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Mexican Goodeid Fishes of the Genus *Characodon,* with Description of a New Species

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ABSTRACT

The goodeid fish genus *Characodon* Günther is revised and diagnosed on the basis of inferred derived characters of the ovary, embryonic trophotaeniae, male anal-fin clasper, and chromosomes. Three species are recognized: *Characodon lateralis, C. audax,* n. sp. from an isolated spring in Durango, Mexico, and the disjunct *C. garmani* herein resurrected as valid.

INTRODUCTION

The genus *Characodon* is readily distinguished from other goodeid fishes on the basis of morphological and chromosomal characters (Miller and Fitzsimons, 1971; Fitzsimons, 1972; Uyeno et al., 1983). The type species, *C. lateralis* Günther, is specialized in several reproductive characters and has usually been considered to comprise a monotypic genus (Hubbs and Turner, 1939, and works above). A second species that shares the reproductive specializations of *C. lateralis* has recently been discovered in an isolated spring near Durango City, State of Durango, Mexico. It is described below. A third species, *C. garmani* Jordan and Evermann, is resurrected from the synonymy of *C. lateralis.* The genus is diagnosed on the basis of characters inferred to be derived.

METHODS: Counts were taken as described by Miller (1948) and, for head canals, by Gosline (1949). The rudimentary anterior anal ray is included in the anal-ray count and the last two closely approximated rays of the dorsal and anal fins are counted as one ray. In the meristic data below, the number of specimens with each count is given in parentheses and the count for the holotype is indicated by an asterisk. For paired fins and head ca-

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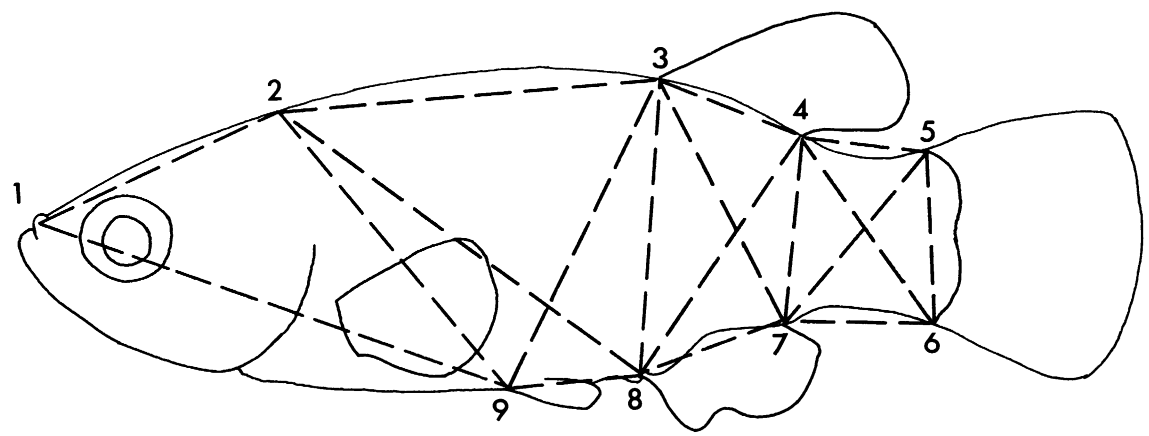

FIG. 1. Morphometric variables forming the elements of a truss network superimposed on the outline of *Characodon lateralis*. Numbered points indicate the landmarks of measurements given in table 1.

nals, the count for each side of the specimen is reported.

In order to include morphometric information from all parts of the body, short straight-line segments were measured between discrete anatomical landmarks (Humphries et al., 1981) and measurements were taken from a pattern of trusses (fig. 1, table 1) as suggested by Strauss and Bookstein (1982). All measurements were made with dial calipers reading to 0.1 mm.

Principal components were calculated from the covariance matrix for log-transformed distance measurements, and bivariate scatter diagrams were examined for patterns revealing morphological differences in pairwise and overall comparisons of populations from the separate drainages.

Material is catalogued in the Academy of Natural Sciences of Philadelphia (ANSP), American Museum of Natural History (AMNH), Arizona State University (ASU), British Museum of Natural History (BMNH), Museum of Comparative Zoology (MCZ), and University of Michigan Museum of Zoology (UMMZ).

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SYSTEMATICS

Characodon Günther

Type species, *Characodon lateralis* Günther.

DIAGNOSIS: Goodeid fishes distinguished by the following derived characters: the two bilateral ovarian chambers are separated by an undivided septum with ovigerous tissue localized in the dorsal part of the septum and the dorsolateral ovarian walls; embryonic trophotaeniae comprise a pair of elongate, sheathed processes with no lateral branches; the anal-fin clasper in males consists of eight modified, shortened rays, of which ray 1 is

TABLE 1
Proportional Measurements of *Characodon*, Expressed as Thousandths of Standard Length

Measurement (numbered as in fig. 1)	*C. lateralis*, 16♂♂ Range	*C. lateralis*, 16♂♂ Mean	*C. lateralis*, 16♀♀ Range	*C. lateralis*, 16♀♀ Mean	*C. audax*, 14♂♂ Holotype	*C. audax*, 14♂♂ Range	*C. audax*, 14♂♂ Mean	*C. audax*, 14♀♀ Range	*C. audax*, 14♀♀ Mean	*C. garmani*, 1♀ Holotype
Standard length, mm	20.7–41.6	31.9	26.5–62.8	37.7	38.3	22.4–42.6	31.9	20.8–48.5	35.5	27.0
1–2	169–251	214	177–247	209	204	176–237	206	192–240	217	259
1–9	521–579	547	528–592	562	574	524–574	548	546–581	562	570
2–3	489–573	526	483–582	545	546	496–580	539	504–581	548	526
2–8	514–585	551	502–600	560	574	531–593	562	529–606	560	578
2–9	384–454	418	392–476	439	452	404–452	425	406–478	442	441
3–9	346–418	383	321–407	358	431	357–431	383	303–408	363	300
8–9	133–186	154	124–194	161	178	138–178	159	120–193	159	163
3–4	116–170	149	103–134	118	138	116–158	142	96–126	111	107
3–7	248–305	273	215–275	232	261	219–291	258	202–249	228	218
3–8	298–346	322	253–318	274	329	290–336	315	248–295	273	244
7–8	104–138	120	77–108	96	104	98–133	117	82–94	87	70
4–8	260–317	294	228–280	253	298	268–312	291	231–279	255	218
4–7	184–230	205	167–214	185	198	183–221	201	163–207	186	174
4–5	115–155	137	137–192	160	136	116–170	141	137–175	157	174
4–6	225–253	237	215–258	234	238	217–248	234	209–260	242	233
5–7	244–309	274	250–290	268	272	249–281	268	259–295	277	259
6–7	165–219	192	164–238	203	217	171–217	191	182–224	205	200
5–6	156–202	179	142–193	160	178	156–200	176	144–183	165	144
Predorsal length	700–763	726	713–770	735	739	692–756	732	725–762	742	733
Head length	308–360	332	276–343	308	316	314–353	329	294–348	320	344
Eye length	74–116	88	56–94	77	81	73–96	85	67–98	81	96
Pectoral-fin length	165–195	181	135–186	157	175	170–217	187	146–180	169	188
Pelvic-fin length	82–130	99	87–115	100	104	85–104	93	77–101	90	81
Dorsal-fin length	222–286	258	176–217	203	253	219–299	260	178–216	204	204
Anal-fin length	164–207	190	145–181	164	180	170–210	187	138–184	157	167
Caudal-fin length	188–244	215	180–226	199	198	180–232	208	171–223	202	—

reduced to a nob, rays 1–7 are unbranched, and the bases of rays 1–7 are partially enclosed in a pocket formed by folds of the adjacent epidermis; the diploid chromosome complement is unique in the family and consists of 24 large metacentric chromosomes. Branchiostegal rays are four in number. The number of rays in the dorsal and anal fins is sexually dimorphic, with more rays in males than in females.

Characodon audax, new species
Bold Characodon
Figures 2, 3

Characodon sp. Anon., 1984, p. 15 ("El Toboso Black"). Radda, 1984, p. 22 (photograph of live male; "Coahuila" erroneously given as locality). Meyer et al., 1985, p. 88 (color photograph of live male; "Coahuila"). Smith and Miller, 1986, Table 13.3 (listed). Miller, 1986 (habitat, range).

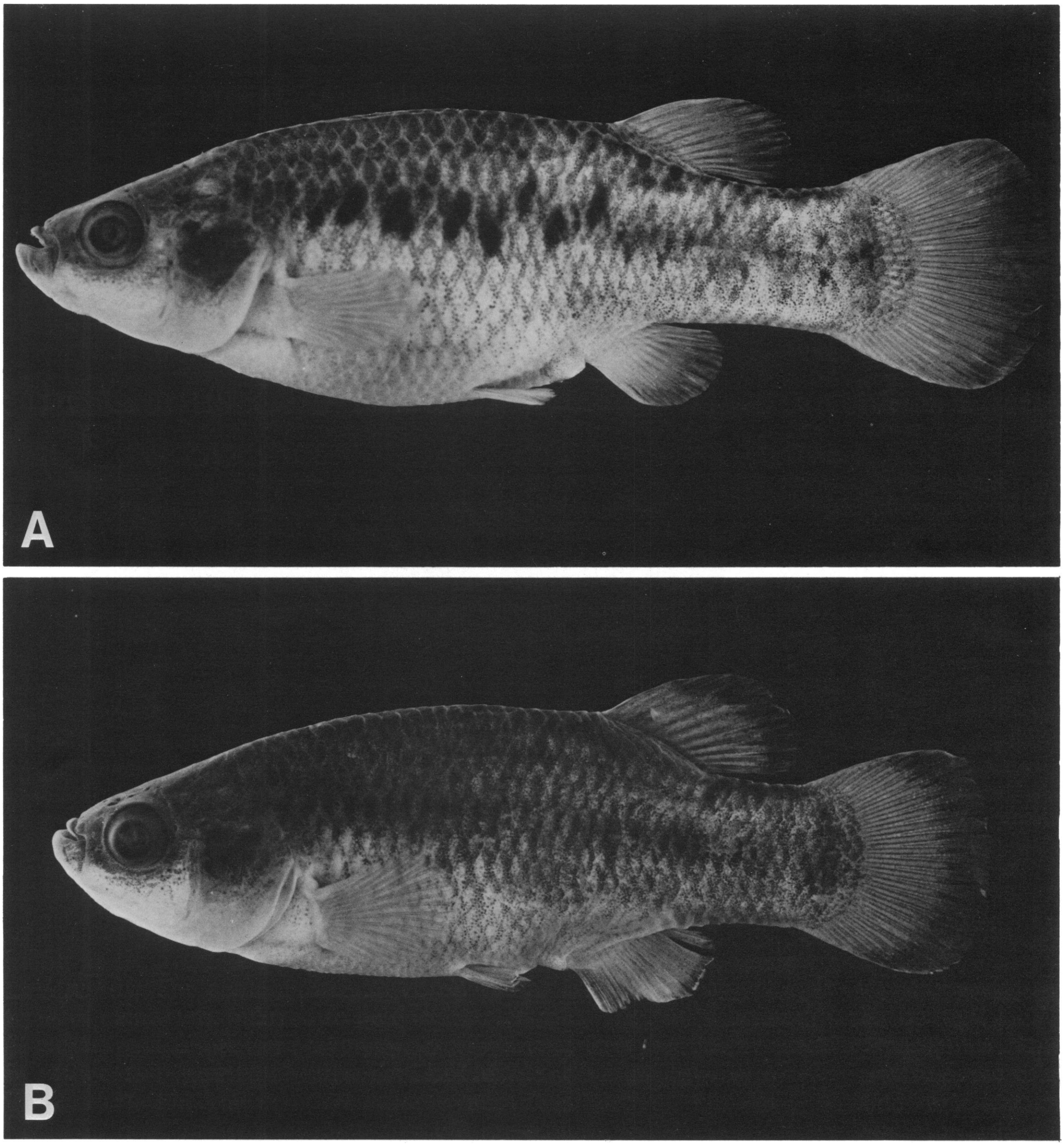

FIG. 2. **A.** *Characodon lateralis* female, 38.6 mm; **B.** *C. lateralis* male, 31.9 mm; UMMZ 211063.

MATERIAL: The holotype (UMMZ 213302), a mature male 38.5 mm in standard length (SL), was collected in a spring-fed pond at El Ojo de Agua de Las Mujeres, near the village of El Toboso, 10.4 km north of Highway 40, State of Durango, Mexico (Sta. M82-58), by R. R. Miller, F. H. Miller, and others, March 16, 1982; 24°16′35″N lat., 104°34′50″W long. The allotype (UMMZ 213303) is an adult female 45.4 mm SL. Taken with the holotype and allotype were 36 juvenile to adult paratypes (UMMZ 211061), 16–46 mm SL, including mature males and females. Four paratypes (UMMZ 213319), two males and two females, 29.7–32.1 mm SL, reared from stock collected at the type locality on April 13, 1983, were karyotyped. Additional paratypes from the type locality taken May 5,

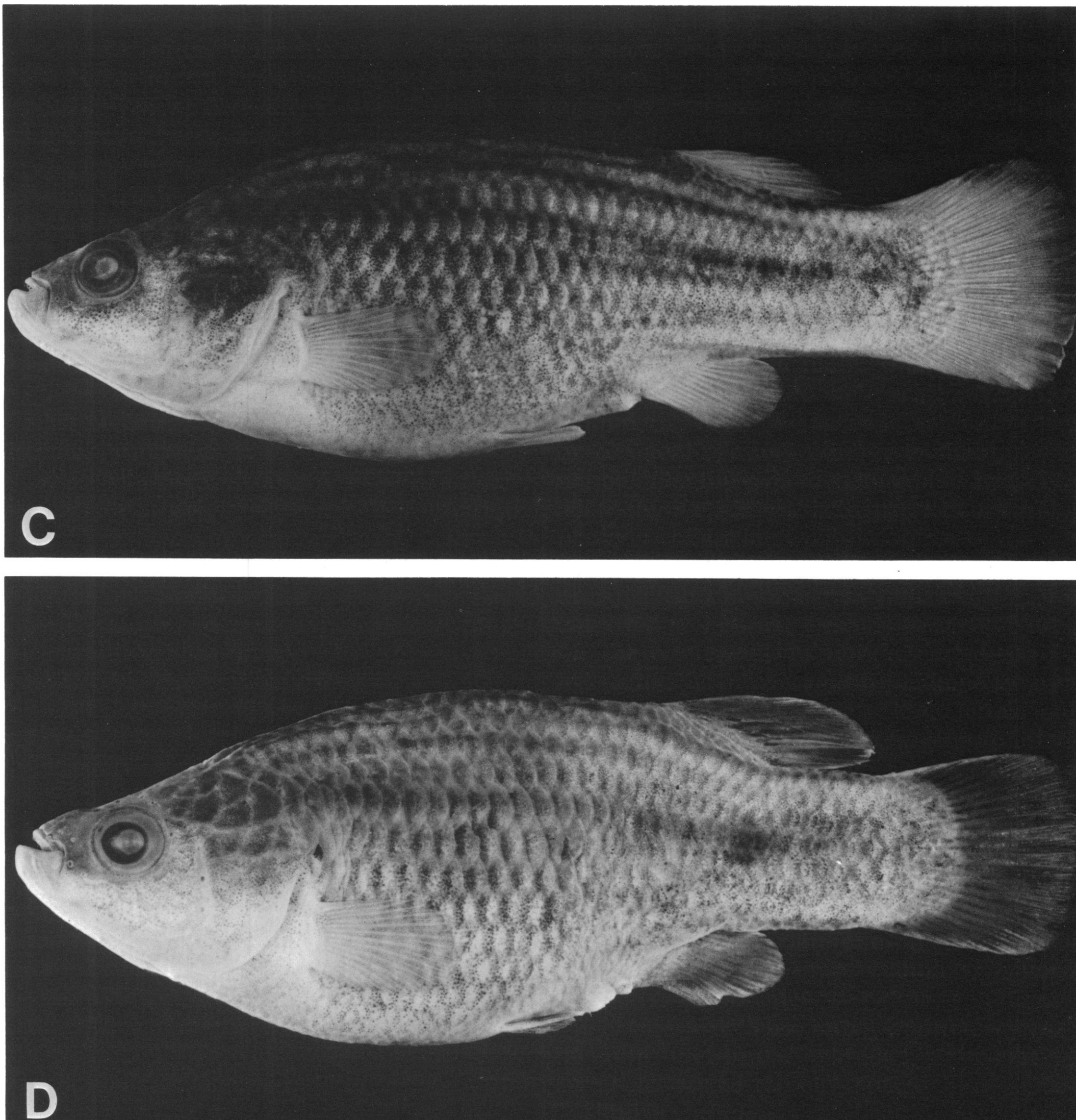

FIG. 2. **C.** *C. audax* female, 45.8 mm; **D.** *C. audax* male, 38.3 mm, UMMZ 211061.

1985, by R. R. Miller, F. H. Miller, and E. Uribe, are distributed as follows: 168, 21.4–47.8 mm SL (UMMZ 213312); 20 ♂ and ♀, 24.7–41.5 mm SL (AMNH 57006); 20 ♂ and ♀, 23.8–41.4 mm SL (ANSP 157641); and 20 ♂ and ♀, 23.8–44.4 mm SL (USNM 274718).

DIAGNOSIS: A medium-size goodeid (to 48 mm SL) with dorsal-fin rays typically 11 in males, 10 in females; outer-series teeth mostly bicuspid, occasionally blunt or conic, attached firmly to jaws; pelvic fins not reaching anus in males; dorsal profile indented at nape among adults; male coloration unique in goodeids, black over entire back and upper sides of body (above level of pupil) except for basal one-third of pectoral and pelvic fins, breast, and underside of head which are yellowish orange; outer two-thirds of interradial membranes of paired fins are black; some scales on sides of body have an iridescent silvery or light blue sheen.

DESCRIPTION AND COMPARISONS: General

morphology and pigmentation of preserved specimens are shown in figure 2 and morphometric data are given in table 1. The body is deep, robust, and moderately compressed. The dorsal and anal fins are set far back on the body, the dorsal origin slightly behind the anal origin.

The upper and lower jaws bear two series of teeth. Those in the outer series are mostly bicuspid, but a few smaller teeth (laterad from the symphysis) are conic. Tricuspid teeth have not been observed. The outer teeth are firmly attached to the jaws as in *Allodontichthys, Allotoca,* and others (see Hubbs and Turner, 1939) rather than loosely attached as in *Ataeniobius, Goodea,* and *Skiffia.* Teeth of the inner series are smaller and conic; they are arranged in a single row or band, narrower than in *C. lateralis,* and barely emerge from the oral epithelium.

Scales in lateral series 30(1 count), 31(9), 32*(28), 33(8), 34(1). Body circumference scale rows 30(3), 31(6), 32(9), 33(11), 34(10), 35(1). Caudal peduncle scale rows 17*(3), 18(33), 19(6), 20(1). Dorsal-fin rays in males 11*(15), 12(6); in females 9(1), 10(20), 11(5). Anal-fin rays in males 14*(13), 15(16), 16(2); in females 12(3), 13(18), 14(5). Caudal-fin rays 17(2), 18(5), 19(20), 20*(18), 21(2). Pectoral-fin rays 15(6), 16(34), 17*(9). Total gill rakers, right anterior arch 13(5), 14(15), 15(13), 16*(8), 17(1). Total vertebrae (including hypural) 32(2), 33(18), 34(26), 35(1).

The acoustico-lateralis system on the head consists of a combination of pit organs, canals, and pores. The number of pores is as follows: mandibular 4(80); preorbital 4(80); preopercular 6(1), 7(53), 8(23), 9(3). The supraorbital canal is interrupted at several points and modally consists of a canal between pores 1–2a, 2b–4a, 4b–6a, 6b–7. An interruption between pores 6a and 6b has been reported only in species of *Characodon, Xenotoca,* and *Ameca* (Fitzsimons, 1981).

The anterior rays and pterygiophores of the male anal fin are modified to form a lobe that serves as a clasping organ during copulation. Rays 1–8 are reduced in length, 74–85 percent as long as the longest unmodified ray. Ray 1 is a rudimentary nob or splint, formed from bilateral ossifications that fail to undergo addition of terminal segments to form an elongate ray. Rays 1–7 are not bifurcated. Rays 2–5 are crowded, slightly recurved, and segmented throughout their length. Rays 6–7 are thickened proximally and their basal segments undergo anastomosis to form an unsegmented base. The first four proximal radials are crowded and bear only rudimentary keels. Those that follow are uniformly spaced and bear moderate anterior and posterior keels as in *C. lateralis, Girardinichthys viviparus,* and *G. multiradiatus.* Similar keeled radials are not known in other goodeids. Anal fins of some goodeids are described by Turner et al. (1962) and Miller and Fitzsimons (1971). The distance between the pelvic-fin insertion and the anus is greater than in *C. lateralis,* so that the pelvic fins fail to reach the anal opening.

As in other goodeids, the ovary is a single median structure formed by fusion of paired lateral organs (see Turner, 1933). The ovary of the new species resembles that of *C. lateralis* (Hubbs and Turner, 1939) in having a complete ovarian septum and ovigerous tissue localized in the dorsolateral walls of the ovary and dorsal part of the septum.

In 19 freshly killed near-term embryos, the unpigmented trophotaeniae comprised a pair of sheathed, elongate processes of the perianal lip. The processes are of equal length and extend slightly beyond the margin of the caudal fin. Each process consists of a vascularized stroma running from the base to the apex of the process. An external epithelium is attached to one side of the stroma, but is otherwise free. The primary tissue space thus formed is filled with fluid in fresh specimens with the consequence that the processes are turgid and round in cross section. In embryos dissected from alcoholic specimens (UMMZ 211061) the epithelium is collapsed against the stroma and the processes appear as irregularly flattened ribbons. The trophotaeniae resemble those of *C. lateralis* (Turner, 1937; Hubbs and Turner, 1939); they are otherwise unique.

The karyotype was determined from gill epithelial cells of specimens from a live stock collected at the type locality and maintained in aquaria for eight months. Chromosomes were counted in 26 metaphase spreads from two males and two females (UMMZ 213319). The diploid number was 24 chromosomes in all spreads examined, and all chromosomes

FIG. 3. Somatic chromosomes at metaphase of *Characodon audax* (UMMZ 213319).

were large metacentrics (fig. 3). No sexual dimorphism was detected, and gradation in size of chromosomes was so slight that homologues could not be identified. The karyotype matches that of *C. lateralis* (Fitzsimons, 1972) and is inferred to be derived because it represents the extreme divergence from the primitive goodeid karyotype of 48 telocentric chromosomes (Uyeno et al., 1983).

SEXUAL DIMORPHISM AND COLORATION: The sexes in *C. audax* are distinguished by structural modifications of the male anal fin to form an organ associated with copulation (see Mohsen, 1961a, 1961b; Miller and Fitzsimons, 1971; Nelson, 1975). Both the dorsal and anal fins are longer and bear more rays in males than in females.

Coloration also distinguishes the sexes. In life, adult males are dark gray or black on the back, upper sides of the head, and on the lower body from the pelvic fins to the caudal fin. The sides of the body have a black background that is broken into a reticulated pattern by the scales which have an iridescent silvery or light blue sheen. The dorsal fin is black except for a narrow milky border. The caudal and anal fins are mostly black, but their posterior margins and the anal-fin lobe are usually chalky. The pectoral and pelvic fins are black on the interradial membranes. The underside of the head and sometimes the breast beneath the pectoral fins are light yellowish to deep orange. The tips of the outer-series teeth are brown to black, becoming darker as the fish grows.

In ethyl alcohol, the yellowish orange and iridescent colors disappear. The pigmented areas of the fins remain black or dark gray. The sides of the body become lighter, revealing a dark lateral stripe, as wide as the midlateral scale row, that runs from the upper limit of the opercular cleft to the base of the caudal fin.

In life, adult females have olivaceous to greenish sides, top of head, nape, and back. The scale centers are pale silvery. The region between the pelvics and anal fin is greenish blue, extending upward as a wedge for a short distance. There is some pale yellow color on the throat and branchiostegals. The back is dark olive, the belly pale to bluish gray. A midlateral series of irregular melanic blotches extends from the upper limit of the opercular cleft to the caudal-fin base. The blotches sometimes coalesce to form a solid midlateral stripe, particularly in the region anterior to the median fins, but may extend more posteriorly. Irregular, scattered blotches may mark the sides of the caudal peduncle in the smaller females. An iridescent silvery sheen (less pronounced in males than in females) extends from seven to eight scale rows from behind the head to the anal fin, four rows onto caudal peduncle, and over the thoracic region. The lower jaw, sides of the head beneath the eye, and the breast area beneath the pectoral fins are light yellow-orange or silvery with a light orange cast. The median fins are mostly clear but have a yellowish cast at the base that sometimes extends over the whole fin; the interradial membranes are dusky or light gray. There is no terminal band of gray on the caudal fin as in some large females of *C. lateralis*. The pelvic fins have gray interradial membranes and the pectoral fins are clear.

In ethyl alcohol, yellow and gray-green colors disappear, leaving a brown color dorsally with buff below. As other colors fade, the midlateral stripe or blotches become more prominent, and melanophores on the margins of the scales form a reticulated pattern on the back and sides.

ETYMOLOGY: The Latin epithet, *audax*, meaning bold or daring, refers to the aggressive behavior of the new species.

HABITAT: *C. audax* has been collected only in the outflow of El Ojo de Agua de Las Mujeres at El Toboso, State of Durango, Mexico. This is one of several isolated springs that rise in the semiarid basin of Laguna El Toboso, an ephemeral lake that was dry in March 1982, April 1983, and May 1985. By local account, the flow of the springs is sufficient during periods of high runoff to coalesce and reach the ephemeral lake, but the lake does not fill sufficiently to achieve a surface outlet. The bed of Laguna El Toboso is separated by a low divide (less than 50 m, judged from topographic maps) from the Río de la Sauceda, a stream 6 km distant in the Río Tunal drainage. This divide is the only barrier between the ranges of *C. audax* and *C. lateralis*.

At El Ojo de Agua de Las Mujeres, water issues from several springs and flows about 60 m as a small brook (maximum width, 100 cm; maximum depth, 20 cm) to a pond about 30 × 35 m in major dimensions. The main spring rises in a pool 80 cm in diameter and 20 cm deep and contains no fish. *C. audax* was seen in the brook over mud, sand, and some gravel. Collections were made in the pond where the substrate consisted of deep, silty mud, dense floating and submerged mats of filamentous algae, and basaltic boulders. The water temperature was 22°C on March 16, 1982 and on succeeding visits. When the large spring at Ojo el Mescal, 2.2 airline km west of El Ojo de Agua de Las Mujeres, was visited on May 5, 1985, no fish were seen. This spring also drains toward Laguna El Toboso. *C. audax* is the only species of fish at the type locality.

Characodon lateralis Günther
Rainbow Characodon
Figure 2

Characodon lateralis Günther, 1866, p. 308 (original description; "Central America"); 1869, p. 480, pl. 82, fig. 2 (description; "Central America"). Bean, 1887, pp. 370–371 (comparison). Eigenmann, 1893, p. 56 (listed). Jordan and Evermann, 1896, p. 668 (in key; description from Günther); 1896a, p. 314 (listed); 1898, pp. 2831–2832 (in synonymy of *C. garmani*). Pellegrin, 1901, p. 205 (Jalisco, error in identification or locality). Meek, 1902, pp. 87, 96 (listed); 1903, p. 779; 1904, pp. xl, 1, 119, 121 (description from Günther). Philippi, 1906, pp. 235–237 (viviparity). Regan, 1906–1908, pp. 88–90 (in part; description; *garmani* as synonym). Eigenmann, 1909, p. 304; 1910, p. 455 (listed). Jordan et al., 1930, p. 183 (listed). Turner, 1937, pp. 496, 506, 512, pl. 3, fig. 14 (trophotaeniae). Hubbs and Turner, 1939, pp. 12, 15, 32, 56–57, 74, pl. 1, fig. 8, pl. 2, fig. 9 (in part; characters in keys; types attributed to Mexican Plateau rather than Central America). Gosline, 1949, p. 9 (sensory pores). Fitzsimons, 1972, pp. 731–739, figs. 1–2 (in part; diagnosis; description; range; karyotype; courtship); 1981, p. 6 (cephalic sensory canals). Nelson, 1975, pp. 475–480 (male urogenital organ). Parenti, 1981, pp. 420, 437, figs. 33, 39, 40, 57, 70, 71 (osteological characters). Uyeno et al., 1983, pp. 500, 503, fig. 3 (karyotype). Smith et al., 1984, p. 399 (zoogeography).

Radda, 1984, pp. 19–20 (in part; characters; black-and-white and color photographs of live male). Meyer et al., 1985, p. 88 (in part; characters; color photograph of male; cultured). Smith and Miller, 1986, p. 463 (listed).

Characodon garmani Meek, 1904, pp. 121–122 (in part; description; "Río Mezquital near Durango, spring at Labor . . ."). Contreras-Balderas, 1975, p. 191 (Río Tunal).

DIAGNOSIS: A *Characodon* (to 63 mm SL) with dorsal-fin rays typically 12 in males, 11 in females; outer-series teeth conic, bicuspid or tricuspid; pelvic fins usually reaching or surpassing anus in males; dorsal profile convex. Coloration of adult males distinguishes the species from all other goodeids: median fins bear a proximal band of red or orange followed by a broad black band; lower parts of body are bright red, orange, or yellow, extending dorsally to midline on sides and caudal peduncle; outer two-thirds of paired fins are clear.

DESCRIPTION AND COMPARISONS: Fitzsimons (1972) described the general morphology, chromosomes, and behavior of *C. lateralis*. Proportional measures are compared to those of other *Characodon* in table 1.

Inner-series teeth are conic or hooked and are arranged in a band that is wider than that in *C. audax*. The outer-series teeth are conic in embryos and juveniles, but tend to be replaced by bicuspid teeth as the fish grows (Fitzsimons, 1972). Large adults bear a few tricuspid teeth, and all tooth forms may be present in a single individual. Tricuspid teeth are known in only one other goodeid, *Allodontichthys hubbsi*. Differences in tooth ontogeny suggest, however, that tricuspid teeth are not homologous in the two species. In *A. hubbsi*, the outer-series teeth of juveniles are spatulate rather than conic. Replacement teeth are shouldered and, in adults, the shoulders are developed as small, sharply pointed cusps lateral to a prominent central cusp (Miller and Uyeno, 1980, fig. 2); intermediate bicuspid teeth similar to those of *Characodon* do not occur in *Allodontichthys*.

Characodon garmani Jordan and Evermann
Parras Characodon

Characodon lateralis Garman, 1895, p. 36, pl. 1, fig. 9 (description; teeth figured; Parras, Coahuila, Mexico). Regan, 1906–1908, pp. 89–90 (in part; range; *garmani* synonymized). Hubbs and Turner, 1939, p. 57 (in part; synonymy of *garmani* accepted). Fitzsimons, 1972, p. 733 (in part; meristics). Radda, 1984, pp. 19–20 (in part; distribution). Meyer et al., 1985, p. 88 (in part; distribution). Smith and Miller, 1986, table 13.1 (habitat, range, extinction). Williams et al., 1985, table 1 (Parras).

Characodon garmani Jordan and Evermann, 1898, pp. 2831–2832 (new name given based on Garman's (1895) description; Parras, Coahuila, Mexico). Meek, 1903, p. 778 (distribution); 1904, pp. 121–122 (in part; description based on material of *lateralis*). Eigenmann, 1910, p. 455 (range). Jordan et al., 1930 (listed). Smith et al., 1984, p. 399 (zoogeography).

DIAGNOSIS: An extinct *Characodon,* known only from the female, which is distinguished from females of other *Characodon* by shorter base of anal fin, shorter pelvic fins, lesser body depth between dorsal and anal fins, greater distance between snout and occiput, and longer pectoral fins. Dorsal profile convex.

DESCRIPTION: The holotype (MCZ 27704) has 11 dorsal-fin rays, 12 anal-fin rays, 19 caudal-fin rays, 16-16 pectoral-fin rays, 6-5 pelvic-fin rays, 33 vertebrae, and 4 branchiostegal rays. Outer-series teeth are blunt, conic, or bicuspid; inner-series teeth are conic or hooked (Garman, 1895, pl. I, fig. 9). Morphometric data are given in table 1.

NOMENCLATURE: Garman (1895) reported a single female goodeid collected by Edward Palmer from a spring or endorheic stream near Parras, Coahuila (fig. 4), a locality remote from the range of other goodeids. He described the specimen and identified it as *C. lateralis*. Jordan and Evermann (1896–1900), however, restricted the name *C. lateralis* to specimens reported to have been collected in "Central America" (Günther, 1866, 1869); they renamed the Parras fish *C. garmani* solely on the basis of Garman's description without distinguishing it from *C. lateralis*. Apparently, Meek's (1904) treatment of the species of *Characodon* was also based on their presumed distribution. He used the name *garmani* for specimens from Parras and the Río Mezquital (both in northern Mexico), and applied the name *lateralis* to material that he believed to have come from "Lowland streams from Central America north to the State of Jalisco" (Meek, 1904, p. 121). We agree with Fitzsimons (1972) that the latter two localities are dubious, and we identify Günther's syntypes as conspecific with our collections from the upper Río Mezquital basin. Regan (1906–1908) synonymized *C. garmani* with *C. lateralis* because "Garman's description appears about equally applicable to *C. lateralis* .... Specimens collected by Dr. Meek at Durango and sent as *C. garmani* are identical with *C. lateralis.*" This synonymy has been generally accepted (Hubbs and Turner, 1939; Alvarez, 1970; Fitzsimons, 1972). Regan did not, however, reexamine the holotype from Parras. That specimen differs from other *Characodon*, including Meek's material from Durango, in several morphometric features (see Diagnosis above and table 1) and we therefore recognize *C. garmani* as a valid species.

DISTRIBUTION

The species are distributed in the remnants of an inferred former stream system on the interior slope of the Central Plateau. Meek (1904) first suggested that the upper Río Mezquital (now a Pacific-slope stream) formerly flowed to the Rio Grande, and ichthyological evidence that it has been part of an interior drainage is discussed by Smith and Miller (1986). The species of *Characodon* are allopatric in three independent hydrographic units (fig. 4). *C. audax* is known only from an isolated spring that sometimes flows to the intermittent lake, Laguna El Toboso, that is not known to have had an outlet during historic time. *C. lateralis* is widespread in springs, creeks, and ponds in the upper Río Mezquital which flows onto the Pacific versant. *C. garmani* was collected in an endorheic system of springs that flowed toward the dry lake bed of Laguna de Mayrán, the terminus of the Río Nazas. This distribution in remnant aquatic habitats is suggestive of speciation subsequent to vicariance.

LOCALITY RECORDS: The localities below are plotted in figure 4. Each locality is followed by the date of collection; numbers of specimens are given in parentheses. Localities for *C. lateralis* and *C. audax* are in the State of Durango; that of *C. garmani* is in the State of Coahuila. *C. lateralis:* UMMZ 65228 (2), Río Mezquital near Durango City, 1903; UMMZ 160880 (25), springs at Berros, 1946; UMMZ 161689 (92), reservoir ca. 25 km E Durango City, 1951; UMMZ 166708 (275), hot springs 9 km E Durango City, 1952; UMMZ 167728 (18), Río de la Sauceda 13 km NE Durango City, 1949; UMMZ 179647 (20), reservoir in Río Tunal ca. 31 km E Durango City, 1961; UMMZ 179655 (2), Río Tunal 9 km SE Durango City, 1961; UMMZ 189091 (308), Ojo de Agua de San Juan near Berros, 1968; UMMZ 192459 (83), below dam at Presa Peñon del Aguila 7 km N Morcillo, 1969; UMMZ 192461 (42), Río Mezquital and ponds 14 km NE Durango City, 1969; UMMZ 199015 (31), spring at Nombre de Dios, 1971; UMMZ 203230 (40), spring near 27 de Noviembre, NE Durango City, 1976; UMMZ 209814 (2), Berros, 1968; UMMZ 211058 (60), Ojo de Agua de San Juan near Berros, 1982; UMMZ 211063 (265), spring 8 km SE Guadalupe Aguilera, 1982; UMMZ 211091 (108), arroyo 16 km N Canatlán, 1982; UMMZ 211096 (77), spring at Cerro Gordo, 15 km S Guadalupe Aguilera, 1982; ASU 6420 (70), spring at Amado Nervo, 1971; BMNH 1855.9.19:317–320, 1566–1569 (14), syntypes, Central America (presumably by error). *C. audax:* UMMZ 213302 (holotype), 213303 (allotype), 211061 (35), 1982; UMMZ 213319 (4), 1983; UMMZ 213312 (168), AMNH 57006 (20), ANSP 157641 (20), USNM 274718 (20), 1985; all from Ojo de Agua de Las Mujeres near El Toboso. *C. garmani:* MCZ 27704 (1), springs or stream at Parras, probably 1880.

DISCUSSION

Morphometric differences among the species of *Characodon* were sought by analyzing bivariate scatter diagrams of principal components scores. Males and females were treated separately, and comparisons included all possible pairs of populations as well as overall comparisons.

The analysis showed *Characodon audax* and *C. lateralis* to be quite similar in general body shape, and scores of specimens formed clusters that overlapped broadly. Although the new species can be reliably identified by shape of the dorsal profile (indented in *C. audax,* convex in *C. lateralis* and *C. garmani*; fig. 2), this feature of the body outline is not bounded by discrete, homologous landmarks and was not recovered in the analysis. Males of *C. audax* and *C. lateralis* can usually be distinguished by position of the anus which is covered by the pelvic fins in all populations of *C. lateralis* except that at Nombre de Dios, Durango. In *C. audax,* the pelvic fins of males consistently fail to reach the anus.

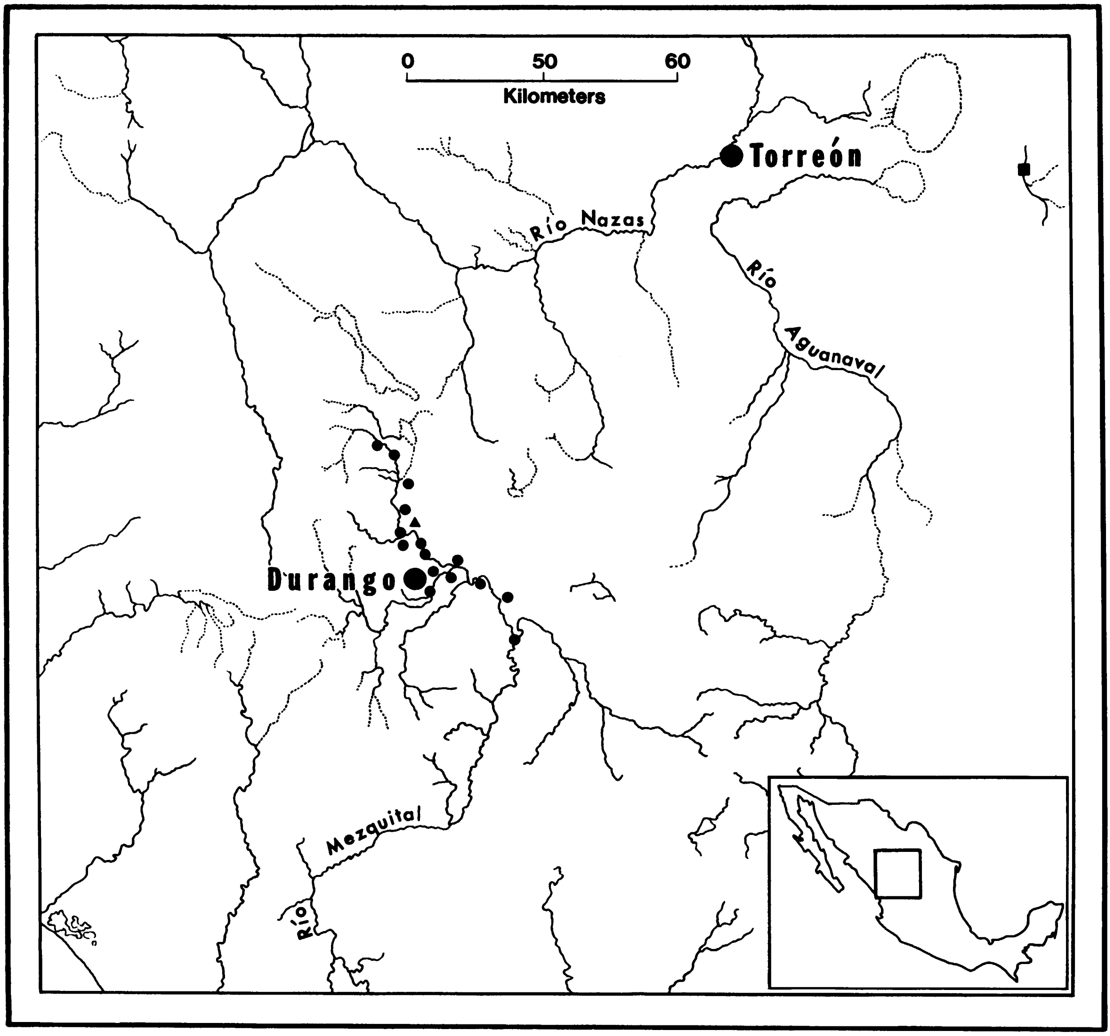

FIG. 4. Distribution of the species of *Characodon* based on locality records listed in text. Dots, *C. lateralis*; triangle, *C. audax*; square, *C. garmani*. Not all collections at a given locality are indicated.

Characodon garmani is known from a single female specimen. When compared to clusters of scores for females of *C. lateralis* and *C. audax*, the specimen of *C. garmani* was consistently found in an outlying position due to proportional characters given in its diagnosis (above). The scores of females of *C. lateralis* and *C. audax* formed overlapping clusters.

We have considered the possibility that the proportional characters that diagnose *C. garmani* are artifacts resulting from long storage in spirits (the single specimen was preserved before 1895). The measurements involving the pelvic-fin and anal-fin origins (segments between landmarks 3–9, 3–8, 7–8, and 4–8; fig. 1, table 1) are particularly suspicious because they could be affected by deterioration of the abdominal wall. We note, however, that the anal-fin base and pelvic fins are proportionately short compared to those of other *Characodon,* while the pectoral fin is proportionately long. We judge it unlikely that these characters are the result of storage.

CONSERVATION STATUS

The natural populations of *Characodon* have been greatly reduced because these fishes occupy limited aquatic habitats in an arid region that has been subject to development for agriculture. *C. garmani* was part of a small but distinctive fish fauna at Parras that also included the monotypic stumptooth minnow (*Stypodon signifer*) and the Parras pupfish (*Cyprinodon latifasciatus*) (Williams et al., 1985; Smith and Miller, 1986). Sometime between 1900 and 1953, the goodeid, as well as the other two extinct fishes just listed, disappeared as determined by C. L. and L. C. Hubbs (see Miller, 1961, p. 380). Testimony obtained by them in 1953 indicated that natural springs no longer exist in Parras Valley, and that spring water was concentrated in a reservoir (containing carp) from which it was diverted by ditches into a cotton mill and onto fields. Flow in the arroyo (fed originally by natural springs) was affected by industrial and domestic sewage. These factors combined to eliminate most of the endemic fish fauna. At present the Parras fish fauna is dominated by exotics, with only one or two of the six or seven native species still surviving in minimal habitat and small numbers (Contreras-Balderas, 1985).

Characodon lateralis has seriously declined in abundance and distribution during the last 25 years; it is listed as a threatened species by Deacon et al. (1979). By 1968, it could no longer be found in the Río Tunal, south of Durango City, where it was common in 1963 (Contreras-Balderas, 1975). Exotic fishes (*Cyprinus carpio, Carassius auratus, Lepomis macrochirus,* and *Micropterus salmoides*) were taken there for the first time in 1968. By 1975, this section of the river yielded none of the 10 native fishes collected there by Meek in 1903 (Meek, 1904, p. xxxvii). *Gambusia senilis* appeared in the basin by 1976 (UMMZ 203232). In 1982 and 1983, a survey of the habitats of *Cyprinodon meeki* (which is frequently an associate of *Characodon lateralis*) revealed the goodeid at only seven springs or spring-fed habitats, except for one sample from an upper tributary to Río Canatlán, about 17 km north of Canatlán. Factors responsible for the depletion of *C. lateralis* apparently include pollution, habitat destruction, and competition with exotic fishes. Although we know of no immediate threat to *C. audax,* its very restricted range is cause for concern.

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