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STATUS OF THE NOMINAL SPECIES OF THE FISH GENUS *XENOOPHORUS* (GOODEIDAE, CYPRINODONTIFORMES) FROM MEXICO

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Xenoophorus captivus (Hubbs, 1924), *X. erro* Hubbs and Turner, 1939, and *X. exsul* Hubbs and Turner, 1939, are members of the Goodeidae, a family of about 35 species of fishes largely restricted to the central highlands of México. The known distribution of *Xenoophorus* in western San Luis Potosí marks the northeastern limit of the family from its center of abundance and presumed center of origin in the basin of the Río Lerma. *Xenoophorus captivus* was based on a holotype male, 46 mm SL, and at least 10 paratypes taken by Meek from an upper tributary of the Río Santa María of the Río Panuco system at Jesús María, a small village near the railroad, about 35 km south of the city of San Luis Potosí (collection date unknown). In a report on reproductive anatomy in the Goodeidae, Turner (1937) first used the name *Xenoophorus erro* and provided a description and figure of nutritive structures in embryos of the species. Turner indicated the name was taken from a manuscript that appeared two years later (Hubbs and Turner, 1939), in which Hubbs and he provided a complete redescription of *X. erro* after expressing doubt whether it was "recognizably differentiated" in Turner's report. *X. erro* was described more fully from a holotype female, 48 mm SL, and 128 paratypes collected 21 March 1932 by Gordon, Whetzel, and Ross in the Río Santa María at the town of Santa María del Río, 46 km southeast by road from San Luis Potosí. The north-

ernmost species of the genus, *Xenoophorus exsul* was based on a holotype female, 45 mm SL, and 594 paratypes obtained by Lundell and others on 21 July 1934 at Agua del Medio, halfway between Venado and Moctezuma, about 76 km north of San Luis Potosí; additional paratypes collected by Lundell and party included 101 fish from a spring-fed stream at Venado, 11 July 1934, and 705 from a mountain stream at Moctezuma, 20 July 1934.

The redescriptions of *Xenoophorus captivus* and *X. erro* and the original description of *X. exsul* in 1939 by Hubbs and Turner were part of an exhaustive family revision based primarily on reproductive anatomy—specifically the structure of the ovary and trophotaeniae, nutritive rosette or ribbon-like anal processes known in embryos of all but one member [*Ataeniobius toweri* (Meek)] of the family. Since the Hubbs-Turner revision, the use of reproductive anatomy to ally the members of the Goodeidae into a natural, monophyletic group has gone unquestioned. However, recent studies (Mendoza, 1965; Miller and Fitzsimons, 1971; Fitzsimons, 1972) demonstrated that some aspects of ovarian and trophotaenial anatomy are sufficiently variable in certain species to question their being used alone to define species and determine relationships in the family. This paper re-examines the reproductive anatomy and other features used by Hubbs and Turner in the classification of *Xenoophorus* and, with new data, evaluates the status of the species now included in the genus.

Materials and Methods

Preserved specimens examined from the fish collections at the University of Michigan Museum of Zoology and the Louisiana State University Museum of Zoology included UMMZ 178225 (paratypes), 161661, 189027, 189578, LSUMZ 21, 262, 1276, 1277, and 1281 for *Xenoophorus captivus*, UMMZ 108555 (holotype), 108556 (paratypes), 189579, LSUMZ 1278, and 1286 for *X. erro*, and UMMZ 118122 (holotype), 118120 (paratypes), 118121 (paratypes), 118123 (paratypes), 189575, 189576, LSUMZ 1285, and 1287 for *X. exsul*.

Live fish for brood data were from a stock maintained in the UMMZ aquarium facility directed by Robert R. Miller: *Xenoophorus erro*, Río Santa María del Río, ca. 5 km by road above town of same name, San Luis Potosí, Miller and Huddle, 29 April 1966.

Methods of counting and measuring were those of Miller (1948) and Hubbs and Lagler (1958). The anteriormost anal ray (Miller and Fitzsimons, 1971) was not included in the count because in goodeids the ray is poorly developed and usually not readily visible in small specimens.

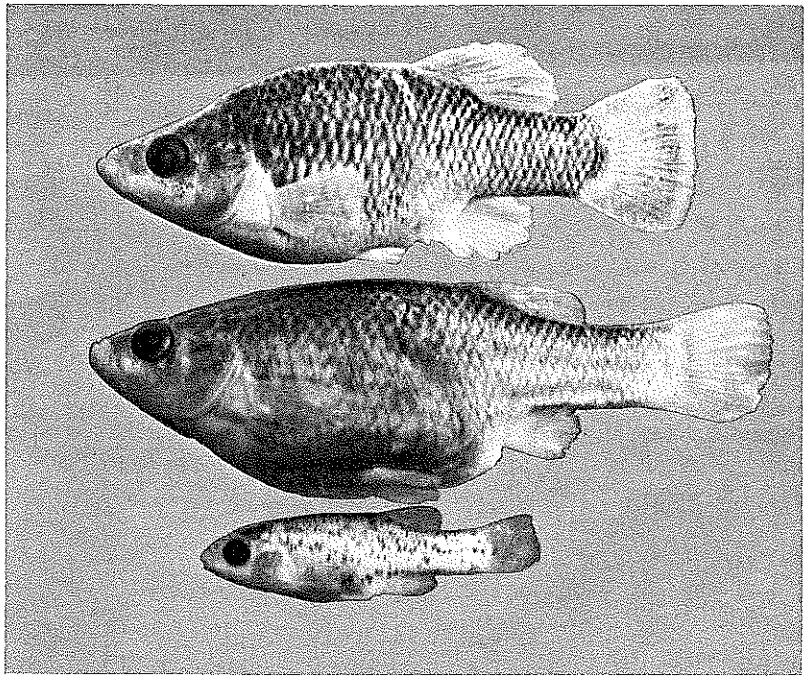

FIGURE 1. *Xenoophorus captivus* ♂ 41.0 mm SL, ♀ 47.5, and immature 23.5, LSUMZ 1286 Río Santa María, San Luis Potosí.

Results and Discussion

Reproductive anatomy.—As in other goodeids, *Xenoophorus* has a single, median ovary formed by the union of right and left organ rudiments whose fused walls comprise a vertical septum that usually extends the length of the ovary. Hubbs and Turner assigned *Xenoophorus* to the subfamily Goodeinae, which includes fishes with egg-producing tissue in the dorsal and ventral wall and septum of the ovary. *Zoogoneticus* Meek is reportedly exceptional in being the only genus of the subfamily to have ovigerous tissue also in the lateral ovarian wall. My inspection of ovaries from females representing the three species in *Xenoophorus* revealed location of ovigerous tissue to depend on the female's maturity and gestational stage of embryos, as in *Characodon* Guenther and *Xenotoca* Hubbs and Turner

(Mendoza, 1965; Fitzsimons, 1972). A gradual posterior proliferation of ovigerous tissue accompanies the development of embryos; new eggs likely cannot be fertilized and the production of a new brood begun until the existing one is evacuated. Egg-producing tissue usually extended throughout the length and height of the ovarian wall and septum in immature females (22-28 mm SL). Ovigerous tissue was usually limited to the anteriormost portion of the ovary at the juncture of the walls and septum in females with early embryonic stages (fertilized eggs or embryos to about 1.8 mm TL), and occurred in the anterior third of the dorsal, lateral, and ventral wall and anterior fourth of the septum in females with embryos about 4 to 8 mm TL, and in the anterior two-thirds of the dorsal, upper lateral, and ventral wall and anterior third of the septum in females with near-term young. In pregnant females the posteriormost extension of ovigerous tissue was mostly in a pair of short bands in the dorsal and upper lateral walls and upper part of the septum. Oocytes were absent or, less frequently, restricted to a small patch of tissue at the anterior dorsal apex of the ovary in the largest females (51-57 mm SL). With few exceptions these large females lacked embryos. The reduction or lack of ovigerous tissue and absence of embryos in older females are likely related to Robert R. Miller's observations (pers. comm.) of reproductive senescence in lab-reared goodeids.

Selected cross sections through the ovary of *Xenoophorus* females of various ages and reproductive condition revealed locations of ovigerous tissue unreported for any goodeid species; other sections were indistinguishable from those described by Hubbs and Turner for other members of the Goodeinae, including *Zoogoneticus*, and from those of the monotypic subfamilies Ataeniobiinae and Characodontinae.

According to Hubbs and Turner, the ovarian septum in *Xenoophorus* is divided near the middle into two flaps attached dorsally and ventrally, about equal in length, unbranched, and strongly rolled in opposite directions. My observations confirm the description above as the predominant condition in mature females of *Xenoophorus*, but the septum was frequently entire (undivided) in immature females, and, in mature females, the dorsal flap was occasionally much longer (to 4X) than the ventral flap in the anterior fourth of the ovary. In a few females with the ovary expanded by near-term embryos, the flaps were only slightly rolled. In four small, but mature females (32.0-35.0 mm SL), septal flaps were rolled in the same direction, a characteristic of *Allotoca* Hubbs and Turner, and, in two large females (45.0 and 47.5 mm SL), the ventral flap was branched at its mid-length, a condition noted by Hubbs and Turner throughout the length of the septum in *Neoophorus* Hubbs and Turner.

After examining embryos from many more collections than were available to Hubbs and Turner, I am able to amend their description of trophotaeniae in *Xenoophorus* only slightly. The longest trophotaeniae, reaching, as reported by Hubbs and Turner, to near the end of the caudal fin, were observed in embryos judged about halfway (4-6 mm TL) through a 45 to 60-day gestation period. Trophotaeniae extended, at most, to about the posterior edge of the anal fin in near-term embryos or neonates (10-15 mm TL). The shortening of trophotaeniae during embryogeny indicates that resorption, which occurs in certain other goodeids for a few days to more than a week after birth, begins in *Xenoophorus* before birth. Trophotaeniae were predominantly in an asymmetrical arrangement but the long trunk originated from the right side, not only the left, with almost equal frequency. Occasionally two long trunks were developed, one from the right and the other from the left, but they were rarely of equal length. My counts indicate a smaller number of trophotaeniae: 3-7 (5.0 ± 1.30) in *Xenoophorus captivus*, 3-7 (5.0 ± 0.96) in *X. erro*, and 3-8 (5.4 ± 0.81) in *X. exsul* rather than 8 as Hubbs and Turner reported. The primary tissue space of a trophotaenia, which separates the central core or medulla of connective and vascular tissue from the outer epithelial covering, varied between embryos and even along the length of a single process. The tissue space was narrow or absent in early tailbud embryos, widest in embryos 8 to 10 mm TL, and again narrow or absent in embryos near birth. The tissue space was usually widest near the mid-length of a trophotaenia and very narrow or absent at the base and tip. Hubbs and Turner described the primary tissue space for all three species as greatly reduced but did not refer to position along the length of a process or to the developmental stage of the embryo.

Although Hubbs and Turner used ovarian and trophotaenial traits to distinguish species in all other goodeid genera, they did not point out species-specific differences in *Xenoophorus*. I also found none.

Reproduction.—The presence of embryos in females of *Xenoophorus captivus*, *X. erro*, and *X. exsul* from collections at various seasons, and the laboratory production of *X. erro* young in all months except February, April, and May, indicate females of *Xenoophorus* likely bear young throughout the year in México if ambient temperatures are kept adequately high in

winter by the constant-temperature springs relatively common in San Luis Potosí. Four wild-caught and three laboratory F_1 females of *X. erro*, 34 to 48 mm SL, produced 231 young in 33 broods. Brood intervals averaged 57.4 days (40-70, mostly 45-60). Brood size ranged from 1 to 17, usually 3 to 9, with an average of seven neonates that were 9 to 16, mostly 13 to 15, mm TL. In contrast to certain other livebearing cyprinodontoids, *Xenoophorus* and probably all goodeids lack interbrood sperm storage and superfetation, the simultaneous development of more than one embryonic stage. Members of a single brood of near-term embryos or neonates usually varied less than 2 mm TL. Intraovarian competition, death, and resorption of embryos were suggested by the much smaller numbers (1/2 to 1/5) of near-term embryos or neonates than those of embryos at earlier developmental stages. Turner (1933) noted that 2/3 to 1/2 of the embryos are resorbed in *Skiffia bilineata* and suggested that resorption of these embryos provided an important energy source for development in the surviving embryos.

Color.—No appreciable differences in color or pigment patterns were indicated for the species of *Xenoophorus* by Hubbs (1924) and Hubbs and Turner (1939). When combined, their descriptions afford an accurate summary of the total range of variation for a single population. The following description of coloration in *Xenoophorus* is derived from a combination of their reports and my observations of more recently collected specimens.

Although interpopulational differences were not detected, coloration in *Xenoophorus* (Fig. 1) was highly variable according to age and sex. Marked sexual dichromism contrasted large males in breeding color with females and immatures of both sexes. Males 30 mm SL and larger were usually much darker on the body, dorsally and laterally, and on the dorsal and caudal fins. The condition was maximized in the largest males, 40 mm SL and larger, by a nearly uniform black or dark brown on the head, nape, back, face, upper half to two-thirds of the body, and sides of the caudal peduncle; in these large males the dorsal and caudal fins were dusky to black, with the latter exhibiting a clear margin, about half an eye diameter, along its trailing edge. Contrary to a statement by Hubbs and Turner, the terminal band of unpigmented tissue on the caudal fin of males was about equally conspicuous in specimens from more recent collections representing *X. captivus*, *X. erro*, and *X. exsul*. Lighter colored, often smaller males, 30 to 35 mm SL, had a dark, irregular stripe along the midside of the caudal peduncle and posterior half of the body. In light-colored males, females, and immatures, scale margins were light and the dorsum often about as light or only slightly darker than the sides. In lighter males and females above 30 mm SL, a vague stripe, most distinct at the origin of the dorsal fin, extended forward over the nape and either faded near the top of the head or merged into the broad, darker area on the head. This predorsal stripe was indiscernible in large males with general darkening of the dorsum and sides. Conspicuous spots were concentrated on the upper and lower edges of the caudal peduncle, dorsum of the body excluding the head, and along the midside of neonates, immatures, and adult females. The spots were indistinct or lost against the darker background of large breeding males and were smaller or diffuse in large, light-colored females. The dorsal and caudal fins of large females were often dusky but never as dark as those of males of similar size. The chin, lower half of the cheek, breast, belly, and ventral surface of the caudal peduncle were pale brown or yellow, and the pectoral, pelvic, and anal fins were usually clear in fish of both sexes and all ages. In live animals, pale areas of the lower head and body appeared silvery. The pelvic and anal fins of courting males had a luminescent light-blue sheen not visible in preserved fish or even in live animals out of water.

Meristics.—Differences in numbers of fin rays, scales, and gill rakers among *Xenoophorus captivus*, *X. erro*, and *X. exsul* (Table 1) were far less than those conventionally required for even subspecies recognition (e.g., Bailey et al., 1954; Géry, 1962; Mayr, 1969). Branchiostegal rays invariably occurred as four pairs in specimens representing the three species.

Very slight north-south clinal variation was found in the numbers of dorsal, anal, and pectoral fin rays, caudal-peduncle scales, and gill rakers, but no marked character changes in these meristic features were detected throughout the geographic range of the genus.

My counts (Table 1), which include specimens examined by Hubbs and Turner, serve little more than to reveal closer averages between the three groups of *Xenoophorus* and to expand slightly the ranges they reported. Based on branched rays, the caudal count is the only total fin-ray count in *Xenoophorus* that varies with fish size. Smaller fish have fewer branched rays in the caudal fin. As noted by Hubbs and Turner, pelvic fin rays were almost invariably six in each fin with the innermost rays slightly separated.

TABLE 1.—MERISTIC CHARACTERS IN *Xenoophorus* [NUMBER OF SPECIMENS: RANGE (MEAN ± ONE STANDARD DEVIATION)].

	X. captivus	*X. erro*		*X. exsul*	
	Paratypes & others	Holotype	Paratypes & others	Holotype	Paratypes & others
D	56:12-14 (13.01±0.30)	13.0	40:12-14 (13.10±0.64)	13.0	60:12-14 (12.95±0.43)
A	56:13-16 (14.46±0.64)	14.0	40:13-15 (14.20±0.52)	14.0	60:13-16 (14.67±0.54)
P_1	92:13-15 (14.14±0.44)	14.5	59:13-15 (14.46±0.55)	13.0	119:11-16 (14.08±0.77)
P_2	92:0 (6.00±0)	6.0	60:0 (6.00±0)	6.0	118:4-6 (5.91±0.24)
C	55:18-22 (19.62±0.31)	20.0	40:18-20 (19.35±0.75)	19.0	57:16-20 (19.18±0.35)
l.ser.	59:33-36 (34.77±0.95)	35.5	39:34-36 (35.05±0.78)	33.5	87:33-36 (34.80±0.74)
c.ped.	52:17-19 (17.55±0.68)	17.0	40:17-20 (18.0±0.73)	17.0	55:16-18 (17.52±0.56)
body	52:34-40 (36.15±0.84)	35.0	40:33-40 (35.60±0.70)	36.0	55:29-38 (34.62±1.67)
pred.	49:22-35 (28.01±2.32)	30.0	40:24-30 (27.50±2.19)	30.0	39:23-29 (25.62±1.53)
G R	54:20-26 (24.8±1.51)	27.0	40:23-27 (24.70±1.42)	26.0	55:19-25 (23.02±1.82)

Sexual differences in meristics were noted in the number of unbranched rays in the anal fin. In both sexes, progressively larger fish had more branched rays in all fins, but, in fish of similar size, males had fewer branched rays in the anterior portion of the anal fin than females. In males 27 to 48 mm SL the first four anal rays were usually unbranched, and, in larger males, the anteriormost ray remained unbranched, a condition recorded earlier in males of *Xenoophorus exsul* (Turner et al., 1962). In contrast to Hubbs' description for *Goodea captiva* (Hubbs, 1924), only one adult of *X. captivus*, 31 mm SL, and two immature males of *X. erro*, 17.5 and 22 mm SL, lacked branching in the first six anal rays. Females 25.5 to 42 mm SL most often lacked branching only in the first two anal days. All but the anteriormost ray was branched in large females above about 48 mm SL.

Proportional measurements.—Head, body, and fin proportions (Tables 2 and 3) do not reveal species-specific differences between the populations currently recognized as *Xenoophorus captivus*, *X. erro*, and *X. exsul*.

Slight north-south clinal variation in proportional measurements was indicated in the three populations of *Xenoophorus*. However, allometric growth and inaccuracy of measurements, both reflected at least partly in the relatively large ranges and standard deviations for most characters, probably mask clinal variation in some features while falsely indicating it in others.

In distinguishing between the species of *Xenoophorus*, Hubbs and Turner emphasized four proportional features in the analytical key and species descriptions: head length, least depth of the caudal peduncle in adult females, distance from the anal fin origin to the base of the caudal fin, and shape of the anterior profile (dorsolateral outline of the nape, head, and snout) in adult males. My observations indicate that differences in these features either do not exist or are of such small magnitude to be unreliable in distinguishing species groups. The disparity between the Hubbs-Turner report and mine stems from their having, in 1939, only seven collections of *Xenoophorus* upon which to base decisions. Nearly 40 years later I had the opportunity to examine, in addition to the material available to them, 15 other collections from a greater range of localities and collection times. Their small number of samples and, for *X. captivus*, the small number of fish per sample, likely caused allometric and sexual differences in a few morphometric features to appear species-specific. Hubbs (1924) and Hubbs and Turner (1939) also pointed out a number of other proportional measurements, as body depth, caudal-peduncle length, snout length, eye length,

TABLE 2.—PROPORTIONAL MEASUREMENTS, IN HUNDREDTHS OF STANDARD LENGTH, IN MALES OF *Xenoophorus* [NUMBER OF SPECIMENS: RANGE (MEAN ± ONE STANDARD DEVIATION)].

	X. captivus	*X. erro*	*X. exsul*
	Paratypes & others	Paratypes & others	Paratypes & others
standard length mm	39:32.0-46.0 (35.28±8.21)	28:27.5-45.0 (33.12±3.78)	40:29.5-47.0 (35.21±4.32)
predorsal length	39:62.5-70.0 (66.34±2.17)	28:65.0-67.5 (66.61±0.71)	40:66.1±70.4 (68.10±1.19)
prepelvic length	39:51.4-61.8 (55.21±3.54)	28:52.6-65.2 (56.82±4.93)	40:51.2-58.1 (54.62±1.93)
anal origin to caudal base	39:33.8-40.6 (36.89±1.77)	28:36.1-40.6 (37.51±1.11)	40:33.9-39.5 (36.71±1.52)
body, greatest depth	39:31.2-45.9 (37.52±2.56)	28:32.7-44.0 (37.21±2.48)	40:32.3-43.2 (37.28±2.81)
body, greatest width	39:16.5-21.7 (19.91±1.39)	28:18.2-22.7 (19.79±1.80)	40:17.7-24.2 (20.61±1.82)
head length	39:29.7-32.8 (31.11±1.12)	28:30.0-33.3 (31.21±0.55)	40:30.1-34.2 (31.58±1.17)
head depth	39:17.6-21.6 (20.11±0.91)	28:19.7-25.3 (21.63±1.43)	40:16.1-23.7 (19.94±1.78)
head width	39:18.1-23.5 (20.48±1.49)	28:19.7-22.0 (20.25±0.61)	40:20.0-23.3 (22.10±1.41)
caud. ped. length	39:23.5-28.1 (25.31±1.77)	28:24.0-31.9 (25.51±2.01)	40:23.9-27.9 (25.82±1.43)
caud. ped. least depth	39:13.8-18.6 (17.42±1.28)	28:14.5-18.7 (17.1±1.52)	40:12.9-19.4 (16.49±1.86)
interorb. width	39:10.8-14.9 (13.55±0.71)	28:12.7-15.4 (13.78±1.06)	40:11.6-15.3 (13.51±0.85)
preorb. width	39:3.3-6.2 (4.78±0.83)	28:4.9-5.4 (5.16±0.23)	40:4.1-8.3 (5.42±1.09)

TABLE 2. (continued)

	X. captivus	*X. erro*	*X. exsul*
	Paratypes & others	Paratypes & others	Paratypes & others
opercle, greatest length	39:10.0-13.0 (11.38±0.62)	28:10.0-13.3 (11.7±0.91)	40:9.7-13.3 (11.85±0.98)
snout length	39:8.3-11.9 (10.03±0.87)	28:9.8-11.0 (10.32±0.49)	40:9.0-12.5 (11.10±1.21)
orbit length	39:8.6-10.9 (9.73±0.62)	28:8.8-11.5 (10.21±0.86)	40:8.7-14.5 (10.47±1.11)
mouth width	39:8.2-11.4 (10.18±1.04)	28:10.5-13.3 (10.4±1.09)	40:9.7-14.5 (10.44±1.21)
upper jaw length	39:4.2-7.8 (5.61±1.41)	28:5.3-8.3 (7.67±0.72)	40:5.8-10.2 (7.31±1.28)
mandible length	39:4.2-9.1 (6.41±1.98)	28:5.3-8.3 (7.71±0.81)	40:6.4-10.7 (7.52±1.31)
dorsal fin basal length	39:16.2-18.8 (17.73±0.61)	28:16.4-18.8 (17.91±0.43)	40:16.4-19.8 (18.32±0.94)
anal fin basal length	39:9.7-15.6 (12.31±1.32)	28:9.2-12.7 (11.61±0.82)	40:11.0-15.2 (13.04±1.11)
dorsal fin depr. length	39:29.2-35.3 (32.11±1.22)	28:31.1-34.5 (33.09±1.19)	40:30.0-35.1 (33.00±1.69)
anal fin depr. length	39:22.2-27.0 (24.12±1.17)	28:21.1-25.0 (23.71±0.86)	40:21.5-26.9 (24.22±1.51)
mid. caud. rays length	39:18.5-23.7 (21.31±1.61)	28:18.7-21.8 (20.91±1.21)	40:17.7-23.9 (21.55±2.01)
length longest pect. ray	39:18.0-23.5 (21.31±1.29)	28:18.8-21.8 (20.78±1.14)	40:19.8-22.7 (21.55±1.09)
length longest pelvic ray	39:11.0-13.9 (12.62±0.99)	28:10.0-13.3 (12.20±0.87)	40:10.0-16.1 (12.46±1.12)

TABLE 3.—PROPORTIONAL MEASUREMENTS, IN HUNDREDTHS OF STANDARD LENGTH, IN FEMALES OF *Xenoophorus* [NUMBER OF SPECIMENS: RANGE (MEAN ± ONE STANDARD DEVIATION)].

	X. captivus	*X. erro*		*X. exsul*	
	Paratypes & others	Holotype	Paratype & others	Holotype	Paratype & others
standard length mm	37:31.0-48.0 (39.1±6.12)	48.0	28:35.0-41.0 (38.00±2.79)	45.0	23:27.0-64.0 (37.07±8.39)
predorsal length	37:65.1-68.2 (66.91±1.83)	68.8	28:65.2-68.8 (67.25±1.31)	68.9	23:65.6-71.4 (68.56±1.76)
prepelvic length	37:51.3-60.8 (54.67±2.44)	54.2	28:52.8-60.0 (56.23±2.17)	53.3	23:51.3-59.7 (55.45±1.90)
anal origin to caudal base	37:30.9-39.7 (35.81±2.36)	33.3	28:32.8-36.2 (34.54±1.04)	31.1	23:31.4-36.7 (34.37±1.71)
body, greatest depth	37:27.4-39.5 (34.48±3.01)	36.5	28:34.5-40.0 (35.26±2.58)	37.8	23:31.5-38.9 (34.55±1.97)
body, greatest width	37:15.1-21.2 (18.61±1.73)	20.8	28:16.7-20.8 (18.95±1.24)	20.0	23:17.1-24.2 (20.22±1.70)
head length	37:27.5-32.3 (29.37±1.11)	30.2	28:27.8-30.0 (29.26±0.73)	28.9	23:28.0-32.3 (30.23±1.32)
head depth	37:17.1-21.2 (18.41±0.98)	19.8	28:18.8-21.4 (20.01±1.03)	20.0	23:16.2-23.7 (19.41±1.99)
head width	37:16.4-21.6 (19.54±1.55)	20.8	28:15.9-22.0 (18.65±1.83)	21.1	23:18.8-23.1 (20.93±1.16)
caud. ped. length	37:22.9-35.5 (27.86±2.29)	25.0	28:25.0-28.6 (26.86±1.11)	24.4	23:22.9-27.8 (25.17±1.54)
caud. ped. least depth	37:13.2-17.5 (15.11±1.42)	15.6	28:13.3-17.1 (14.91±1.26)	15.6	23:13.5-18.2 (15.53±2.12)
interorb. width	37:11.0-15.0 (12.10±1.09)	12.5	28:11.6-13.8 (12.50±0.73)	11.1	23:9.4-14.1 (12.80±1.35)
preorb. width	37:3.5-5.5 (4.48±0.52)	4.2	28:3.9-5.3 (4.59±0.48)	4.4	23:3.7-8.3 (5.40±1.39)

TABLE 3. (continued)

	X. captivus	*X. erro*		*X. exsul*	
	Paratypes & others	Holotype	Paratype & others	Holotype	Paratype & others
opercle greatest length	37:8.3-12.8 (10.65±1.23)	11.5	28:9.8-11.8 (10.85±0.73)	11.1	23:9.4-14.5 (11.41±1.47)
snout length	37:7.0-11.0 (8.89±1.14)	10.4	28:8.0-10.5 (9.35±0.84)	8.9	23:7.4-12.9 (10.31±1.38)
orbit length	37:8.1-11.0 (9.42±0.81)	8.3	28:8.3-9.5 (8.86±0.42)	8.9	23:7.0-12.1 (10.18±1.26)
mouth width	37:8.1-11.2 (9.35±1.17)	12.5	28:8.3-10.7 (9.51±0.90)	11.1	23:8.6-12.9 (10.51±1.28)
upper jaw length	37:3.2-8.2 (6.14±1.68)	7.3	28:4.8-7.9 (6.45±1.24)	6.7	23:5.3-9.7 (7.30±1.32)
mandible length	37:3.2-8.2 (6.12±1.88)	8.3	28:4.8-7.9 (6.45±1.24)	7.8	23:6.4-9.7 (8.07±1.17)
dorsal fin basal length	37:11.8-16.14 (14.21±1.37)	14.6	28:13.2-15.0 (13.99±0.65)	15.6	23:12.9-16.7 (15.04±1.38)
anal fin basal length	37:9.3-13.7 (10.41±1.41)	10.4	28:8.5-11.2 (9.85±0.81)	10.0	23:8.1-13.3 (11.29±1.68)
dorsal fin depr. length	37:22.1-25.7 (24.28±1.33)	22.9	28:20.7-24.6 (22.75±1.52)	24.4	23:20.6-26.0 (23.52±2.02)
anal fin depr. length	37:16.1-21.9 (18.71±1.98)	16.7	28:16.0-18.6 (17.48±0.88)	16.7	23:15.8-22.7 (18.70±2.06)
mid. caud. rays length	37:16.2-21.9 (20.03±1.76)...	19.8	28:15.7-20.3 (19.41±0.85)	20.0	23:15.6-22.6 (19.63±1.71)
length longest pect. ray	37:16.3-20.6 (18.54±0.97)	18.8	28:17.3-21.2 (18.73±1.49)	17.8	23:11.1-22.7 (17.55±3.65)
length longest pelvic ray	37:9.7-13.7 (11.36±1.02)	10.4	28:9.3-12.5 (10.33±1.03)	10.0	23:8.8-14.5 (10.96±1.42)

interorbital width, mouth width, dorsal-fin origin to end of middle caudal ray, dorsal origin to caudal base, length of depressed dorsal fin, length of middle ray of caudal fin, and a few others, which although overlapping between populations, exhibited species-typical averages. Significant divergence in species' averages for these traits is not supported by the expanded data provided in this study (Tables 2 and 3).

Dentition.—In the original description of *Goodea captiva,* Hubbs (1924) noted two tooth types: 1) distally dilated, bifid incisors which form an outer row of movable, biserially alternating elements in the upper and lower jaws and 2) conic, villiform teeth which comprise an inner series in both jaws. In the family revision in which *Xenoophorus captivus* was briefly redescribed and *X. erro* and *X. exsul* proposed as new species, no differences in dentition were indicated for the three species; rather the description of teeth in *Goodea captiva* was slightly expanded and included as a set of generic characters for *Xenoophorus* (Hubbs and Turner, 1939:30). My observations agree with those of Hubbs and Turner, and I, too, was unable to detect species-specific differences in tooth type, number, or arrangement among these animals. However, considerable but similar ontogenetic variation in dentition was revealed in an examination of 45 specimens from the three groups of *Xenoophorus.* Outer-row teeth were conic in embryos, neonates, and young to about 16 mm SL. Fish 20-25 mm SL had conic teeth laterally in the outer rows of both jaws with about the medial ¾ of the complement ranging from flat-topped to markedly bifid. Specimens 30 mm SL and larger had only strongly bifid teeth in the outer rows. Hubbs (1924) and Hubbs and Turner (1939) reported outer-row teeth, ranging from 15 to 30 in each jaw, to be long, slender, and loosely attached in a weakly to moderately alternating arrangement. My counts for immature fish 16-28 mm SL ranged from 9 to 14 (mostly 10-12) teeth in the outer row of the upper jaw and 11 to 18 (11-13) in the lower jaw. Adult fish 30-54 mm SL had 10 to 22 (15-20) in the upper jaw and 11 to 28 (15-19) in the lower jaw. No sexual differences in tooth number were noted. Degree of alternation of outer-row teeth is a result of crowding and the ease with which the loosely attached teeth can be displaced distally. Young fish with fewer teeth than adults showed little or no alternation of outer-row teeth. Adults 40 to 50 mm SL with 18 to 20 outer-row teeth closely packed in each jaw exhibited marked tooth alternation, but equally large fish with considerable tooth loss sometimes lacked alternation entirely. Inner teeth of the upper and lower jaws were conic, much smaller than outer-row teeth, and occurred in a fairly wide band with conspicuous backward lateral extensions (Hubbs and Turner, 1939). Counts of teeth forming the inner tooth bands were not attempted because of their small size, large number, and deep implantation in soft tissue. In specimens about 40 mm SL and larger, a few broader-based truncate or slightly bifid teeth were scattered among conic teeth and occasionally were most frequent near the anterior median edge of the band formed by conic teeth (see also Miller and Fitzsimons, 1971:12).

Sensory canals of the head.—Examination of 85 specimens of *Xenoophorus captivus,* 40 of *X. erro,* and 66 of *X. exsul* revealed no significant species or population-specific differences in the pattern or number of preopercular, mandibular, and preorbital sensory pores. In all specimens the supraorbital canal system conformed to Group II of Gosline's classification (1949), Pl. 1) in which the canal is discontinuous between the second and third anteriormost pores (Gosline's 2a and 2b). Most adults greater than 35 mm SL had nine supraorbital pores with a second break between the fifth and sixth ones, a pattern represented by the formula 1-2a 2b-4a 4b-7 in Gosline's numbering system. This pattern occurred in five of the six paratypes of *X. captivus,* in the holotype and in seven of 10 paratypes of *X. erro,* and in eight of 10 paratypes of *X. exsul.* The holotype of *X. exsul* has discontinuities between the second and third and between the fifth and sixth pores as in the animals above, but has eight rather than nine pores in each of its supraorbital canals; the dorsal sensory-pore pattern is 1-2a 2b-4a 4b-6. In *Xenoophorus* the number of pores and the number and position of disruptions in the supraorbital canals are related to fish size. The canals of near-term embryos, neonates, and young fish 11-19 mm SL usually occurred as open grooves. Formulae and size ranges for larger fish included 1-2a 2b-open 4a-open 6a-7 (16-24 mm SL), 1-2a, 2b-5a 5b-8 (23-25), 1-2a 2b-4a 4b-5a 5b-6 (27-30), 1-2a 2b-4a 4b-6a 6b-7 (23-39), 1-2a 2b-4a 4b-7 (23-48), 1-2a 2b-7 (33-47), 1-2a 2b-4a 4b-6 (44-45), and 1-2a 2b-6a 6b-7 (44-49). Although eight supraorbital canal formulae were noted for specimens of *Xenoophorus* ranging from embryos to large adults, the fifth pattern in the list, as indicated earlier, was more frequent (3-7X) than any other.

Karyology.—Teruya Uyeno (Nippon Luther Shingaku Daigaku, Tokyo), Robert R. Miller (University of Michigan), and I recently completed a study preparatory to a report of karyotypic variation in the Goodeidae. The manuscript will describe, compare, and, where possible, interpret the

phylogenetic significance of chromosome complements in the species of *Xenoophorus* and other goodeid genera. Chromosome microslides of *Xenoophorus* were prepared from specimens taken near the type locality for each species. The same karyotype, a diploid complement of two submetacentric and 46 subtelocentric to telocentric chromosomes, was obtained for each species.

Recommendations

Species status.—Hubbs and Turner (1939:54) remarked that "later collections of *Xenoophorus* may indicate further intergradation of characters, calling for the reduction of the 3 species as here differentiated to subspecific rank." Similarly, Miller and Fitzsimons (1971:11) commented that few taxa in the Goodeidae "have been studied in sufficient detail to determine limits of variation, and additional species recognized in 1939 may eventually be combined, as in *Xenoophorus*." The supplementary information on the species of *Xenoophorus* supplied by this report requires concurrence with the prediction above. I recommend that the known populations of *Xenoophorus* be regarded as conspecific and that the older epithet *captivus* be considered a senior synonym of *erro* and *exsul*. Subspecies designations are not justified by the data provided herein.

My only reservation in recommending these synonymies is the lack of extensive hybridization experiments and comparative ethological data, particularly courtship analyses and discrimination tests, for the populations of *Xenoophorus*. Experimental approaches proved valuable in a revision of the goodeid genera *Characodon* and *Xenotoca* (Fitzsimons, 1972) and sometimes were more useful in judging relationships than information from conventional sources (meristics, proportional measurements, and others) because the criterion of interbreeding was imposed and because attention was drawn to features that the animals themselves used in species recognition (Fitzsimons, 1974, 1976).

Relationships of Xenoophorus.—Limited comparative data for the Goodeidae indicate *Xenoophorus* is most similar to *Xenotoca*, particularly *X. variata* (see Fitzsimons, 1972). However, I am unable to determine whether the resemblances between *Xenoophorus* and *Xenotoca* are the result of parallel or convergent evolution because comparable data are lacking for 15 of the family's 18 genera. The combined effects of the similar aquatic environments on the Mexican Plateau and the relatively short evolutionary

history of the Goodeidae since about the Pliocene probably have produced parallelism in many features among closely related fishes. If further studies detailing specific and generic limits throughout the family attribute the similarity of *Xenoophorus* and *Xenotoca* to a lack of divergence, a combination of the two genera may be expedient.

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