Bonneville basin, Bear and Snake River drainages).

Representatives of the three major clades (western, shiner, and chub) of Coburn and Cavender (1992) were also examined, with special emphasis on hypothesized sister taxa to plagopterins. These names will be used throughout manuscript. Chubs were *Camptostoma anomalum*, *Couesius plumbeus*, *Hybognathus hankinsoni*, *Margariscus margarita*, *Nocomis micropogon*, and *Semotilus atromaculatus*. Shiners included *Cyprinella spiloptera*, *Luxilus chrysocephalus*, and *Pimephales notatus*. Representatives of the western clade were *Acrocheilus alutaceus*, *Agosia chrysogaster*, *Gila cypha*, *Moapa coriacea*, *Orthodon microlepidotum*, and *Rhinichthys atratulus*. Based on relationships inferred from morphological characters (Cavender and Coburn, 1992; Coburn and Cavender, 1992), sequences from the leuciscins *Abramis brama* (Briolay et al., 1998; GenBank accession number Y10441) and *Notemigonus crysoleucas* (Schmidt and Gold, 1995; GenBank accession number U01318) were used as outgroups.

Sequencing.—Sequences were obtained from PCR products by either standard dideoxy sequencing or cycle-sequencing and deposited in GenBank (accession numbers in Material Examined). In the standard method, templates were obtained through two rounds of amplification. In the first, a double-stranded product was generated as follows: 1–5 μ l (approximately 1–5 ng) of genomic DNA; 0.25 units of *Taq* DNA polymerase [from Promega Corp. or purified from a clone as described by Pluthero (1993)]; 4 μ l of dNTP mix (final concentration of 200 μ M of each of the four dNTPs); 2.5 μ l $MgCl_2$ stock (final concentration of 2.5 mM); 2.5 μ l of 10 \times buffer stock [provided by the enzyme supplier or as described in Pluthero (1993)]; 1.25 μ l of each primer (final concentration of 0.5 μ M of each); sterile-distilled water to a final volume of 25 μ l. Amplification was performed by 20 cycles of denaturation at 94 C for 1 min, an-

TABLE 1. SEQUENCES OF PRIMERS USED FOR AMPLIFICATION AND SEQUENCING OF *CYTB*.

Primer ^a	Position ^b	Sequence
LA-a	15248	5' GTG ACT TGA AAA ACC ACC GTT G 3'
LC-s	15536	5' ATA CAT GCC AAC GGA GCA TC 3'
HD-a	15894	5' GGG TTG TTT GAT CCT GTT TCG T 3'
LD-a	15848	5' CCA TTC GTC ATC GCC GGT GC 3'
LD _{IB} -a	15768	5' ACC CTT GTT CAA TGA ATC TG 3'
LD _{LUX} -a	15812	5' ACA TTA ACA CGA TTC TTC GC 3'
LE-s	16084	5' CCC ACC ACA CAT TCA ACC 3'
HA-a	16462	5' CAA CGA TCT CCG GTT TAC AAG AC 3'

^a Primers are designated by strand (L = light, H = heavy) and application (a = amplification and sequencing, s = sequencing only).

^b Position is identified relative to the published sequence for carp, *Cyprinus carpio*, (Chang et al., 1994).

nealing at 48 C for 1 min, and extension at 72 C for 2 min.

Single-stranded DNA for sequencing was generated by using 10 µl of 1:100 dilution of this double-stranded PCR product. Conditions for amplification were identical except that one of the primers was diluted (1:100) and annealed at 52 C. Single-stranded products were cleaned by centrifugation (Millipore Corp.), as indicated by the supplier, and sequenced using the Sequenase 2.0 kit (U.S. Biochemical) as described in Dowling and Naylor (1997). Alternatively sequences were obtained from cleaned, double-stranded PCR products by cycle sequencing, following recommendations of the manufacturer (Perkin-Elmer), or by automated sequencing of dye-labeled products (using an ABI377).

Most primers (Table 1) were designed by T. R. Schmidt from a series of sequences from eastern North American cyprinids (described in Schmidt and Gold, 1993); however, it was necessary to redesign some internal primers from sequences of several other minnows obtained with external primers. External primers (LA and HA) were positioned in conserved flanking tRNA genes. Because of its large size, sequences for the entire gene were obtained from two separate sets of primers (LA-HD and LD, LD_{IB}, or LD_{LUX}-HA, respectively, Table 1), producing fragments approximately 600 bp in length. The complete sequence of each fragment was obtained using two sets of primers, the limiting external primer in the asymmetric amplification reaction and an internal primer from the same strand (Table 1).

Data analysis.—Sequences were aligned by eye using the homologous sequence of *Cyprinus carpio* (Chang et al., 1994) as reference. Although this can be a problem for noncoding sequences, the alignment attained for the protein-coding sequence was unambiguous. Phylogenetic analysis was performed using PAUP4.0b8w (D. L.

Swofford, Sinauer Associates, Sunderland, MA, 1998, unpubl.). Topologies were obtained by heuristic search using the tree bisection-reconnection (TBR) method with 50 random-addition sequences and uninformative characters excluded. Relative strength of nodes was determined by completion of 1000 bootstrap replicates (Felsenstein, 1985; Hillis and Bull, 1993) in PAUP, using the fast-search option. Neighbour-joining trees were also generated with PAUP, using Tamura-Nei distances corrected for rate variation using the alpha value (alpha = 0.3) estimated by maximum likelihood from a larger study of *cytb* variation in western cyprinids (Smith et al., in press). Relative strength of nodes was determined by completion of 1000 bootstrap replicates in PAUP.

Estimation of divergence times.—Rates of molecular evolution were estimated from match of fossil to molecular data in the context of the molecular phylogeny (Table 2). This method permits calculation of estimated rates of divergence, which then enable estimates of divergence times for biogeographic units. Numerators in the rate equation are pairwise Tamura-Nei distances expressed as percentage sequence divergence of *cytb*. Denominators in the rate equation are estimated times (in millions of years = Ma) of divergence for those taxa. The fossil record provides estimates of times of divergence as inferred from oldest fossil occurrences of diagnostic apomorphies of lineages (Smith et al., in press). Regression of pairwise percentage divergence against time of first appearance in the fossil record yields an estimated rate of divergence for *cytb* in cyprinids (Fig. 2). When the intercept is constrained to pass through the origin (Hillis et al., 1996), this estimate is 1.31% sequence divergence per pairwise comparison per Ma (or 0.66% per lineage per Ma), with an error of 10% to 25% (Smith et al., in press). This assumes no genetic diver-

TABLE 2. AGE OF FIRST APPEARANCE OF FOSSILS IN MILLIONS OF YEARS (Ma) AND ESTIMATES OF SEQUENCE DIVERGENCE USED IN RATE ESTIMATION (Fig. 2). Diagnostic characters, stratigraphic, geographic, and age data from Smith et al., 1982; Smith et al., 2000; and Smith et al., in press.

Fossil taxon	Diagnostic character	Locality	Sister taxon	Diagnostic character	Locality	Time (Ma)	% divergence
<i>Lavinia</i>	Striated pharyngeal teeth	Chalk Hills formation, ID	<i>Mylopharodon</i>	Molariform pharyngeal teeth	Glenns Ferry formation, ID	6	8.1
<i>Mylopharodon</i>	Molariform pharyngeal teeth	Glenns Ferry formation, ID	<i>Siphateles</i>	One row sharp pharyngeal teeth	Truckee formation, NV	12	15.0
<i>Mylocheilus inflexus</i>	Molar pharyngeal teeth	Below Chalk Hills formation, NV	<i>Richardsonius</i>	Long, slender pharyngeal teeth	Glenns Ferry formation, ID	7	21.0
<i>Gila turneri</i>	Two rows hooked pharyngeal teeth	Stewart Valley, NV	<i>Siphateles</i>	One row sharp pharyngeal teeth	Truckee formation, NV	12	11.5
<i>Siphateles bicolor</i>	Broad anterior frontal	Chewaucan Valley, OR	<i>Siphateles b. obesus</i>	Narrow anterior frontal	Lahontan deposits, NV	0.1	3.1
<i>Gila a. atraria</i>	Two rows hooked pharyngeal teeth	Bonneville deposits, UT	<i>G. a. subspecies</i>	Short articular angular	Bear Lake, UT, ID	0.03	0.9
<i>Klamathella milleri</i>	Long, slender pharyngeal arch	Salt Lake formation, UT	<i>Gila atraria</i>	Robust, curved pharyngeal arch	Bonneville deposits, UT	6	6.2
<i>Aerocheilus</i>	Sharp, slicing pharyngeal teeth	Chalk Hills formation, ID	<i>Klamathella milleri</i>	Hooked, non-slicing teeth	Salt Lake formation, UT	7	6.4
<i>Psychocheilus</i>	Conical canine pharyngeal teeth	Priest Rapids, Miocene, ID	<i>Gila turneri</i>	Robust, curved pharyngeal arch	Truckee formation, NV	15	10.3
<i>Psychocheilus</i>	Conical canine pharyngeal teeth	Priest Rapids, Miocene, ID	<i>Mylocheilus</i> sp.	Opposing molar teeth	Salt Lake formation, UT	15	27.0

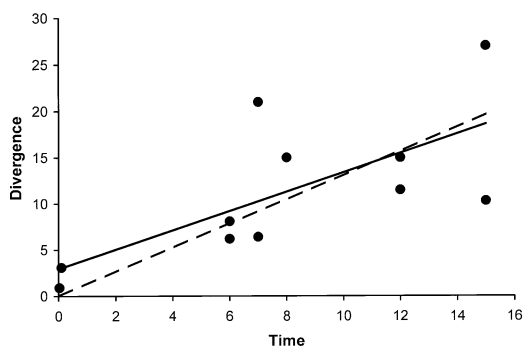


Fig. 2. Scatter of pairwise sequence divergences against time since initial divergence [millions of years (Ma)], as estimated from first appearance of diagnostic apomorphy in the fossil record (from Table 2). Lines identify regressions unconstrained (solid, $R^2 = 0.48$) and forced through the origin (dashed, $R^2 = 0.44$), yielding estimated divergence rates of 0.53% and 0.66%/lineage/ma, respectively.

gence at the time of branching and unbiased estimates of the denominator. This method probably overestimates the rates of molecular evolution because the first appearance of fossil taxa are almost surely underestimated but has the advantage of being based on a sample of values for numerators and denominators, rather than a single assumption. If, however, estimates of ages of ancestors are biased toward underestimation, the regression should not be constrained, producing a line with a positive intercept and shallower slope of 1.05% per million years (or 0.53% per lineage per million years).

Constancy of evolutionary rates was examined using the relative rates test as implemented in the program PHYLTEST (vers. 2.0, S. Kumar, Pennsylvania State University, University Park, PA, 1996). Estimates of divergence time were corrected for variation in rates of evolution among lineages by calculating branch lengths for each lineage using MEGA2 (S. Kumar, K. Tamura, I. B. Jakobsen, and M. Nei, Arizona State University, Tempe, AZ, 2001). Because it is difficult to determine whether constrained or unconstrained estimates are more appropriate, minimum and maximum divergence estimates were derived using the constrained (0.66% per Ma) and unconstrained calibrations (0.53% per Ma).

RESULTS

Of the 1140 bp of *cytb*, 425 were informative. Patterns of variation were typical, with most variable characters (335) in the third position, fewest in the second (14), and an intermediate

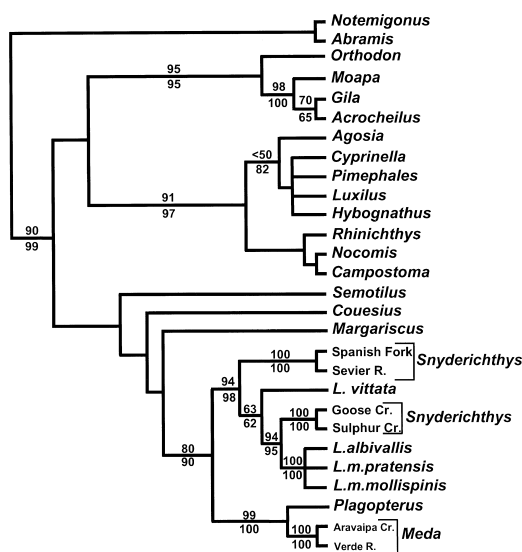


Fig. 3. Results from parsimony analysis of *cytb* sequences. Unweighted and weighted analyses produced similar results; therefore, only the more resolved topology (weighted) is presented. This topology represents a strict consensus of six most-parsimonious trees with transversions given twice the weight of transitions. Numbers above and below branches identify bootstrap values (percent) from unweighted and weighted analyses, respectively. Bootstrap values not provided are less than 60%.

number (76) in the first position. Heuristic search with all characters weighted equally recovered 15 most-parsimonious trees of 2040 steps (CI = 0.34, RI = 0.54). A strict consensus of these (not shown) identified a polytomy of three major lineages: (1) western clade (*Acrocheilus*, *Gila*, *Moapa*, and *Orthodon*); (2) an unresolved group of chubs and shiners (*Campostoma*, *Cyprinella*, *Hybognathus*, *Luxilus*, *Nocomis*, and *Pimephales*) that included the western clade members *Agosia* and *Rhinichthys*; and (3) a well-resolved clade containing members of the western and chub clades (plagopterins, *Snyderichthys*, *Couesius*, *Margariscus*, and *Semotilus*) and consistent with the creek-chub clade + plagopterin grouping identified by Simons and Mayden (1997). Further evaluation by bootstrap analysis (Fig. 3) indicated monophyly of the western and chub + shiner clades (including *Agosia* and *Rhinichthys*), with these groups occurring in 95% and 91% of replicates, respectively. The relationship of *Couesius*, *Margariscus*, or *Semotilus* to the plagopterins was not strongly supported, because they formed a monophyletic group in less than 50% of replicates.

Relationships among the plagopterins were generally well resolved (Fig. 3). This monophy-

letic group (80% of bootstrap replicates) was divided into a southern clade containing *Meda* and *Plagopterus* (99% of replicates) and a northern lineage including all *Lepidomeda* and *Snyderichthys* (94% of replicates). The northern lineage was further divided into four groups inconsistent with current taxonomy and biogeography (Fig. 1). Two forms of *L. mollispinis* and *L. albivallis* formed an unresolved trichotomy (100% of bootstrap replicates) that was most closely related to *Snyderichthys* from the Snake and Bear River drainages (94% of bootstrap replicates). *Lepidomeda vittata* was the sister to this clade (63% of bootstrap replicates), and *Snyderichthys* from the central and southern Bonneville basin was the most basal lineage.

The impact of differential weighting was tested by giving transversions twice the weight of transitions. This weighting scheme was selected because it reflects the minimum transition:transversion ratio for this group of taxa (calculated using PAUP). Heuristic search recovered six most-parsimonious trees (2494 steps) similar to those obtained in the unweighted analysis, with the western clade sister to a chub + shiner clade and the creek chub + plagopterin clade of Simons and Mayden (Fig. 3). Unlike the previous analysis, shiners and chubs (including *Agozia* as a shiner and *Rhinichthys* as a chub) were sister groups (found in 82% and 51% of bootstrap replicates, respectively), with only placement of the chub *Hybognathus* discordant with previously hypothesized relationships. Bootstrap support for the western and chub + shiner clades was strong (95% and 97% of replicates, respectively). Monophyly of the creek chub + plagopterin clade occurred in more bootstrap replicates (60%); however, relationships of *Couesius*, *Margariscus*, or *Semotilus* to plagopterins were again poorly supported.

Relationships and levels of support among plagopterins were similar to those found in the unweighted analysis when transversions were weighted twice as much as transitions. That is, plagopterins (including *Snyderichthys*) were monophyletic in 90% of bootstrap replicates. Remaining relationships and bootstrap values were essentially unchanged.

Pairwise estimates of sequence divergence were clustered by neighbor-joining, using gamma-corrected Tamura-Nei distances to correct for differences in levels of variation among sites (Table 3). Standard errors on divergence estimates were generally small, typically 15–20% within the plagopterin lineage. This analysis recovered groupings similar to those found through parsimony analysis (Fig. 4). The chub + shiner group was most similar to the plagop-

terin + creek-chub lineage sensu Simons and Mayden, western minnows were more divergent, and *Semotilus* was the most divergent lineage. Bootstrap values supported monophyly of the western, chub + shiner, and plagopterin (including *Snyderichthys*) groups (100%, 99%, and 87% of replicates, respectively), but relationships among the major lineages and *Couesius*, *Margariscus*, and *Semotilus* were not well resolved. Taxonomic groupings and levels of bootstrap support for plagopterins provided by the neighbor-joining analysis were similar to those found in parsimony analyses. Plagopterins (plus *Snyderichthys*) formed a monophyletic clade in 93% of bootstrap replicates, and relationships among *Snyderichthys*, *Lepidomeda*, *Meda*, and *Plagopterus* were identical to unweighted and weighted parsimony results, with all bootstrap values higher than 70%.

DISCUSSION

Phylogenetic position of the Plagopterini.—Sequences of the *cytb* gene indicate that *Snyderichthys* is a member of Plagopterini as suggested by DeMarais (1992) and Simons and Mayden (1997). Monophyly was strongly supported, with bootstrap values $\geq 80\%$ in all analyses.

These results are also consistent with the conclusion of Simons and Mayden (1997) that plagopterins are related to *Margariscus*, *Couesius*, and perhaps *Semotilus*. When using unweighted and weighted parsimony, plagopterins fall within the monophyletic creek chub clade, with *Margariscus* their closest relative. In the neighbor-joining topology, a group consisting of *Couesius* and *Margariscus* was the sister lineage to plagopterins; however, the creek chub clade (sensu Simons and Mayden) was not monophyletic as *Semotilus* was the most divergent North American cyprinid. The three results are similar, however, and consistent with results of Simons and Mayden (1997) using 12S rDNA. Unfortunately, neither study provided strong bootstrap support, indicating that additional data are necessary to further test these relationships. A close relationship of the plagopterins with *Margariscus* and *Couesius* is supported by biogeography. The present distribution of these northern genera complements that of the plagopterins near the Continental Divide in western Wyoming (Fig. 1).

Relationships within the Plagopterini.—Studies of allozyme variation (DeMarais, 1992) supported a close relationship of *Snyderichthys* to plagopterins, rendering them polyphyletic. The examination by Simons and Mayden (1997) indi-

cated *Snyderichthys* was more closely related to *Lepidomeda vittata* than to *Meda fulgida*. These relationships, however, were not strongly supported by bootstrap analysis of weighted characters as the *Snyderichthys* + *L. vittata* node occurred in 64% of bootstrap replicates while monophyly of plagopterins was indicated in 58% of replicates.

In this analysis, sequence variation at *cytb* produced highly resolved relationships supported by high bootstrap values. In all analyses, *Lepidomeda* [*L. m. mollispinis* and *L. m. pratensis* from the Virgin River drainage and *L. albivallis* from the adjacent pluvial White River, a Pleistocene-Holocene tributary to Virgin River (Fig. 1)] formed a trichotomy most closely related to Snake River samples of *Snyderichthys*. The sister species to this group is *L. vittata* of the Little Colorado River. *Snyderichthys* from the central and southern Bonneville basin are the most divergent.

Although previous studies found *Snyderichthys* closely affiliated with *Lepidomeda*, none had sufficient geographic samples to identify polyphyly of the species and existence of two forms of *Snyderichthys*. As reported here, analyses of several additional populations from several drainages (Johnson and Jordan, 2000) showed differentiation of northern and southern *Snyderichthys*. Previous studies of life-history variation (Johnson et al., 1995, and references therein) identified differences in spawning time between Main Creek (Bonneville basin) and Sulphur Creek, Wyoming (Bear River), providing further evidence for differentiation. Given this, *Snyderichthys* should be considered a possible synonym of the genus *Lepidomeda* and possibly divided into two species. As yet, however, we have not found diagnostic morphological characters to differentiate *S. copei* of the upper Snake and Bear Rivers (type locality "tributary of Bear River at Evanston, Wyoming," Jordan and Gilbert, 1881) and what may be *S. aliciae* (Jouy, 1881; type locality Provo River at Utah Lake).

Biogeographic implications.—The broader relationships hypothesized here corroborate patterns derived from allozymes, morphology, and karyology (DeMarais, 1992; Miller and Hubbs, 1960; Uyeno and Miller, 1973). Divergence times were estimated with the method of Smith et al. (in press) using the neighbor-joining tree (Fig. 4), allowing comparison of biogeographic hypotheses and geologic events. Tests for variation in rates of evolution among nodes of interest were conducted, with only the deepest node within the plagopterin lineage (*Lepidomeda* +

Snyderichthys and *Plagopterus* + *Meda*) exhibiting significant deviation from equal rates. Although variation in rates among lineages may cause estimates of divergence from the mean and standard errors to be misleading, the shortest and longest branches from the common ancestor were used to provide minimum and maximum estimates of divergence time, respectively (S. Kumar, pers. comm.).

The *Meda* + *Plagopterus*, *Lepidomeda*, and *Snyderichthys* clades last shared a common ancestor 17 to 40 Ma (Table 4), corresponding to or predating the initial formation of the southern Colorado Plateau margin 22 to 25 Ma (Potochnik, 1989) and the beginning of extensional faulting of adjacent terrains > 20 Ma (Dokka and Ross, 1995) to form the Basin-and-Range Physiographic Province. Divergence of *Meda* and *Plagopterus* also was early, 19 to 34 Ma (Table 4), and may have occurred when the Gila and Colorado paleorivers (Howard, 1996) were isolated from one another, or associated with any one of the numerous closed basins that were formed south of the Plateau (Nations et al., 1982, 1985; Peirce, 1987). Divergence of *Meda* populations in the Verde and upper Gila basins occurred 0.9 to 3.4 Ma. This separation might be attributable to habitat isolation because of a proclivity of the genus for hard-bottomed streams, separated by the sand-bottomed, erosive nature of the mainstem lower Gila River. Alternatively, it might also have resulted from isolation in endorheic drainage basins (e.g., Douglas et al., 1999).

Differentiation of the southern and central Bonneville basin *Snyderichthys* and *L. vittata* (presently in only the Little Colorado River basin) from a common progenitor, 7.8 to 11.6 Ma and 6.3 to 8.6 Ma, respectively, was also likely related to isolation through Plateau uplift and extensional collapse of Basin-and-Range. These time estimates are bracketed by estimated plateau-margin development as recent as approximately 6.0 Ma on its extreme southwest (Luchitta, 1979, 1984) and other Bonneville Basin-rim structures like the Wasatch Front (30 Ma or before; Anderson and Mehnert, 1979).

A limited time of differentiation (0.0–1.3 Ma) exists for *Lepidomeda* taxa of the Virgin River basin [*L. m. mollispinis* of the Virgin River, *L. m. pratensis* from Meadow Valley Wash (= pluvial Carpenter River, a recent tributary of the Virgin), and *L. albivallis* of pluvial White River]. *Lepidomeda altivelis*, an extinct White River species was in this clade as well. Similar divergence times between our middle Snake and Bear river samples (0.0–0.4 Ma) and Central and Southern Bonneville samples (0.6–0.9 Ma) of *Snyderichthys* from north and south of the "Old River Bed"

TABLE 3. TAMURA-NEI DISTANCES AND THEIR STANDARD ERRORS (BELOW AND ABOVE THE DIAGONAL, RESPECTIVELY). POPULATIONS ARE ABBREVIATED AS IN FIGURE 1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1. <i>Notemigonus</i>		0.028	0.039	0.044	0.052	0.043	0.069	0.054	0.044	0.055	0.057	0.064	0.053	0.047
2. <i>Abramis</i>	0.192		0.037	0.040	0.049	0.039	0.065	0.053	0.048	0.059	0.056	0.063	0.046	0.056
3. <i>Orthodon</i>	0.289	0.257		0.023	0.027	0.026	0.061	0.057	0.044	0.065	0.057	0.063	0.067	0.069
4. <i>Gila</i>	0.296	0.267	0.162		0.011	0.011	0.059	0.060	0.055	0.057	0.062	0.059	0.064	0.056
5. <i>Moapa</i>	0.356	0.320	0.191	0.072		0.016	0.062	0.058	0.063	0.062	0.060	0.061	0.064	0.064
6. <i>Acrocheilus</i>	0.309	0.265	0.187	0.069	0.103		0.054	0.061	0.060	0.060	0.057	0.049	0.055	0.055
7. <i>Cyprinella</i>	0.495	0.470	0.438	0.420	0.443	0.398		0.040	0.045	0.054	0.059	0.059	0.051	0.052
8. <i>Luxilus</i>	0.392	0.374	0.396	0.393	0.423	0.401	0.287		0.029	0.033	0.035	0.042	0.032	0.039
9. <i>Pimephales</i>	0.336	0.349	0.322	0.370	0.423	0.402	0.327	0.210		0.048	0.044	0.048	0.034	0.047
10. <i>Nocomis</i>	0.402	0.407	0.445	0.394	0.431	0.414	0.394	0.245	0.346		0.038	0.040	0.041	0.062
11. <i>Rhinichthys</i>	0.418	0.402	0.398	0.422	0.421	0.396	0.419	0.260	0.314	0.276		0.038	0.049	0.047
12. <i>Campostoma</i>	0.447	0.391	0.450	0.422	0.440	0.359	0.430	0.321	0.345	0.301	0.291		0.042	0.059
13. <i>Hybognathus</i>	0.390	0.352	0.459	0.426	0.440	0.392	0.344	0.157	0.249	0.304	0.353	0.326		0.038
14. <i>Agosia</i>	0.368	0.411	0.490	0.413	0.460	0.405	0.380	0.287	0.341	0.432	0.344	0.429	0.281	
15. <i>Margariscus</i>	0.337	0.328	0.286	0.277	0.283	0.296	0.435	0.372	0.458	0.400	0.429	0.404	0.401	0.428
16. <i>Semotilus</i>	0.318	0.279	0.327	0.310	0.390	0.331	0.507	0.480	0.468	0.401	0.505	0.462	0.439	0.444
17. <i>Conesus</i>	0.351	0.321	0.357	0.306	0.366	0.300	0.388	0.386	0.460	0.425	0.387	0.425	0.431	0.367
18. <i>S. copei</i> SF	0.352	0.327	0.377	0.342	0.357	0.340	0.489	0.375	0.473	0.446	0.415	0.447	0.393	0.438
19. <i>S. copei</i> SR	0.357	0.329	0.364	0.326	0.342	0.318	0.485	0.383	0.469	0.443	0.431	0.443	0.404	0.449
20. <i>S. copei</i> GC	0.372	0.391	0.417	0.378	0.407	0.413	0.478	0.444	0.459	0.488	0.483	0.435	0.461	0.485
21. <i>S. copei</i> SC	0.368	0.395	0.411	0.383	0.403	0.408	0.489	0.443	0.459	0.488	0.471	0.445	0.450	0.474
22. <i>L. vittata</i>	0.350	0.362	0.388	0.355	0.352	0.351	0.433	0.442	0.448	0.470	0.440	0.408	0.436	0.456
23. <i>L. albigallis</i>	0.324	0.341	0.395	0.361	0.359	0.360	0.451	0.392	0.416	0.444	0.404	0.421	0.436	0.480
24. <i>Platypherus</i>	0.450	0.451	0.460	0.413	0.452	0.415	0.554	0.483	0.500	0.499	0.465	0.538	0.455	0.588
25. <i>L. m. pratensis</i>	0.311	0.336	0.390	0.347	0.344	0.344	0.454	0.395	0.412	0.438	0.387	0.417	0.426	0.463
26. <i>L. m. mollispinus</i>	0.329	0.337	0.401	0.367	0.356	0.366	0.468	0.399	0.422	0.451	0.410	0.427	0.438	0.483
27. <i>M. fulgida</i> AR	0.498	0.541	0.555	0.523	0.617	0.578	0.539	0.592	0.558	0.524	0.435	0.582	0.564	0.506
28. <i>M. fulgida</i> UV	0.479	0.514	0.537	0.510	0.569	0.528	0.548	0.560	0.519	0.507	0.437	0.557	0.555	0.522

TABLE 3. CONTINUED

	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1. <i>Noemigonus</i>	0.045	0.042	0.048	0.048	0.049	0.049	0.049	0.047	0.043	0.064	0.041	0.044	0.072	0.067
2. <i>Abramis</i>	0.045	0.037	0.045	0.044	0.044	0.055	0.055	0.049	0.047	0.066	0.047	0.046	0.085	0.079
3. <i>Orthodon</i>	0.039	0.048	0.052	0.053	0.050	0.058	0.058	0.054	0.056	0.066	0.056	0.057	0.079	0.076
4. <i>Gila</i>	0.039	0.043	0.043	0.047	0.044	0.052	0.053	0.049	0.050	0.057	0.048	0.051	0.075	0.073
5. <i>Moapa</i>	0.038	0.056	0.052	0.048	0.046	0.057	0.056	0.048	0.049	0.065	0.047	0.048	0.103	0.089
6. <i>Acrocheilus</i>	0.040	0.047	0.041	0.045	0.042	0.057	0.057	0.048	0.049	0.057	0.046	0.050	0.088	0.077
7. <i>Cyprinella</i>	0.059	0.070	0.052	0.067	0.067	0.066	0.067	0.058	0.062	0.080	0.063	0.065	0.075	0.077
8. <i>Luxilus</i>	0.050	0.070	0.054	0.053	0.055	0.063	0.063	0.063	0.056	0.069	0.057	0.057	0.084	0.079
9. <i>Pimephales</i>	0.063	0.072	0.070	0.066	0.066	0.063	0.063	0.060	0.058	0.070	0.059	0.060	0.075	0.069
10. <i>Nocomis</i>	0.056	0.056	0.062	0.060	0.060	0.068	0.068	0.065	0.062	0.071	0.061	0.063	0.074	0.070
11. <i>Rhinichthys</i>	0.060	0.076	0.053	0.057	0.059	0.069	0.067	0.061	0.055	0.067	0.053	0.056	0.058	0.058
12. <i>Campostoma</i>	0.054	0.065	0.058	0.060	0.060	0.058	0.060	0.054	0.056	0.077	0.055	0.057	0.083	0.078
13. <i>Hybognathus</i>	0.055	0.064	0.059	0.053	0.055	0.064	0.062	0.059	0.061	0.064	0.060	0.061	0.079	0.079
14. <i>Agosia</i>	0.056	0.061	0.049	0.060	0.062	0.067	0.065	0.063	0.066	0.091	0.064	0.067	0.067	0.069
15. <i>Margariscus</i>	0.056	0.048	0.032	0.032	0.031	0.039	0.038	0.032	0.035	0.052	0.034	0.036	0.073	0.072
16. <i>Semotilus</i>	0.337		0.045	0.043	0.043	0.049	0.048	0.043	0.043	0.062	0.043	0.044	0.078	0.083
17. <i>Couesius</i>	0.238	0.320		0.040	0.041	0.040	0.040	0.036	0.034	0.054	0.034	0.035	0.060	0.063
18. <i>S. copei</i> SF	0.241	0.317	0.291		0.003	0.018	0.018	0.017	0.019	0.044	0.018	0.019	0.054	0.054
19. <i>S. copei</i> SR	0.233	0.318	0.296	0.008		0.019	0.018	0.017	0.020	0.043	0.019	0.020	0.056	0.055
20. <i>S. copei</i> GC	0.289	0.356	0.296	0.118	0.121		0.001	0.014	0.009	0.051	0.009	0.010	0.059	0.059
21. <i>S. copei</i> SC	0.286	0.352	0.293	0.116	0.120	0.002		0.014	0.009	0.050	0.010	0.010	0.059	0.059
22. <i>L. vittata</i>	0.249	0.320	0.273	0.112	0.111	0.087	0.088		0.015	0.045	0.015	0.016	0.059	0.057
23. <i>L. albivallis</i>	0.205	0.317	0.251	0.127	0.131	0.048	0.048	0.098		0.043	0.002	0.002	0.050	0.049
24. <i>Plagopterus</i>	0.349	0.445	0.352	0.298	0.288	0.330	0.327	0.298	0.295	0.285	0.040	0.043	0.047	0.051
25. <i>L. m. pratensis</i>	0.256	0.313	0.255	0.122	0.125	0.049	0.049	0.096	0.006	0.285		0.002	0.049	0.050
26. <i>L. m. mollispinus</i>	0.269	0.322	0.258	0.127	0.131	0.049	0.050	0.100	0.006	0.295	0.006		0.050	0.052
27. <i>M. fulgida</i> AR	0.470	0.536	0.418	0.356	0.359	0.363	0.365	0.363	0.319	0.299	0.314	0.319		0.005
28. <i>M. fulgida</i> UV	0.457	0.559	0.424	0.351	0.357	0.355	0.357	0.354	0.317	0.311	0.318	0.323	0.022	

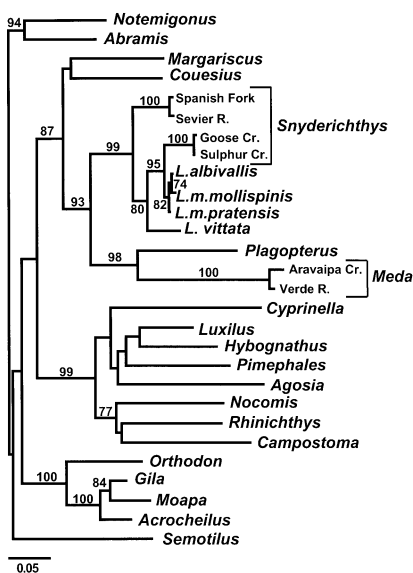


Fig. 4. Neighbor-joining tree generated by clustering gamma corrected Tamura-Nei distances ($\alpha = 0.3$). Numbers by branches identify bootstrap values (percent). Only bootstrap values $\geq 70\%$ are shown. Scale represents number of substitutions/site.

are consistent with geological history (Oviatt et al., 1992).

Affinities of the Bear and Snake River populations to each other rather than to the central and southern Bonneville populations (Bear River is now tributary to the Bonneville basin) must reflect Middle to Late Pleistocene divergence, before Bear River's most recent connection ($\sim 34,000$ years ago; Bright, 1963) with the Bonneville system. It will be of interest to examine *Snyderichthys* from Wood River, Idaho. Miller (1945) found morphological differences; since Wood River enters the middle Snake, molecular characters are predicted to resemble the middle Snake River form.

Highlands dating to Early Miocene or before

(Minckley et al., 1986; Drummond et al., 1993) contain the Bear River watershed that now flows into the Bonneville basin from Wyoming, Idaho, and Utah. Bear Lake basin also hosted a succession of Miocene to Recent lakes (Peale 1879; Hubbs and Miller, 1948; Miller, 1965). Three lake-adapted, endemic whitefishes (Snyder, 1919) and an endemic *Cottus* attest to both its antiquity and drainage relations. Exchange of Bear River between the Snake and Bonneville basins caused by block faulting and volcanism (Morrison, 1965; Stokes, 1979) are also corroborated by fossil fishes. A relative of the Bear Lake whitefishes occurs in Mio-Pliocene deposits of the Snake River Plain, southern Idaho (Smith, 1975), and two others were in the Bonneville system in Pleistocene (Smith, 1981); an endemic *Cottus* in Utah Lake (also Bonneville) is a possible Pleistocene relative of the Bear Lake endemic (Smith et al., 1968); and Bright (1967) reported a fossil lakesucker (*Chasmistes*) related to taxa in the upper Snake or Bonneville (Utah Lake) from Thatcher Basin, along Bear River's path during the most recent, Late Pleistocene diversion from the (Bear River into Lake Bonneville).

The sister relationship (1.3–7.4 Ma; Table 4) between *Snyderichthys* of the Bear River-Snake complex and *L. mollispinus* (plus *L. albivallis* and presumably *L. altivelis*) of the Virgin-pluvial White system is more difficult to rationalize. It corresponds in part with a past hypothesis of Snake-Bonneville-Virgin River drainage connections by Keyes (1917, 1918), who proposed the upper Snake River as a former Bonneville-system tributary that ultimately flowed into the lower Colorado River. Geologists did not take Keyes seriously (Stokes, 1979). Hubbs and Miller (1948:31) rejected his proposal and provided biogeographic evidence against it in a later monograph (Hubbs et al., 1974) on fishes of western Nevada. Ives (1948) identified a poten-

TABLE 4. MINIMUM AND MAXIMUM DIVERGENCE TIME ESTIMATES (IN MILLIONS OF YEARS) FOR PLAGOPTERIN TAXA. Abbreviations for each group are provided in parentheses following first use.

Divergence time for:	Minimum	Maximum
<i>L. albivallis</i> (LA), <i>L. m. mollispinus</i> (LMM), and <i>L. m. pratensis</i> (LMP)	0.0	1.3
<i>Snyderichthys</i> Goose (SCGC) and Sulphur Creeks (SCSC)	0.0	0.4
LA + LMM + LMP and SCGC + SCSC	1.3	7.4
LA + LMM + LMP + SCGC + SCSC and <i>L. vittata</i> (LV)	6.3	8.6
<i>Snyderichthys</i> Spanish Fork R. (SCSF) and Sevier R. (SCSR)	0.6	0.9
LA + LMM + LMP + SCGC + SCSC + LV and SCSF + SCSR	7.8	11.6
<i>Meda</i> Aravaipa Cr. (MFA) and Verde R. (MFV)	0.9	3.4
MFA + MFV and Plagopterus (PL)	19.0	33.7
MFA + MFV + PL and LA + LMM + LMP + SCGC + SCSC + LV + SCSF + SCSR	16.6	40.0

tial connection from the Escalante Basin of Lake Bonneville southward through Meadow Valley Wash (hence to Virgin River). Smith (1966) and Smith and Koehn (1971) found morphologic and genetic evidence for such communication. Taylor (1985) proposed a Late Miocene or Pliocene connection based on molluscan distributions from upper Snake River through the Bonneville area and pluvial White River to the lower Colorado basin.

Molecular similarity between Virgin River *Lepidomeda* and Bear-Upper Snake River *Snyderichthys* suggests connections between these drainages about 5 to 6 Ma. At this time, the Salt Lake Formation in northern Utah and southern Idaho was separate from the Snake River drainage on the Western Snake River Plain (Taylor, 1985). The Snake River was connected to the Sacramento (Wheeler and Cook, 1954; K. R. Fecht, S. P. Reidel, and A. M. Talklman, 1982, unpubl.) and Klamath drainages (Taylor, 1960; Smith et al., 2000). Based on molecular data linking northern *Snyderichthys* to Virgin River *Lepidomeda*, we hypothesize connections following structural alignments of basin-and-range topography in the vicinity of the Bonneville Basin, which was not lacustrine at the time (G. K. Gilbert, Lake Bonneville, U.S. Geological Survey V, 1890, unpubl.).

If this pattern is the consequence of vicariance, the progenitor of *Lepidomeda* and *Snyderichthys* was distributed throughout the Lower Colorado and Upper Snake Rivers around 12 Ma and survived to differentiate as relicts of tectonism disrupting a continuous distribution. The populations now represented in the Bonneville (*Snyderichthys*) and Little Colorado (*L. vittata*) were connected until 6.3 to 8.6 Ma. More recently diverged forms (e.g., *L. m. mollispinus*, *L. m. pratensis*, *L. albivallis*, *L. altivelis*) likely resulted from disruption of water connections through recent aridification of the region (Axelrod, 1979; Winograd et al., 1992). These temporal relationships demonstrate the importance of tectonism and reliction in speciation of western fishes.

If the vicariance hypothesis is correct, *Snyderichthys* will become a synonym of *Lepidomeda* and the southern form will be recognized as a separate species, possibly *L. aliciae* (Jouy). At this time, however, we must also consider two other possibilities. Polyphyly of *Snyderichthys* mtDNA lineages could also result from stochastic processes associated with the sorting of different lineages (Neigel and Avise, 1986); however, the high levels of sequence divergence among them would make this alternative less likely. A possible alternative could be introgressive transfer of

mtDNA among lineages. Extensive transfer of mtDNA among species is common in cyprinids (Dowling et al., 1989; Dowling and Hoeh, 1991) including species in these basins (Dowling and DeMarais, 1993; Gerber et al., 2001). Broader sampling and analysis of additional independent loci is necessary to evaluate these alternatives.

Material examined.—General locality information for ingroup sequences used in this study. Precise information available upon request to TED. Sequences generated for this study were deposited in Genbank under the accession numbers AF452072–AF452094. Genbank numbers for sequences from other studies are provided in parentheses. *Acrocheilus alutaceus*, OR, Maries River drainage, Benton County; *Agosia chrysogaster*, AZ, Gila River drainage, Greenlee County; *Campostoma anomalum*, IN, Illinois River drainage, LaPorte County; *Couesius plumbeus*, AK, Yukon River drainage, North Star Borough; *Cyprinella spiloptera*, NY, Susquehanna River drainage, Tioga County (U66605); *Gila cypha*, AZ, Colorado River drainage, Coconino County; *Hybognathus hankinsoni*, MI, Lake Michigan drainage, Charlevoix County; *Lepidomeda albivallis*, NV, White River drainage, Nye County; *Lepidomeda mollispinis mollispinis*, AZ, Virgin River drainage, Mohave County; *Lepidomeda mollispinis pratensis*, NV, Meadow Valley Wash, Lincoln County; *Lepidomeda vittata*, AZ, Chevelon Creek, Little Colorado River drainage, Coconino County; *Luxilus chrysocephalus*, TN, Tennessee River drainage, Blount or Hancock Counties; (U66595); *Margariscus margarita*, MI, Charlevoix County, Lake Michigan drainage; *Meda fulgida*, AZ, Gila River drainage, Graham Co., and AZ, Verde River drainage, Yavapai County; *Moapa coriacea*, NV, Moapa River drainage, Clark County; *Nocomis micropogon*, MI, Raisin River drainage, Washtenaw County; *Orthodon microlepidotum*, CA, King's River drainage, Fresno County; *Pimephales notatus*, MI, Raisin River drainage, Washtenaw County (U66606); *Plagopterus argentissimus*, UT, Virgin River drainage, Washington County; *Rhinichthys atratulus*, MI, Rouge River drainage, Macomb County; *Semotilus atromaculatus*, MI, Raisin River drainage, Washtenaw Co.; *Snyderichthys copei*, ID, Goose Creek drainage, Cassia County; WY, Bear River drainage, Uinta County; UT, Sevier River drainage, Garfield County; and UT, Spanish Fork River drainage, Utah County.

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- (TED, CAT, WLM) DEPARTMENT OF BIOLOGY, ARIZONA STATE UNIVERSITY, TEMPE, ARIZONA 85287-1501; AND (GRS) MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, ANN ARBOR, MICHIGAN 48109. WLM DECEASED 22 JUNE 2001. E-mail: (TED) thomas.dowling@asu.edu. Send reprint requests to TED. Submitted: 4 June 2001. Accepted: 13 Feb. 2002. Section editor: J. D. McEachran.