The Southwestern Naturalist 25(4): 485–503

TAXONOMIC STATUS AND MORPHOLOGY OF ISOLATED POPULATIONS OF THE WHITE RIVER SPRINGFISH, CRENICHTHYS BAILEYI (CYPRINODONTIDAE)

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ABSTRACT. Crenichthys baileyi (Gilbert) is endemic to a series of isolated springs along the approximately 325 km pluvial White River system of southeastern Nevada. The preference of Crenichthys for spring habitats and the drying of the pluvial White River have resulted in isolation of various populations in the remaining spring habitats. Geographic isolation coupled with the environmental diversity that prevails among the spring habitats caused considerable morphological divergence among several spring populations. Taxonomic analyses indicate that several populations are distinct, and are herein described as new subspecies. Five subspecies of the formerly monotypic C. baileyi are described. One population of C. baileyi has been extirpated and others are endangered by loss of habitat through introductions of exotic fish species and physical alterations.

Crenichthys baileyi (Gilbert), the White River springfish, inhabits warm springs throughout the White River system of southeastern Nevada. In pluvial times, this river system was tributary to the Colorado River, but is now disjunct except at its most southerly extent; there, numerous springs provide water for the Moapa River, which flows into the Colorado River by way of Lake Mead (Blackwelder 1943, Hubbs and Miller 1948a). The pluvial White River is now represented by the White River Valley, Pahranagat Valley, and the Moapa River. Flows reduced from pluvial times, 10,000 to 30,000 years ago, and the obligatory spring existence of Crenichthys have resulted in isolation of populations in the remaining suitable spring habitats along the course of the pluvial White River (Fig. 1) (Hubbs et al. 1974). Robert R. Miller (pers. comm. to R. H. Reider) suggested that these springs may have been isolated for approximately 10,000 years.

The spring habitats occupied by *C. baileyi* vary considerably in temperature and minimum dissolved oxygen values (Table 1). Temperature and minimum oxygen values are relatively constant within each spring.

The ability of *C. baileyi* to thrive in springs of high temperature and low oxygen has been examined by Hubbs and Hettler (1964). They concluded that the high resistance of certain *C. baileyi* populations to environmental stress was due to their unique genetic makeup. The statement that certain populations have become adapted to their own particular environment implies that some of these populations may be distinct taxonomic units. This hypothesis is supported by the experiments of Sumner and Sargent (1940), where they transferred *C. baileyi* between Mormon Spring (37°C and 0.7 ppm oxygen) and Preston Spring (21°C and 3.3 ppm oxygen). Of the over 80 fish from Preston

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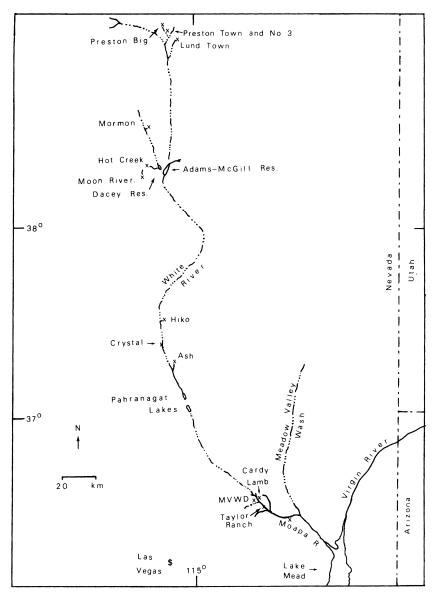


Fig. 1. Map of the southeast Nevada region, showing locations (x) of Crenichthys baileyi populations.

Spring which were acclimated and transferred to Mormon Spring, none survived the harsher environment; whereas those transferred from Mormon to Preston Spring survived.

Differences in the physical properties (especially temperature and oxygen) of the various springs and each population's apparently different resistance to these factors, coupled with the extended period of isolation, prompted examination of the taxonomy

TABLE 1. Temperature and minimum dissolved oxygen values of the spring source in waters containing Crenichthys baileyi. Data from Hubbs and Hettler (1964) and personal observation.

SPRING	TEMPERATURE (°C)	OXYGEN (ppm
PRESTON BIG	21.0	3.3
MORMON	37.0	0.7
HOT CREEK	31.3	1.6
MOON RIVER	33.3	_
HIKO	26.3	3.0
CRYSTAL	26.0-27.0	1.6-3.0
ASH HEADPOOL	35.9	2.4
OUTFLOW CREEK	34.0	2.1 - 2.6
MOAPA HEADWATER SPRINGS	30.0-31.1	4.0-5.8
TAYLOR (=HOME)	31.0	5.7

of various populations of C. baileyi. The need for such an investigation was made urgent by the recent loss of the Hiko Spring population due to exotic fish introductions. Largemouth bass (Micropterus salmoides) apparently were introduced into Hiko Spring in February 1965 (B. L. Wilson, pers. comm.). Shortfin mollies (Poecilia mexicana) and mosquito fish (Gambusia affinis) were introduced into Hiko in January or February 1965. Shortfin mollies, mosquitofish, and largemouth bass increased in abundance through 1965. By February 1966, springfish were rare, and were extinct in June 1967. Part of the Crenichthys decline also is attributable to a parasite, Lernaea, that probably was introduced along with the exotic fishes. Crenichthys baileyi of Hot Creek Spring were thought to have been extirpated in the early 1970's when largemouth bass entered the spring from Dacey Reservoir, where they had been introduced as game fish. Fortunately, a recently discovered group of the springfish from Hot Creek survived because they were isolated by dense emergent vegetation from the main pool area. Exotic species (Poecilia mexicana, P. reticulata, Gambusia affinis, and Cichlasoma nigrofasciatum) have been introduced into other springs inhabited by Crenichthys baileyi (Deacon and Bradley 1972, Hubbs and Deacon 1964). Establishment of exotic species has resulted in depressed activity cycles and reduced population numbers of C. baileyi in these springs (Deacon and Wilson 1967, Deacon et al. 1964). Exotic species also have been indicated as sources of Lernaea (Copepoda) and Contracaecum (Nematoda) that parasitize Crenichthys baileyi in Moapa River headwater springs (Wilson et al. 1966). The current status of each population will be treated in later sections.

The published material relating to this species usually has centered around the fish's ability to inhabit seemingly hostile environments (Hubbs and Hettler 1964) and their resulting activity patterns (Deacon and Wilson 1967, Hubbs et al. 1967). Kopec (1949) reported on aspects of early life history of *C. baileyi*. Relatively little attention has been afforded the taxonomy of this species despite the suggestion by work on other cyprinodonts in the southwestern United States that subspecific status might be warranted for certain populations (Miller 1948). Reider (1971) compared the morphology of four spring populations of *Crenichthys baileyi*. However, his failure to examine specimens from other springs or to separate data by sex hampered interpretations of his results and no attempt at describing distinct populations was made.

MATERIALS AND METHODS. During the course of this study we attempted to examine specimens of *Crenichthys baileyi* from every locality where they exist or have historically existed. Specifically, we based our study on series of 30 adult fish from the following springs: Preston Big,

Mormon, Hot Creek, Hiko, Ash, Moapa Valley Water District (MVWD), and Cardy Lamb. Due to a lack of specimens and/or the rare occurrence of *C. baileyi* in a particular habitat, only small numbers of specimens were examined from Lund Town Spring, Moon River Spring, Adams-McGill Reservoir, and the Moapa River at Taylor (= Home) Ranch. Specimens were provided by The University of Michigan Museum of Zoology (UMMZ); Arizona State University (ASU); University of Nevada, Las Vegas (UNLV); and field collections. Type material is deposited at UMMZ and UNLV. Field notes taken by Carl L. Hubbs when his party collected specimens from most *C. baileyi* populations during the summer of 1938 provided the basis for subspecies color diagnoses.

Morphometric and meristic analyses were made as described for cyprinodonts by Miller (1948) with the following exception. Greatest body depth, a measurement of the greatest vertical distance between the dorsal and ventral margins, was measured with one end of the calipers placed just anterior to the origin of the dorsal fin and the other end on the ventral margin directly below the calipers on the dorsal margin. Gill filaments were measured and enumerated on the first arch on the left side.

Morphometric measurements were made with precision dial calipers to the nearest 0.1 mm. Morphometrics were analyzed by the graphical methods of Hubbs and Hubbs (1953). The basal line indicates the sample range and the hatched rectangle represents plus and minus one standard error of the mean (vertical line). The larger rectangle indicates 0.675 standard deviation on either side of the mean. If no overlap occurs between the larger rectangles of two samples, the populations are considered separable for that character at the 75% level, an accepted value of subspecific separation (Hubbs and Hubbs 1953). Morphometric values are given in thousandths of standard length. Meristic data are presented in frequency tables. Numbers of vertebrae were determined by radiographs for fishes from Preston Big Spring, Mormon Spring, Hiko Spring, the outflow creek below Ash Spring, and Cardy Lamb Spring. Precaudal, caudal, and total vertebrae numbers are reported. The first caudal vertebra was defined as the first vertebra with fused transverse processes. Enumeration of vertebral centra was employed as an indication of vertebrae number.

In many respects, the Preston Big Spring and Mormon Spring populations represent the two extremes in environmental conditions, especially temperature and oxygen. Visually, when examining springfish from these two locations, one is impressed with the relatively small head and large body of the fish from Preston Big Spring, and on the other extreme, the large head and small body of the fish from Mormon Spring. When standard morphometric analysis failed to elucidate these differences adequately, a combination of measurements called "relative head size index" was created. This index compares the relative sizes of head and body by utilizing standard morphological measurements (mean values) in the following manner:

TAXONOMIC HISTORY. Crenichthys baileyi was originally described by Gilbert (1893) as a subspecies of Cyprinodon macularius. The exceedingly brief description by Gilbert was based on 11 small specimens (<20 mm) collected in 1891 by C. H. Merriam and V. Bailey from "Pahranagat Valley, Nevada." The failure of Gilbert to list the specific locality of collection in Pahranagat Valley presents a problem since three springs in the valley, Ash, Crystal, and Hiko, harbored populations of springfish. Hiko would seem to be eliminated as the type locality since it is somewhat removed from the river bed and therefore the route of travel. The area near Ash Spring was frequented by travelers at that time and probably was a stopping place for Merriam and Bailey. That Merriam and Bailey collected fishes at Ash Spring is supported by the report of their collection of Rhinichthys in a spring of 36.11°C as described by Gilbert (1893). Ash spring is the only spring of that temperature in Pahranagat Valley, and therefore, the probable type locality of Crenichthys baileyi. Two of Gilbert's type specimens still exist and are housed at the California Academy of Sciences (SU 709). Jordan and Evermann (1896) considered the fish to be specifically distinct. The genus Crenichthys was erected by Hubbs (1932) when he described C. nevadae, the only other species of the genus, from Railroad Valley, Nevada. Sumner and Sargent (1940), on the advice of Hubbs, then associated baileyi with

the newly created *Crenichthys* (La Rivers 1962). The genus *Crenichthys* is closely allied with *Empetrichthys*, differing principally in the former having uniserially bifid rather than biserially conical teeth, herbivorous feeding habits, and associated modifications (Hubbs 1932). Prior to this work, *C. baileyi* was considered monotypic.

Bailey et al. (1970) listed White River killifish as the common name for *C. baileyi*. However, Hubbs (1932) named *C. nevadae* in reference to its spring habitat (Cren referring to spring). Subsequent editions of "Common and Scientific Names of Fishes" should replace killifish with springfish in the common names of *C. baileyi* and *C. nevadae*.

ACCOUNTS OF SUBSPECIES. Crenichthys baileyi albivallis, n. subsp. Preston White River springfish. (Fig. 7).

Diagnosis.—This subspecies differs from other C. baileyi subspecies in having a shorter head and smaller least bony interorbital width (Figs. 2, 3).

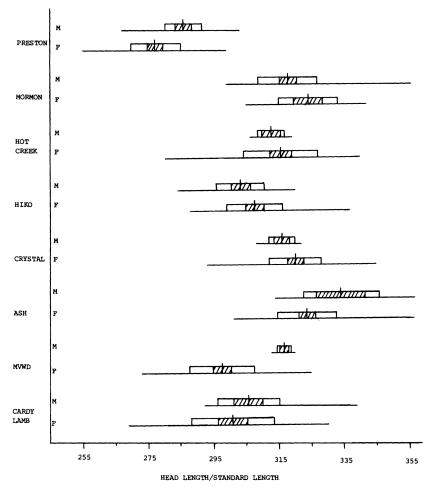
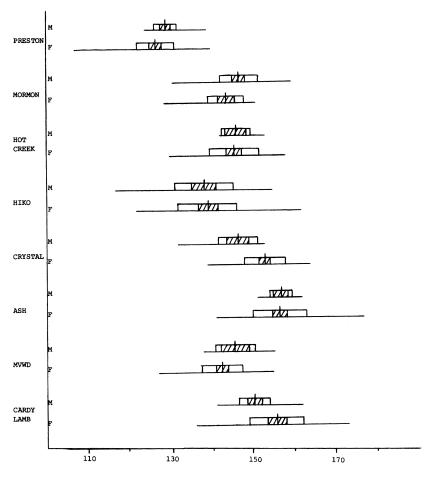


Fig. 2. Comparison of head length in populations of *Crenichthys baileyi*. See text for explanation of figure.



LEAST BONY INTERORBITAL WIDTH/STANDARD LENGTH

Fig. 3. Comparison of least bony interorbital width in populations of *Crenichthys baileyi*. See text for explanation of figure.

Type Material.—Holotype, male (UMMZ 203332), 42.3 mm SL and allotype (UMMZ 203333), 36.0 mm; collected 10 Oct. 1966 by J. E. Deacon from Preston Big Spring along with 28 paratopotypes, UNLV F-952 (30.0-48.7 mm).

Distribution.—The distribution of this subspecies is the northernmost limit of the species, being restricted to springs near the towns of Preston and Lund in White Pine Co., Nevada. The type locality of C. b. albivallis is Preston Big Spring (T 12 N, R 61 E). The known range of this subspecies also includes Preston Town Spring, Preston Spring #3, Arnoldsen Spring, and Cold Spring (all in T 12 N, R 61E, Sec. 12); as well as Indian Spring (T 12 N, R 61 E, Sec 2); and Lund Town Spring (T 11 N, R 62 E, Sec 3).

Species Associates and Status.—The following native fishes are associated with C. b. albivallis: Lepidomeda albivallis (in all springs listed above), Rhinichthys osculus subsp. (in Preston Big, Preston Town, Preston #3, and Lund Town Springs), and Catostomus

clarki intermedius (in Preston Big, Preston Town, Preston #3, Arnoldsen, and Lund Town Springs). In addition to native fishes, an exotic, *Poecilia reticulata*, has become established in all springs except Preston Big. Carassius auratus have been seen in Lund Town Spring. Crenichthys b. albivallis were abundant in Preston Big Spring during November 1977, but were less common during an October 1979 survey. The populations of C. b. albivallis in Preston Town Spring and Preston Spring #3 are apparently reduced, perhaps because of the presence of *Poecilia reticulata*. Springfish were abundant in Arnoldsen, Cold, and Indian Springs during a 1979 survey. No springfish were collected during 1977 in Lund Town Spring, which probably never harbored a large population of the fish (J. E. Deacon, pers. comm.).

Description.—Crenichthys baileyi albivallis is a large-bodied springfish with a relatively small head (Table 2). Adults of this subspecies are commonly 35-40 mm SL, exceeded only by C. b. grandis. The comparatively small head is exemplified in C. b. albivallis by possession of the shortest head length and smallest least bony interorbital width (Figs. 2, 3).

TABLE 2. Comparison of relative head size index in populations of Crenichthys baileyi. Larger values indicate a relatively larger head to body size. See text for explanation.

Location	Index value
Mormon Spring	41.14
Crystal Spring	37.16
Ash Spring	37.00
Cardy Lamb Spring	36.74
Hot Creek Spring	36.68
MVWD Spring	36.42
Hiko Spring	32.87
Preston Big Spring	27.61

Meristics and Morphometrics.—The following values are based on 30 Crenichthys baileyi (10 male, 20 female) from Preston Big Spring, 30.0-48.7 mm SL. Typical fin ray numbers: dorsal 11, anal 12 or 13, caudal 18, and left pectoral 16 (Table 3). Lateral line scales typically 29 and caudal peduncle circumference scales typically 18 (Table 4). For the following characters, in this and subsequent descriptions, the mean value is given first, followed by the range in parentheses. Predorsal length: § 717.60 (707-729), § 714.85 (695-747). Anal to caudal length: § 347.70 (326-367), § 332.75 (314-351). Greatest body depth: ♂ 374.30 (355-398), ♀ 350.00 (332-374). Greatest body width: ♂ 215.80 (197-233), ♀ 209.85 (192-224). Head length: ♂ 286.10 (267-303), ♀ 277.40 (255-299). Head depth: & 255.00 (236-270), \$\frac{2}{2}\$ 240.60 (222-258). Head width: \$\sigma\$ 222.30 (214-236), ♀ 215.40 (202-238). Least bony interorbital width: ♂ 129.30 (124-139), ♀ 126.75 (112-140). Snout length: § 82.20 (79-85), 9. 78.45 (65-92). Orbit length: § 79.70 (64-88), ♀ 74.40 (66-83). Depressed dorsal fin length: ♂ 224.90 (207-256), ♀ 208.85 (188-230). Depressed anal fin length: ♂ 228.00 (214-262), ♀ 213.35 (172-229). Middle ray caudal fin length: 3 201.40 (187-225), 2 195.63 (174-222). The following vertebral counts are based on 20 specimens (UMMZ M123982), with frequency of each count given in parenthesis; precaudal: 11(1), 12(16), 13(3), avg. 12.1; caudal: 15(1), 16(14), 17(5), avg. 16.2; total: 27(2), 28(11), 29(6), 30(1), avg. 28.3.

Etymology.—The name albivallis is from the Latin albus, white, and vallis, valley, in reference to the subspecies inhabiting the White River Valley.

TABLE 3. Frequency distribution of selected fin ray counts in populations of Crenichthys baileyi.

Subspecies	7	8	9		l rays		mean	11	12		il ray		mean
Locality		•		10		12	mean		12	13	14	15	mean
C. b. albivallis													
Preston Big				3	22	5	11.1	1	10	15	3	1	12.8
C. b. thermophilus													
Mormon			3	21	6		10.1		21	4			12.0
Hot Creek	1		1	19	9		10.2	3	18	9			12.2
C. b. grandis													
Hiko				10	17	3	10.8		2	20	8		13.2
Crystal			2	5	17	6	10.9		2	19	9		13.2
C. b. baileyi													
Ash			6	17	6		10.0	6	18	6			12.0
C. b. moapae													
MVWĎ				9	19	2	10.8		3	18	9		13.2
Cardy Lamb			1	11	14	3	10.7		7	17	6		13.0
Subspecies			c	auda	l rays				Le	ft pe	ctoral	rays	6
Locality	16	17	18				mean	14					mean
C. b. albivallis													
Preston Big		2	21	5	2		18.2		4	21	5		16.0
U. b. thermophilus													
C. b. tnermophilus Mormon	2	3	21	3	1		17.9		5	24	l		15.9
	2 2		21 19	3	1 2		17.9 18.0			24 13		3	15.9 16.5
Mormon Hot Creek												3	
		3										3	
Mormon Hot Creek C. <i>b. grandis</i>	2	3	19 14	4	2		18.0		3	13	11 22		16.5
Mormon Hot Creek C. b. grandis Hiko Crystal	2	3 5	19 14	4 7	2		18.0 18.0		3	13 8	11 22		16.5 16.7
Mormon Hot Creek C. b. grandis Hiko Crystal	2 2 2	3 5	19 14 11	4 7	2		18.0 18.0		3	13 8	11 22		16.5 16.7
Mormon Hot Creek C. b. grandis Hiko Crystal C. b. baileyi Ash	2 2 2	3 5 10	19 14 11	4 7 5	2		18.0 18.0 17.8		3	13 8 13	11 22 13		16.5 16.7 16.6
Mormon Hot Creek C. b. grandis Hiko Crystal C. b. baileyi	2 2 2	3 5 10 14	19 14 11	4 7 5	2	1	18.0 18.0 17.8		3	13 8 13 18	11 22 13	3	16.5 16.7 16.6

TABLE 4. Frequency distribution of selected scale counts in populations of Crenichthys baileyi.

0.1	Lateral line scales								Peduncle circumference scales						
Subspecies															
Locality	26	27	28	29	30	31	32	33 1	nean	15	16	17	18	19	mean
C. b. albivallis			3	17	4	5	1		29.5			12	16	2	17.7
Preston															
C. b. thermophilus															
Mormon	1	1	15	5	7	1		7	28.6		16	13	1		16.5
Hot Creek		1	4	7	13	3		2	29.7		5	19	4	2	17.1
C. b. grandis															
Hiko		1	9	18	2			:	28.7	1	13	16			16.5
Crystal			9	15	6				28.9	1	13	13	3		16.7
C. b. baileyi															
Ash		7	15	6	2			:	28.1		4	21	5		17.0
C. b. moapae															
MVWD			12	14	4			:	28.7		11	18	1		16.7
Cardy Lamb		3	16	10	1			:	28.3		11	19			16.6

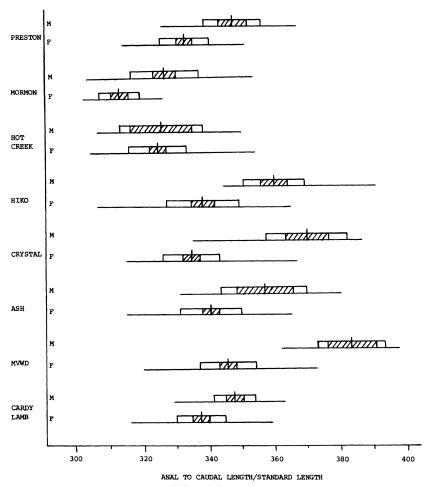


Fig. 4. Comparison of anal to caudal length in populations of *Crenichthys baileyi*. See text for explanation of figure.

Crenichthys baileyi thermophilus, n. subsp. Mormon White River springfish (fig. 8).

Diagnosis.—This subspecies differs from other C. baileyi subspecies in having the most posteriorly positioned median fins, resulting in a shorter anal to caudal length (Fig. 4). Crenichthys b. thermophilus also is characterized by a long snout (Fig. 5).

Type Material.—Holotype, male (UMMZ 203334), 32.4 mm SL collected 4 Apr. 1965 by J. E. Deacon from Mormon Spring along with 6 paratopotypes, UNLV-124 (15.8-29.8 mm). Allotype (UMMZ 203335), 31.6 mm; collected 29 Jan. 1965 by J. E. Deacon from Mormon Spring along with 12 paratopotypes, UNLV-123 (19.1-33.6 mm). Other paratopotypes collected from Mormon Spring as follows: 4, UNLV-121 (16.8-32.1 mm); 6, UNLV-122 (18.5-30.0).

Distribution.—Crenichthys baileyi thermophilus is restricted to three springs in Nye Co., Nevada. The type locality is Mormon Spring (T 9 N, R 61 E, Sec 32). This subspecies also occurs in Hot Creek Spring (T 6 N, R 61 E, Sec 18) and Moon River Spring (T 6 N, R 60 E, Sec 25). On rare occasions, C. baileyi is collected in Adams-McGill Reservoir. These fish apparently are washed down from Hot Creek and/or Moon River Springs during floods or are transported by fishermen. No viable population of springfish exist in Adams-McGill Reservoir.

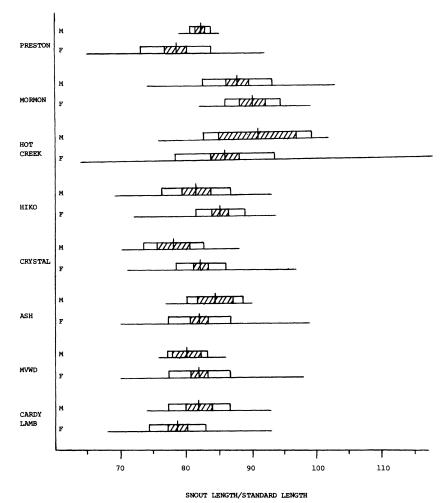


Fig. 5. Comparison of snout length in populations of *Crenichthys baileyi*. See text for explanation of figure.

Species Associates and Status.—No fish species other than springfish normally exist in the springs inhabited by C. b. thermophilus. Location on a tributary of the White River and the high water temperature of Mormon, Hot Creek, and Moon River Springs apparently restricted these waters to a single native fish. Largemouth bass (Micropterus salmoides) entered Hot Creek Spring in the early 1970's from Dacey Reservoir, where they had been introduced as game fish. It was thought that the bass had extirpated the springfish until personnel from the Nevada Department of Fish and Game discovered a group of springfish separated from the main pool area by dense emergent vegetation. Hot Creek Spring was poisoned and the isolated springfish were introduced into the main pool area after a barrier to prohibit entry of bass was repaired. Despite the barrier, one bass, probably introduced by fishermen, was observed in the main pool area in 1979. The proximity of bass to Hot Creek Spring can be expected to result in additional intentional or accidental introductions in the future. Viable populations currently exist in all springs inhabited by C. b. thermophilus. This subspecies formerly was common in the warm outflow of Hot Creek Spring. It has been extirpated there by largemouth bass.

Description.—Crenichthys baileyi thermophilus is the smallest subspecies of C. baileyi. Adult specimens of this subspecies average near 30 mm SL. Median fins are relatively posterior in position, resulting in a reduced anal to caudal length. (Fig. 4).

Meristics and Morphometrics.—The following values are based on 30 Crenichthys baileyi (20 male, 10 female) from Mormon Spring, 26.3-45.0 mm SL. Typical fin ray numbers: dorsal 10, anal 12, caudal 18, and left pectoral 16 (Table 3). Lateral line scales typically 28 and caudal peduncle circumference scales 16 or 17 (Table 4). Predorsal length: \$\display 728.80 (701-767), \quad 731.70 (711-760). Anal to caudal length: \$\display 326.60 (303-354), § 313.30 (302-326). Greatest body depth: § 320.70 (292-361), § 297.10 (265-316). Greatest body width: § 212.85 (201-224), § 211.70 (200-224). Head length: ♂ 317.90 (299-356), ♀ 324.30 (305-342). Head depth: ♂ 249.25 (231-274), ♀ 245.90 (234-253). Head width: δ 227.20 (214-247), ♀ 232.40 (222-253). Least bony interorbital width: \$\displant 147.00 (131-160), \cong 143.70 (129-151). Snout length: \$\displant 87.85 (74-103), \cong 90.10(82-99). Orbit length: \$\displant 78.05(64-89), \quad 81.20(71-93). Depressed dorsal fin length: ¿ 213.20 (190-229), ♀ 206.40 (198-221). Depressed anal fin length: ♂ 220.70 (189-255), [♀] 214.40 (197-226). Middle ray caudal fin length: ♂ 201.80 (183-214), ♀ 207.70 (197-225). The following vertebral counts are based on 20 specimens (UMMZ M124987), with frequency of each count given in parenthesis; precaudal: 11(2), 12(13), 13(5), avg. 12.2; caudal: 15(3), 16(11), 17(5), 18(1), avg. 16.6; total: 26(1), 27(1), 28(7), 29(11), avg. 28.4.

Etymology.—The name thermophilus is from the Greek therme, warm, and philos, having an affinity for, in reference to the subspecies inhabiting warm spring waters.

Crenichthys baileyi grandis, n. subsp. Hiko White River springfish (Fig. 9).

Diagnosis.—This subspecies differs from other C baileyi subspecies in being of large size (adults average longer than 40 mm SL). Crenichthys b. grandis differs from C. b. albivallis in having a longer head (Fig. 2). Crenichthys b. grandis differs from C. b. thermophilus and C. b. baileyi in possessing more dorsal and anal fin rays (Table 3). Crenichthys b. grandis can be distinguished from C. b. moapae and other C. baileyi subspecies on the basis of color. Males of C. b. grandis have much more yellow than any other C. baileyi subspecies. The ventral surface of head and body of the males are brilliant lemon yellow. This color extends onto the caudal fin, becoming deep orange.

Type Material.—Holotype, male (UMMZ 203336), 45.5 mm SL and allotype (UMMZ 203337), 45.4 mm; collected 3-4 Jun. 1966 by J. E. Deacon from Hiko Spring along with 29 paratopotypes ASU-3942 (31.3-65.5 mm). Additional paratopotypes collected from Hiko Spring as follows: 44, UNLV-142 (26.4-40.3 mm) collected 4 Jun. 1964 by J. E. Deacon; 40, UMMZ 124998 (part of a collection of 1626 specimens 13.0-71.0 mm) collected 28 Aug. 1938 by C. L. Hubbs.

Distribution.—Crenichthys b. grandis inhabits Hiko Spring (T 4 S, R 60 E, Sec 14) and Crystal Spring (T 5 S, R 60 E, Sec 10), in Pahranagat Valley, Lincoln Co., Nevada.

Species Associates and Status.—Two native fishes, Gila robusta jordani and Rhinichthys osculus velifer, were associated with C. b. grandis in Hiko Spring. This springfish population became extinct in 1967 after largemouth bass, shortfin mollies, and mosquitofish became established in Hiko Spring. Largemouth bass apparently invaded Hiko Spring by swimming up the irrigation ditch flowing into a reservoir on the Key Pittman Wildlife Management Area. Shortfin mollies and mosquitofish probably were introduced directly into Hiko Spring. Gila robusta jordani, Rhinichthys osculus velifer, and Catostomus clarki intermedius were associated with C. b. grandis in Crystal Spring (C. L. Hubbs' field notes). Recently, Cichlasoma nigrofasciatum has become established in Crystal Spring, resulting in reduced numbers of springfish.

Description.-Crenichthys b. grandis is the largest subspecies of C. baileyi. Adult

specimens of C. b. grandis average over 40 mm SL, occasionally exceeding 65 mm.

Meristics and Morphometrics.—The following values are based on 30 Crenichthys baileyi (12 male, 18 female) from Hiko Spring, 31.9-65.5 mm SL. Typical fin ray numbers: dorsal 10 or 11, anal 13, caudal 18, and left pectoral 17 (Table 3). Lateral line scales typically 29 and caudal peduncle circumference scales typically 16 or 17 (Table 4). Predorsal length: ∂ 712.42 (705-722), ♀ 712.44 (684-732). Anal to caudal length: ∂ 360.17 (344-391), § 377.83 (306-365). Greatest body depth: \$ 383.50 (336-432), § 331.00 (293-370). Greatest body width: \$\darkappa 218.92 (192-237), \quap 210.11 (196-234). Head length: 3 303.58 (284-320), 2 307.67 (289-337). Head depth: 3 252.33 (236-274), 2 247.89 (233-277). Head width: § 224.17 (212-245), § 229.61 (211-248). Least bony interorbital width: \$\delta\$ 138.42 (117-155), \$\dagger\$ 139.50 (122-162). Shout length: \$\darger\$ 81.25 (69-93), ♀ 85.22 (72-94). Orbit length: ♂ 79.08 (69-87), ♀ 76.39 (64-85). Depressed dorsal fin length: ∂ 243.67 (221-272), ♀ 217.22 (198-247). Depressed anal fin length: ♂ 247.25(201-294), ? 213.00(192-234). Middle ray caudal fin length: 3 201.40(182-216), 2 200.88 (182-224). The following vertebral counts are based on 20 specimens (UMMZ M124998), with frequency of each count given in parenthesis; precaudal: 12(17), 13(3), avg. 12.2; caudal: 15(1), 16(6), 17(13), avg. 16.6; total: 28(5), 29(15), avg. 28.8.

Etymology.—The Latin name grandis refers to the relatively large size of this subspecies.

Crenichthys b. baileyi (Gilbert). White River springfish (Fig. 10).

Diagnosis.—Crenichthys b. baileyi differs from C. b. albivallis in having a longer head and greater least bony interorbital width (Figs. 2, 3). Crenichthys b. baileyi differs from C. b. thermophilus in possessing a longer anal to caudal length (Fig. 4). Crenichthys b. baileyi differs from C. b. grandis and C. b. moapae in having fewer fin rays (Table 3).

Type Material.—Two of the original type specimens utilized by Gilbert (1893) to describe Cyprinodon macularius baileyi (now Crenichthys baileyi) are deposited at the California Academy of Sciences (SU 709). Since the syntypes of Gilbert were immature (< 20 mm SL), two topotypes, one of each sex, have been chosen to serve as representative specimens of C. b. baileyi. Representative topotypes, male (UMMZ 203331), 30.1 mm (SL); and female (UMMZ 203331), 35.4 mm; collected 10 Jun. 1967 by J. E. Deacon from Ash Spring along with 29 additional specimens, ASU-5196 (21.0-40.0 mm).

Distribution.—Crenichthys b. baileyi is restricted to a single spring, Ash (T 6 S, R 61 E, Sec 6) in Pahranagat Valley, Lincoln Co., Nevada. The Crenichthys baileyi that inhabit the outflow creek below Ash Spring exhibit some integration of meristic and color characters with C. b. grandis. Crystal Spring is located in the main river channel just upstream from Ash Spring. Crenichthys prefer and predominately inhabit springs; however, the location of Crystal Spring in the main river channel makes it susceptible to floods and therefore provides a mechanism to disperse springfish downstream into the extensive outflow creek of Ash Spring. The head pool population of Crenichthys in Ash Spring is separated from the outflow creek by precipitous topography, preventing movement of springfish from the outflow creek into the head pool, insuring the genetic purity of the head pool fish.

Species Associates and Status.—Gila robusta jordani, Rhinichthys osculus velifer, Catostomus clarki intermedius, and Lepidomeda altivelis were associated with Crenicnthys in the Ash Spring outflow (Miller and Hubbs 1960). The description of Rhinichthys o. velifer by Gilbert (1893) indicates its association with Crenichthys in the head pool area. Several exotic species (Gambusia affinis, Poecilia mexicana, P. latipinna, and Cichlasoma nigrofasciatum) have become established in the main pool area (Hubbs and Deacon 1964). Due to the establishment of these exotic species, Crenichthys b. baileyi is very rare.

Description.—Crenichthys b. baileyi is a moderately sized C. baileyi subspecies. Many

characteristics of this subspecies are intermediate between the large bodied *albivallis* and *grandis* subspecies and the small bodied *C. b. thermophilus*.

Meristics and Morphometrics.—The following values are based on 30 C. baileyi (5 male, 25 female) from Ash Spring, 27.2-38.5 mm SL. Typical fin ray numbers: dorsal 10, anal 12, caudal 17, and left pectoral 16 (Table 3). Lateral line scales typically 28 and candal peduncle circumference scales typically 17 (Table 4). Predorsal length: 3 720.80 (704-729), ♀ 705.00 (685-736). Anal to caudal length: ♂ 357.00 (331-380), ♀ 340.28 (315-365). Greatest body depth: § 355.20 (317-412), § 300.04 (259-352). Greatest body width: δ 226.00 (207-244), ♀ 214.68 (192-238). Head length: δ 334.20 (314-357), ♀ 323.88 (301-357). Head depth: δ 245.00 (234-261), ♀ 255.36 (205-252). Head width: δ 235.60 (220-244), 2 225.88 (208-252). Least bony interorbital width: 3 156.80 (151-162), ♀ 156.48 (141-178). Snout length: ♂ 84.40 (77-90), ♀ 82.16 (79-99). Orbit length: ♂ 86.80 (76-103), \$\gamma \text{81.16 (79-92)}. Depressed dorsal fin length: \$\delta \text{218.80 (199-231)}, \$\gamma\$ 195.28 (164-223). Depressed anal fin length: δ 220.80 (192-241), ♀ 206.08 (180-234). Middle ray caudal fin length: δ 191.40 (172-210), ♀ 191.72 (170-208). The following vertebral counts are based on 20 specimens (UMMZ M125006), with frequency of each count given in parenthesis; precaudal: 11(5), 12(15), avg. 11.8; caudal: 15(1), 16(6), 17(13), avg. 16.6; total: 27(5), 28(3), 29(12), avg. 28.4.

Etymology.—Gilbert (1893) named the fish in honor of V. Bailey, one of the collectors of the type specimens.

Crenichthys b. moapae, n. subsp. Moapa White River springfish (Fig. 11).

Diagnosis.—This subspecies is separable from C. b. albivallis in having a longer head and greater least bony interorbital width (Figs. 2, 3). Crenichthys b. moapae differs from C. b. thermophilus in possessing a longer anal to caudal length (Fig. 4). Crenichthys b. moapae can be distinguished from C. b. grandis by coloration. The deep green middorsal stripe and the bright blue bands to either side are less prominent in C. b. moapae than in C. b. grandis. The yellow color on males of C. b. moapae is reduced, being displayed only as orange-yellow pectoral fin bases and occasionally in parts of the caudal peduncle. The belly and lower parts of the head are lemon yellow on males of C. b. grandis. Crenichthys b. moapae is separable from C. b. baileyi in the former having more fin rays (Table 3).

Type Material.—Holotype, male (UMMZ 203338), 47.8 mm SL and allotype (UMMZ 203339), 41.9 mm; collected 26 Feb. 1967 by M. Belcher from Cardy Lamb Spring along with 61 paratopotypes ASU-5231 (16.8-56.8 mm).

Distribution.—Crenichthys b. moapae inhabits headwater springs of the Moapa River (T 14 S, R 65 E) in Clark Co., Nevada. An apparently introduced population exists in a spring near Anderson Dairy Farm along the Moapa River (T 15 S, R 66 E, Sec 3). The type locality, Cardy Lamb Spring, is located in the SW¼ of section 9 (T 14 S, R 65 E).

Species Associates and Status.—Several native species (Rhinichthys osculus moapae, Moapa coriacea), the local form of Gila robusta, and Crenichthys baileyi moapae inhabit headwater areas of the Moapa River (Cross 1976, Williams 1978). Exotic species (Gambusia affinis, Poecilia mexicana, and Pimephales promelas) also inhabit Moapa River headwater areas. Crenichthys b. moapae is still abundant in many headwater springs of the Moapa River.

Meristics and Morphometrics.—The following values are based on 30 Crenichthys baileyi (10 male, 20 female) from Cardy Lamb Spring, 29.2-57.1 mm SL. Typical fin ray numbers: dorsal 11, anal 13, caudal 18, and left pectoral 17 (Table 3). Lateral line scales typically 28 and caudal peduncle circumference scales typically 17 (Table 4). Predorsal length: \$\sigma\$ 709.00 (687-729), \$\gamma\$ 711.05 (682-734). Anal to caudal length: \$\sigma\$ 347.36 (329-363), \$\gamma\$ 337.21 (316-359). Greatest body depth: \$\sigma\$ 330.55 (303-360), \$\gamma\$ 303.84 (276-335). Greatest body width: \$\sigma\$ 204.82 (191-228), \$\gamma\$ 211.68 (188-252). Head length: \$\sigma\$ 305.64 (292-339), \$\gamma\$ 301.00 (269-331). Head depth: \$\sigma\$ 253.27 (231-284), \$\gamma\$ 241.16

(205-287). Head width: § 223.27 (213-242), § 228.05 (201-275). Least bony interorbital width: § 150.27 (141-162), § 155.63 (136-173). Snout length: § 81.82 (74-93), § 78.63 (68-93). Orbit length: § 79.73 (66-95), § 78.32 (61-90). Depressed dorsal fin length: § 226.27 (203-261), § 194.68 (174-222). Depressed anal fin length: § 225.27 (205-249), § 195.32 (172-219). Middle ray caudal fin length: § 196.82 (178-211), § 186.63 (165-205). The following vertebral counts are based on 20 specimens (ASU-5231), with frequency of each count given in parenthesis; precaudal: 12(11), 13(8), 14(1), avg. 12.5; caudal: 15(6), 16(8), 17(6), avg. 16.0; total: 28(10), 29(10), avg. 28.5.

Etymology.—The name moapae, of Moapa, refers to endemism of the subspecies in the Moapa River system.

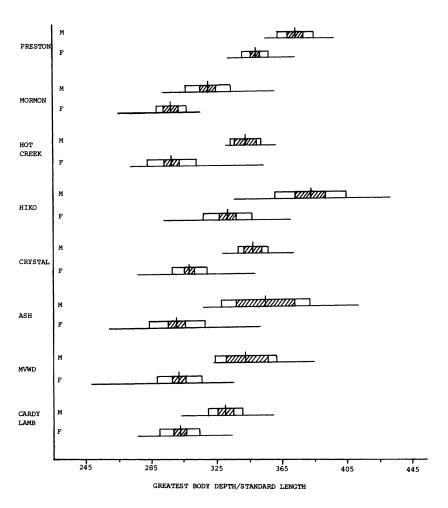


Fig. 6. Comparison of greatest body depth in populations of *Crenichthys baileyi*. See text for explanation of figure.

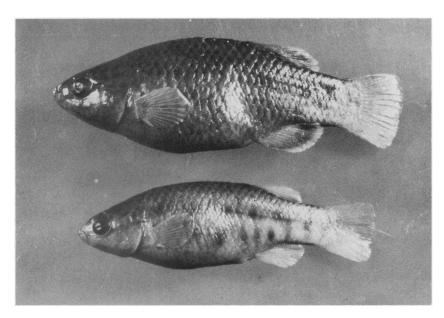


Fig. 7. Crenichthys b. albivallis: above, holotype (42.3 mm SL); below, allotype (36.0).

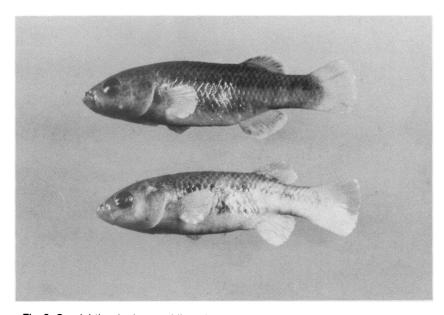


Fig. 8. Crenichthys b. thermophilus: above, holotype (32.4); below, allotype (31.6).

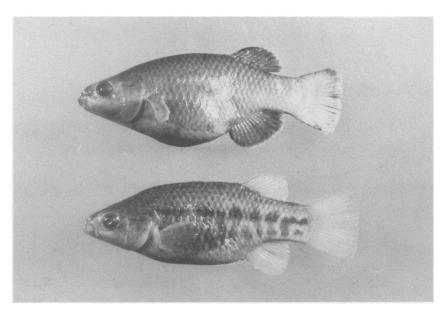


Fig. 9. Crenichthys b. grandis: above, holotype (45.5); below, allotype (45.4).

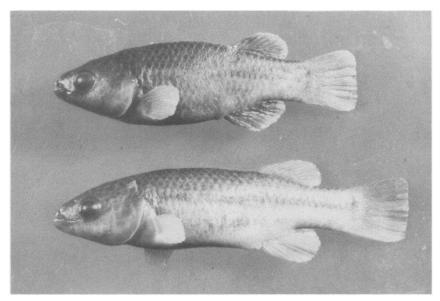


Fig. 10. Crenichthys b. baileyi: above, male topotype (30.1); below, female topotype (35.4).

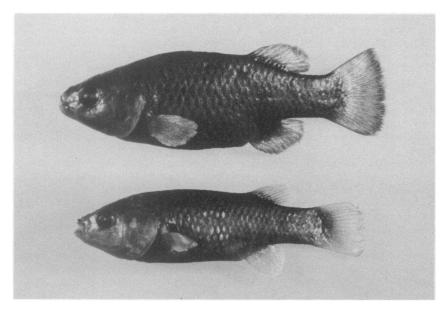


Fig. 11. Crenichthys b. moapae: above, holotype (47.8); below, allotype (41.9).

DISCUSSION. Like many native fishes of the Great Basin, Crenichthys baileyi exhibits a relict distribution. The obligate spring existence of Crenichthys and the drying of the pluvial White River system have resulted in geographic isolation among the many populations of C. baileyi. Geographic isolation has been demonstrated to be a potent force in the evolution of desert fishes (Hubbs and Miller 1948b, Miller 1948). Miller (1948) found geographic isolation to be the most important factor allowing for speciation in Death Valley Cyprinodon populations. Populations of Crenichthys baileyi have probably been isolated for many thousands of years. Geographic isolation persists at present time due to the following: 1) usually dry condition of the White River channel, 2) obligatory spring existence of Crenichthys, 3) extreme distances among some spring populations, and 4) location of the springs a small distance from the river bed. The last three characteristics provide continued isolation among spring populations during flood events. An exception to the isolation occurs in Pahranagat Valley, where Crystal Spring and the outflow creek of Ash Spring occur in the river bed. This permits some contamination of the Ash Spring outflow creek fish by individuals from Crystal Spring during floods. The head pool of Ash Spring is isolated, however, from its outflow creek by precipitous topography, insuring the genetic purity of the head pool fish.

Arid regions of the western United States have provided numerous examples of remnant fish populations in isolated springs evolving relatively rapidly (Hubbs 1941, Hubbs et al. 1974). Much of the rapid evolution in *Crenichthys baileyi* populations can be attributed to differences in temperature and oxygen values among the isolated spring habitats occupied by this species. As the populations became isolated, a divergence of morphological features among the fish populations occurred as they adapted to the unique qualities of their environment. Sumner and Sargent (1940) illustrated this concept by finding that *C. baileyi* from cool, well oxygenated waters of Preston Spring could not survive in the warm, poorly oxygenated waters of Mormon Spring. We attempted to

account for the inability of *C. baileyi* from Preston Spring to survive the more poorly oxygenated waters of Mormon Spring by comparing the gill filament number and length in fishes from the two springs. Insignificant differences existed in gill filament number; however, gill filament length varied significantly. Of 10 *C. baileyi* from Mormon Spring (27.8-37.1 mm), the mean value of longest gill filament was .046 SL (range .040-054). Ten *C. baileyi* from Preston Big Spring (32.6-40.7 mm) exhibited a mean longest gill filament value of .0362 SL (.034-.042). Variation in gill surface area is apparently attributable to evolution of *C. baileyi* populations in springs with different dissolved oxygen concentrations. Deacon and Minckley (1974) attributed the survival of *C. baileyi* in poorly oxygenated water to their proportionately longer gills as compared to other desert fishes.

Both geographic isolation and environmental factors are important considerations in designating the five subspecies herein described. Crenichthys b. albivallis occurs in the seven northernmost springs inhabited by the species. These springs are characterized by cool temperatures (near 20°C) and relatively high dissolved oxygen at the spring source (above 3 ppm). Crenichthys b. thermophilus inhabits three springs near a dry tributary of the pluvial White River approximately 20 km southwest of Lund Town Spring. The springs inhabited by C. b. thermophilus are warm (33.3-37.0°C) and have low dissolved oxygen at the spring source (0.7-2.0 ppm). Over 100 km south of these springs are the springs of Pahranagat Valley and the headwaters of the Moapa River. The Ash Spring population has distinct meristic features, and is therefore considered separable from other C. baileyi populations. Other Pahranagat Valley populations, Hiko and Crystal, are considered distinct from Moapa River populations due to geographic isolation and differences in color.

The authors are indebted to the many people who provided assistance throughout the various stages of this study. Particularly, Carl L. Hubbs and Robert R. Miller deserve acknowledgment for the loan of museum specimens, field notes, radiographs, and their extensive knowledge of these fishes. William N. Eschmeyer kindly loaned the remaining type specimens of *Crenichthys baileyi*. James E. Deacon provided valuable assistance throughout this work and reviewed the manuscript. Clark Hubbs provided a beneficial review of an earlier draft of this paper. Thom B. Hardy kindly provided location data and status reports for several populations. Thanks are due Carl E. Bond for allowing one of us (JW) to work on something besides *Gila*. Cynthia D. Williams typed and reviewed drafts of this paper.

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