

MARION GREY AWARD

This paper by J. Michael Fitzsimons has been selected for support by the Marion Grey Fund, which was established to fund one long and excellent fish paper in honor of Marion Grey. Mrs. Grey had been an associate in the Division of Fishes of the Field Museum of Natural History for 21 years prior to her death the 20th of March, 1964. Mrs. Grey is best known for her major contributions to the study of deep sea fishes.

A Revision of Two Genera of Goodeid Fishes (Cyprinodontiformes, Osteichthyes) from the Mexican Plateau

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A taxonomic revision is presented of Characodon and Xenotoca of the Goodeidae, a family of vivaparous fishes that is virtually restricted to the Mexican Plateau. The most recent family classification was based on anatomical characters of the ovary and trophotaeniae; these characters of the two genera were restudied and evaluated here in combination with added "conventional" information on morphological features and new information on karyotypes, courtship behavior, hybridization experiments, and discrimination tests. The distinctiveness of Characodon and Xenotoca is confirmed. The monotypy of Characodon with C. lateralis is supported, but Xenotoca is found to consist of three species: X. variata, the type species of the genus, X. eiseni, a species here withdrawn from synonymy with variata, and X. melanosoma, a distinctive new species described herein.

Introduction

THE Goodeidae comprise a wholly Mexican family of viviparous freshwater fishes represented by 35 or more species largely restricted to the highlands of the Mesa Central. Its focus of abundance is in the Río Lerma basin where it is the dominant family of fishes (Miller and Fitzsimons, 1971).

Goodeids are generally small; members of two genera, Alloophorus Hubbs and Turner and Goodea Jordan, attain a length of 200 mm, but most grow no larger than 100 mm. They live in a variety of habitats, ranging from deep spring-fed pools to shallow riffles. Some are lake dwellers; others abound in irrigation ditches that may have only a few inches of water. Their body form often

reflects habitat type. Certain river and stream fishes, as Ilyodon Eigenmann, are swift swimmers with slim, stream-lined bodies and large caudal fins. In ponds, lakes, or quiet stream pools, deep-bodied forms, such as Skiffia Meek, are slow moving and maneuver easily in dense vegetation, sculling with the pectoral fins in a manner reminiscent of many resident coral-reef fishes. Members of the genus Allodontichthys Hubbs and Turner look and behave like North American darters (Etheostomatinae), are long-bodied bottom dwellers, and are found only among the rocks and boulders in shallow riffles. Goodeids include all consumer types: carnivores with conic teeth and a short gut, Alloophorus; herbivores with generalized bifid teeth and a long coiled gut, Ameca Miller and Fitzsimons; or omnivores with variable teeth and gut form, Xenotoca Hubbs and Turner, the feeding habits of which range from nearly completely carnivorous to completely herbivorous at different localities.

The unifying features of the family are related to mode of reproduction-internal fertilization and live birth. The distinctive modification of the male anal fin, presence of an internal muscular organ of apparent reproductive function in the male, structure of the ovary, and the development of trophotaeniae in embryos distinguish the Goodeidae from all other cyprinodontoid fishes. The first six or seven rays of the male anal fin are crowded, shortened, and often separated from the rest of the fin by a distinct notch; they probably aid in insemination. The anterior anal rays of the male have been described as a "gonopodium" (Turner, Mendoza, and Reiter, 1962), a term first applied to the elongate male anal fin of poeciliids, but this term may be a misnomer for goodeids since the role of the anal fin in sperm intromission has not been demonstrated (Miller and Fitzsimons, 1971). Goodeid males also have a short, highly muscular tube connecting the sperm ducts to the genital opening; this structure has been termed a "pseudophallus" (Mohsen, 1961, 1965). It is said to expel semen forcibly or to become everted and applied to or placed into the female's genital opening, but, as with the "gonopodium," its function has only been surmised and not demonstrated. Females have a single median ovary formed by the union of lateral organ rudiments, the fused internal walls of which form the median septum. Yolk is resorbed early in embryogeny and its nutritive function is assumed by placenta-like trophotaeniae, rosette or ribbon-like growths which extend from the anal region of developing embryos in all but one species (Turner, 1933, 1937).

The taxonomy of the Goodeidae was last revised by Hubbs and Turner (1939), chiefly on the basis of ovarian and trophotaenial anatomy which is now judged to be too variable to be used alone for distinguishing species or for determining phylogenies (Mendoza, 1965; Miller and Fitzsimons, 1971). Since Hubbs and Turner's revision of more than 30 years ago, the study collections of preserved specimens of the family have increased well over tenfold. Most of this material is housed at The University of Michigan Museum of Zoology where live fishes are also kept representing every described genus and nearly all of the species in the family in the large aquarium facility directed by Dr. Robert R. Miller.

My work is a re-examination of two goodeid genera, Characodon and Xenotoca, and redetermination of their species using conventional morphological data along with those from study methods not used by the early students of these fish groups. These include hybridization experiments, ethology, discrimination tests, and karyology. In Xenotoca a new species, X. melanosoma, is described and another, X. eiseni (Rutter), is resurrected from synonymy.

MATERIALS AND METHODS

Most of the preserved specimens used are from the University of Michigan Museum of Zoology (UMMZ), but material from other important collections was also studied: British Museum (Natural History) (BMNH), United States National Museum (USNM), Tulane University (TU), University of Utah (UT), Louisiana State University Museum of Zoology (LSUMZ), and Harvard Museum of Comparative Zoology (MCZ). Live individuals were from stocks collected in México and transferred to Ann Arbor by R. R. Miller, H. L. Huddle, A. L. Metcalf, W. L. Minckley, C. M. Bogert, and me.

Methods used in counting and measuring are essentially those described by Miller (1948) and Hubbs and Lagler (1958). The anteriormost anal ray of goodeids remains a mere vestige or rudiment; since it typically can be seen only by dissection, clearing and staining, or in radiographs, it is not included

in the count (Hubbs and Turner, 1939, omitted it also). Numbering of sensory head pores and classification of canal types is based on Gosline's study (1949), which included certain goodeids.

Microscope slide preparations of gill tissue to disclose chromosomes followed the method of McPhail and Jones (1966). Designation of centromeric positions on chromosomes adopts the classification of Levan, Fredga, and Sandberg (1964).

Three types of hybridization tests were used: (1) forced crosses; (2) group crosses; and (3) artificial insemination. In "forced" or "no choice" experiments, a male of one species (or population) was isolated in an aquarium with a female of another species. Since goodeids do not have superfetation or interbrood sperm storage, crosses could be set up with wild-caught or conspecifically pregnant females from stock tanks; once the conspecific brood was born, any young produced subsequently were hybrids. When possible, the cross of the female of one species with the male of another species was accompanied by a reciprocal cross set up in another aquarium. If the crosses were not productive within two months, mates were exchanged so that a female was mated with the male of her own species. This procedure was repeated several times with several pairs of fishes to determine whether or not the members of a hybrid cross, although capable of conspecific reproduction, would reproduce with members of the other species under the existing conditions of the experiment.

In "group" or "choice" hybridization experiments, males and nonpregnant females of both species were placed together in an aquarium; subsequently the females that became pregnant were isolated and their young identified as conspecific or hybrid. Since goodeid males and females have indeterminate growth, it was possible to set up a group experiment and, months later, to identify the original parents even after some of their offspring had in turn begun to reproduce. In a long-term experiment, the number of hybrids and individuals of each species was counted and identified as F_1 , F_2 , or backcross young.

In the third hybridization test, which involved artificial insemination, sperm packets were removed from the posterior part of the sperm duct of a dissected male with a glass pipette containing a few drops of 0.8% saline and were injected well into the gona-

ducts of nonpregnant heterospecific females and "control" nonpregnant conspecific females. The females were then isolated in aquaria for gestation.

Ecological data were summarized from original field notes that accompany collections of live fish as well as those catalogued at the UMMZ. In February and March, 1970, personal field observations were made for all species included herein, and specimens of each species were preserved for food analyses. Mendoza's excellent study (1965) on the ovary and trophotaeniae of *Xenotoca eiseni* was used as a guide for the examination of these structures in the other species of *Xenotoca* and in *Characodon lateralis*.

Discrimination tests were based on pairforming movements that occur early in the courtship sequence. Prior to copulation attempt, goodeid males typically exhibit one or more courtship displays-conspicuous movements and postures in which sexually dimorphic features are presented to potential mates. In testing the discriminatory ability of a male, points were scored according to which of two females, heterospecific and conspecific, the displays were directed. Similarly, points were scored for females by noting their Head-Wagging response, a series of rapid lateral head movements which always preceded successful copulation. Behavioral components that were studied quantitatively are capitalized in this text to connote technical significance. To evaluate the number of test points statistically indicative of discrimination or nondiscrimination for an individual fish and, ultimately, its species or population, a closed sequential test grid was used. This grid, devised by Cole (1962) for ecological tolerance experiments, indicates when the experimenter may stop after completing a sufficient number of tests to reveal differences of predetermined statistical significance (in P = 0.9 for discrimination and P = 0.5 for nondiscrimination). Such tests were conducted on fishes of various ages and experience, including exclusively conspecific, exclusively heterospecific, or no experience (i.e., raised in complete isolation).

The account of mating behavior is limited to a qualitative description of male courtship displays based on about 280 hr of aquarium and underwater observations. Extensive evidence, to be presented elsewhere, indicates that the courtship displays of *Characodon* and *Xenotoca* have the complexity, variability, and species-specificity to make

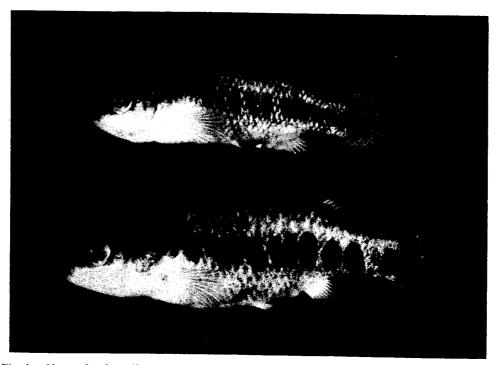


Fig. 1. Characodon lateralis male, 29.5 mm SL, and female, 38 mm SL, from Los Berros, Durango.

them excellent taxonomic characters; indeed, they appear to be the most important traits for species determination by the fishes themselves.

The following live stocks were largely the basis for the hybridization experiments, discrimination tests, ethology, and karyology:

Characodon lateralis: Los Berros, 4 km NE of El Salto, Durango, Metcalf, June, 1968; Ojo de

Agua de San Juan, Durango, underwater observations, 15 February 1970.

Xenotoca variata: Río Santa María, ca. 1.6 km S of Villa de Reyes, San Luis Potosí, Miller and Huddle, 26 March 1968; Presa El Gigante, near Santa María de Gallardo, 21 km NE of Hwy 45 on road to Loreto (at La Dichosa), Aguascalientes, Miller, Huddle, and Gomez, I April 1968; S end Lago de Cuitzeo, Michoacán, Miller and Fitzsimons, 8 March 1970.

Xenotoca eiseni: Manantial El Sacristán, 1.3 km NW plaza of Tepic, Nayarit, Bogert, 1955; Río Tamazula at Hwy 110 bridge, 5 km S of Cd. Guzmán turnoff, Jalisco, Miller and Huddle, 3 May 1966.

Xenotoca melanosoma n. sp.: Río Tamazula at Hwy 110 bridge, 5 km S of Cd. Guzmán turnoff, Jalisco, Miller and Huddle, 3 May 1966; Presa de la Vega, in Río Ameca, 32 km W of jct. of Hwy 15 and Hwy 70 (to Ameca), Jalisco, Miller and Huddle, 5 May 1966.

Ameca splendens: Río Teuchitlán below

Teuchitlán, Jalisco, Miller and Huddle, 5 May

Allotoca dugesi: Presa El Gigante, near Santa María de Gallardo, 21 km NE of Hwy 45 on road to Loreto (at La Dichosa), Aguascalientes, Miller, Huddle, and Gomez, 1 April 1968.

Xenoophorus captivus: Río Santa María del

Río, ca. 5 km by road above town of same name, San Luis Potosí, Miller and Huddle, 29 April 1966.

Characodon Günther Fig. 1

Type species, Characodon lateralis Günther

Diagnosis.-A medium-sized goodeid (to 60 mm SL) with red, yellow, black, and clear curved bands on the median fins of the male, typically 12 (11-13) dorsal rays for the male and 11 (10-12) for the female, 14 or 15 (13-16) anal rays for the male and 13 or 14 (12-14) for the female, 17 (16-18) pectoral rays, 36 or 37 (35-38) scales around the body, usually 7 preopercular sensory pores in adults, 4 branchiostegal rays, 2 ribbon-like trophotaeniae in developing embryos and neonates, a unique diploid chromosome number of 24 metacentrics (Fig. 2), and 4 distinctive male courtship displays.

Relationships.-On the basis of ovarian

and trophotaenial characters, Hubbs and Turner (1939) removed four species from Characodon and placed them in the genera Xenotoca Hubbs and Turner, Chapalichthys Meek, Ilyodon Eigenmann, and Lermichthys Hubbs (regarded as a synonym of Girardinichthys Bleeker; Miller and Fitzsimons, 1971), leaving Characodon monotypic with C. lateralis. Although certain of the ovarian and trophotaenial characters proposed by Hubbs and Turner are of limited systematic use (Mendoza, 1965; Miller and Fitzsimons, 1971), data from ethology, karyology and other anatomical studies confirm the distinctiveness of this genus. However, the phyletic relationships of Characodon are uncertain. This genus is specialized in many characters but its trends away from primitive characteristics are shared by various genera whose relationships are themselves diverse or uncertain. Almost 70% of the Goodeidae have a diploid chromosome number of 48, now widely held to be the basic teleost number. Characodon has the lowest number, 24, for the family. Other low numbers include Allotoca Hubbs and Turner (26), Ameca Miller and Fitzsimons (26), Zoogoneticus Meek (28), Alloophorus Hubbs and Turner (30), and Chapalichthys Meek (36); all except Ameca (position uncertain, Miller and Fitzsimons, 1971) are members of the Goodeinae as defined by Hubbs and Turner. The number of branchiostegal rays, four, observed in Characodon occurs in only three other genera: Xenoophorus Hubbs and Turner of the Goodeinae, Xenotaenia Turner of the Girardinichthyinae, and Allodontichthys Hubbs and Turner of uncertain subfamily affiliation (Turner, 1946). All other goodeids have 5 branchiostegal rays. Besides Characodon, only Girardinichthys Bleeker, subfamily Girardinichthyinae, shows marked sexual differences in dorsal and anal ray counts, but they are much more extreme in the latter genus. The few trophotaeniae (two) in Characodon is most closely approached in the specialized species of Skiffia Meek (three trophotaeniae) of the Girardinichthyinae. and by the monotypic genus Ataeniobius Hubbs and Turner (no trophotaeniae), set aside in the Ataeniobiinae, and reputed to be the most primitive member of the family (Hubbs and Turner, 1939). Comparisons of data for character states common (primitive) throughout the family also do not indicate a greater affinity between Characodon and any particular genus or subfamily. Thus the

segregation of *Characodon* into its own subfamily by Hubbs and Turner, using ovarian and trophotaenial characters, is retained but should be considered tentative until confirmed or invalidated when the interrelationships of the family are more completely understood through redefining species and generic boundaries.

Characodon lateralis Günther

Synonymy.-Günther (1866) described Characodon lateralis from specimens at the British Museum in "Dr. Seeman's collection, who obtained them in Southern Central America." In his subsequent account (1869) Günther remarked on the inadequacy of localities for Seeman's collection. My comparisons of meristic data from the syntypes and from material taken near Durango, México, indicate that all specimens were conspecific. It is likely that the type locality of this species was somewhere on the Mexican plateau, probably in Durango or Coahuila; goodeids are unknown in "southern Central America." Garman (1895) collected and correctly identified C. lateralis from Parras, Coahuila, about 320 km NNE of the city of Durango, but Jordan and Evermann (1898), possibly confused by Günther's erroneous designation of the type locality, named the Parras fish C. garmani solely from Garman's description. Meek (1904) published another description of *G. garmani* from material he collected at Labor, Durango, in the Río Mezquital basin. Although Regan (1906-08) examined Meek's specimens and reported them to be identical to Günther's description of C. lateralis, Jordan, Evermann, and Clark (1930) persisted in listing garmani as a valid species. Hubbs and Turner (1939) re-examined Meek's specimens and confirmed Regan's synonymy but no actual comparison was made of specimens from both Parras and Durango. In 1963 R. R. Miller examined the holotype of Characodon garmani from Parras, Coahuila (MCZ 27704), and has allowed me to use his data in validating the synonymy of C. garmani with C. lateralis.

Distribution.—Characodon lateralis is the northernmost known member of the Goodeidae, now apparently confined to the headwaters of the Río Mezquital in the state of Durango. It once ranged farther north to the enclosed basin near Parras, Coahuila (type locality of C. garmani) but probably



Fig. 2. Diploid chromosome complement of Characodon lateralis.

became extinct there because of the diversion of water for irrigation, increased industrial and domestic sewage, and the introduction of carp (Miller, 1961). Unless misidentified, the species occurred earlier in Jalisco (Pellegrin, 1901), but this southern extension of its known range has not been confirmed by recent collecting.

Material examined.—BMNH 1855-9-19: 317–320, 1566–9 (syntypes); UMMZ 65228, 160880, 161689, 166708, 167728, 179647, 179655, 189091. Data were obtained from 127 specimens.

Description.—The diagnostic characters listed for the genus are the most useful in identifying this species.

Dorsal rays: 11-13 (11.86 ± 0.51) for males; 10-12 (11.09 ± 0.16) for females. Anterior unbranched dorsal rays: 2-6 (3.20 ± 0.82) for males, and 2-5 (3.12 ± 0.82) for females. Branching is correlated with size. Fish of both sexes with only two unbranched dorsal rays were usually 35 mm SL or larger; those with five or six unbranched rays were 30 mm SL or smaller. Anal rays: 13-16 (14.39 ± 0.65) for males; 12-14 (13.19 ± 0.56) for females. Unbranched anal rays: 5-8 (6.20 ± 0.50) in males, and 1-6 (3.44 ± 1.13) in females. Seven or eight unbranched anal rays were seen only in males less than 25 mm

SL; four or more unbranched rays occurred in females 34 mm SL and smaller. Pectoral rays (both fins): 16-18 (16.73 ± 0.04). Pelvic rays (both fins): 5-7 (5.90 ± 0.38). Principal caudal rays: 17-22 (19.35 ± 1.01). Fish 40 mm SL or larger had 19 to 21 principal caudal rays. The syntype male has 12 dorsal rays, 14 anal, 6-6 pelvic, 17-17 pectoral, and 19 principal caudal rays. The syntype females have 10 (1), 11 (8) dorsal rays, 13 (5), 14 (4) anal, 6 (18) pelvic, 16 (4), 17 (13), 18 (1) pectoral, and 19 (4), 20 (3) principal caudal rays.

Scales in lateral series: 31-35 (32.93 ± 0.59). Predorsal scales: 25-33 (28.84 ± 1.77). Scales around body: 35-38 (36.44 ± 0.82). Scales around caudal peduncle: 17-20 (18.06 ± 0.63). The syntype male has 33 lateral-series scales and about 20 around the caudal peduncle. The syntype females have 33 (6) lateral-series scales and 17 (1) or 19 (5) around the caudal peduncle. Accurate predorsal and circum-body counts were not possible for the syntype series.

Vertebrae: 32-35 (33.42 ± 0.75). The syntype male has 33 vertebrae and the syntype females have 33 (7) and 34 (2).

Data for the holotype female of "garmani," taken by Miller, when compared with that for the syntypes and Durango specimens of C. lateralis support the identity of the Parras and Río Mezquital populations. His counts were: dorsal rays 11, anal 12, pectoral 16-16, pelvic 6-5, caudal 19, and vertebrae 33. These values are well encompassed by the ranges recorded for C. lateralis, and, except for number of anal and pectoral rays, they approximate the mean values observed in the syntypes and the samples from Durango.

Gill rakers: 12-17 (14.20 ± 1.44). Specimens larger than 36 mm SL have 14 to 17 gill rakers. The syntype male has 13 gill rakers and the syntype females have 14 (1), 15 (5), 16 (2), 17 (1).

Proportional measurements are summarized in Table 1.

Sensory pores were counted on both sides of the head. Lachrymal: 3-5 (3.99 ± 0.18); mandibular: 3-5 (4.0 ± 0.15); preopercular: 4-9 (7.04 ± 0.46). The syntype male has 4-4 lachrymal, 4-4 mandibular, and 7-7 preopercular pores. The syntype females have 4-4 lachrymal, 4-4 mandibular, and 7-7 (6), 7-8 (3) preopercular pores. The pattern of supraorbital canals on top of the head is type 11, according to Gosline's classification (1949, Pl. 1), in which the canal is discontinuous

Table 1. Proportional Measurements, in Hundredths of Standard Length, of Characodon lateralis and the Three Species of Xenoloca. Means in parentheses.

	C. la	C. lateralis ¹	Х. t	X. variata²	X.	X. eiseni³		Xei	Xenotoca melanosoma ⁴	101-1
	11 males	14 females	10 males	10 females	10 males	10 females	Holo- type	Allo- type	7 males	9 females
Standard length, mm.	27.5-40.0	32.5-53.0	31.0-59.0	36.5-69.0	27.5-51.0	30.5-56.0	65.5	75.5	28.5-66.5	31.0-79.0
	(34.8)	(41.1)	(40.9)	(46.1)	(40.0)	(44.8)			(47.6)	(55.2)
Predorsal length	71-76(72.8)	69-76(73.8)	61-65(62.8)	61-67(64.0)	63-72(67.5)	66-69(67.6)	62	65	62-67(63.0)	62-66(64.3)
Prepelvic length	54-58(56.5)	54-60(57.6)	52-58(54.8)	52-58(54.9)	55-60(57.1)	56-60(57.2)	54	56	54-58(55.3)	54-57(55.3)
A origin to C base	30 - 35(31.3)	28 - 33(30.6)	29 - 37(33.9)	27-37(32.0)	29 - 35(32.2)	29-35(31.5)	35	32	32-37(34.4)	32-35(33.2)
Body, greatest depth	32-40(36.0)	30 - 36(33.6)	32 - 37(34.5)	30 - 37(33.8)	36-48(40.7)	33-41(37.6)	35	36	30-36(33.6)	31-39(34.6)
Width	17-19(18.2)	16-21(18.1)	16-19(17.5)	15-23(19.0)	17-22(18.8)	18-24(20.3)	21	91	16-21(18.1)	16-23(18.9)
Head length	32 - 35(33.8)	30 - 33(31.3)	32 - 34(32.7)	30 - 33(31.4)	30 - 34(32.3)	28 - 32(30.0)	32	32	30 - 32(31.9)	30-32(31.2)
Depth	18–22(19.7)	18-21(19.3)	16-20(17.6)	15-19(17.1)	17-20(18.3)	16-18(17.3)	20	19	18-20(18.7)	16-20(18.2)
Width	19-22(20.3)	19-21(20.1)	18-21(19.1)	16-21(18.8)	18-22(19.7)	17-20(18.7)	22	23	20-21(20.6)	20-23(21.2)
Caudal peduncle length	19-24(21.7)	20-24(21.5)	21-26(24.0)	21-26(24.2)	21 - 25(23.6)	21-26(22.9)	24	55	22-24(23.3)	21-24(23.3)
Least depth	16-19(17.1)	14-17(15.9)	14-16(15.4)	14-19(15.6)	14-19(16.3)	13-17(15.8)	91	91	15-17(16.1)	16-18(16.8)
Interorbital width	13-15(13.8)	12-16(13.8)	11-14(12.5)	10-13(11.6)	11 - 15(13.4)	12 - 14(13.2)	14	15	13-15(13.8)	13-15(13.9)
Preorbital width	4-5 (4.2)	3-6 (4.1)	4-6 (4.8)	4-5 (4.5)	4-7 (5.1)	3-5 (4.1)	4	4	4-5 (4.1)	3-5 (3.8)
Opercle length	12-15(13.3)	11-14(12.5)	11-13(12.0)	10-12(10.9)	11-14(12.5)	11-13(11.7)	13	12	11–13(12.6)	12-13(12.4)
Snout length	7–9 (8.2)	(9.9) $8-9$	5-9 (7.9)	7–9 (8.0)	(9.7) (7.6)	7-8 (7.7)	9	7	6-7 (6.4)	6-8 (6.7)
Orbit length	9-11(9.7)	7-10(9.6)	8-12(10.1)	8-11(9.6)	8-10(8.9)	8-10(8.5)	6	∞	9-11(9.7)	8-11(8.6)
Mouth width	11-13(11.8)	10-13(11.7)	9-12(10.3)	8-12(9.8)	9-12(10.2)	7-10(8.5)	=	Ξ	9–12(10.8)	9-11(10.3)
Opper Jaw Jength	6-9 (7.3)	7-9 (7.7)	6-9 (7.2)	(0.7) $6-9$	4-8 (6.6)	5-8 (6.2)	œ	8	5-9 (6.8)	5-9 (6.8)
Mandible length	7-9 (8.3)	7-10(8.1)	6-10(7.4)	(6.9) 6-9	5-8 (6.7)	5-8 (6.4)	8	6	5-9 (7.0)	5-8 (7.0)
Dorsal fin, basal length	14-18(15.5)	11-13(11.8)	15-19(16.6)	11-16(13.6)	15-20(17.6)	13-17(15.3)	24	21	20-24(21.6)	18-21(18.3)
Depressed length	26-31(29.0)	18-21(20.2)	27 - 32(30.6)	20-26(23.2)	28 - 34(30.8)	23 - 26(24.3)	38	50	30-39(35.4)	24-28(26.3)
Anal fin, basal length	11-15(12.8)	8-10(9.6)	10-12(11.8)	8-12(9.8)	7-12(10.8)	8-12(9.8)	12	01	12-13(12.4)	10-12(10.8)
Depressed length	18-21(19.5)	15-18(16.3)	19-21(20.2)	14-19(17.2)	16-23(19.3)	15-18(16.2)	12	16	19–21(19.8)	15-19(17.7)
Middle caudal rays, length	16-19(17.2)	14-18(15.8)	16-19(17.3)	12-19(15.8)	14-18(15.9)	14-18(15.2)	14	+	14-21(17.1)	12-18(15.3)
Pectoral length	17-19(18.2)	12-17(15.6)	18-21(20.2)	17-21(18.5)	18-21(20.1)	16-20(18.0)	21	81	19–21(20.6)	16-21(18.1)
Pelvic length	9-10(9.5)	8-10(9.3)	13-16(14.2)	12-15(13.2)	12-15(13.2)	10-15(12.4)	14	13	12-16(14.4)	13-15(13.7)

¹ Based on BMNH 1855-9-19: 317-320; 1566-9 and UMMZ 166708. ² Based on UMMZ 179760, 189581, and LSUMZ 6309. ³ Based on UMMZ 17243 and 186290. ⁴ Based on UMMZ 189077, 189078, 189079, and Ut-CDB69-28.

between the second and third anteriormost pores (designated 2a and 2b by Gosline). In fish about 33 mm SL and smaller, another break frequently occurs between the fifth and sixth pores (Gosline's 4a and 4b). Formulae for the supraorbital canal and pores in this species are: 1-2a 2b-7 and 1-2a 2b-4a 4b-7.

Four branchiostegal rays were counted in each of 10 males and 10 females.

Outer row teeth are conic or bifid depending on the size of the fish (Table 2). They number from 17 to 22 (mostly 21 or 22) in the upper jaw and from 18 to 23 (mostly 20–22) in the lower jaw. Inner row teeth, conic in fish of all sizes, number from 32 to 56 (mostly 32–36) in the upper and from 32 to 52 (mostly 32–36) in the lower jaw.

Inner teeth are arranged in an irregular curved band in both jaws.

The diploid chromosome complement of *Characodon lateralis* consists of 24 metacentric chromosomes (Fig. 2).

Dimorphism and coloration.—Sexual dimorphism in this species is marked in the range and average number of dorsal and anal fin rays. As in all goodeid males, the first six or seven anal rays are shortened and crowded and presumably aid in copulation. Proportional measurements (Table 1) indicate some slight sexual differences in body depth, head length, snout length, and perhaps other characters, but the most striking sexual dimorphism occurs in the lengths of the fins. Except for the pelvics, the fins of males are considerably longer than those of females. Even more conspicuous sexual differences occur in the life colors.

Breeding males exhibit a striking rainbowlike pattern of red, yellow, black, and clear curved bands on their median fins. In males 40 mm SL or larger, the basal red band is equal to or slightly greater in width than twice the diameter of the eye. An outer yellow band, equal to or slightly narrower than an eye diameter, borders the red band, and is, in turn, demarcated along its outer margin by a slightly narrower black band. At the margin of the fin an unpigmented zone, approximately the width of the adjacent black zone, forms the outermost band. In immature males only the outer three bands of yellow, black, and clear may be seen; the yellow band is two to four times the width of the black and clear bands. However, as the fish matures, red pigments gradually expand onto the fin membranes and eventually form the broadest and brightest band of color.

TABLE 2. COMPARISON OF OUTER ROW TOOTH TYPES AND BODY LENGTH IN Characodon lateralis.

	Fish with teeth				
Standard length, mm	Conic both	upper conic, lower mostly bifid	mostly bifid* both jaws		
7–11	20 fish				
(newborn)					
12-18	18	2			
22 - 31	4	16			
31-50		3	17		

^{* = 6} or fewer conic per jaw.

Originating at the anal fin insertion is a concomitant proliferation of red pigment that suffuses dorsally and laterally onto the caudal peduncle and belly, often reaching as far as the midside. The top of the head, nape, and back are olive-brown, darkest dorsally and gradually becoming paler down the sides. The chin, cheek below the eye, and most of the opercle are bright yellow. The upper corner of the opercle and scales just anterior to the pectoral fin are silvery. Paired fins are pale gray to clear. Speckling or spotting is seen on the sides in males of all sizes but is most discernible in preserved material.

The ground color in females is also olivebrown but the vivid colors of the males are lacking. The fins are pale gray to clear except for a slight concentration of very pale yellow on the proximal membranes of the dorsal, caudal, and, less frequently, the anal fins of large females. The chin, cheek, and opercle are pale yellow to yellow-white. Pale red-gold reflections can be seen at the upper edge of the opercle. Live females are variously spotted and speckled over the body, but, as in males, these pigment patterns are most clearly seen in preserved fish.

In preservative the bright red and yellow colors of the males and the pale yellow of the females fade completely. Areas of the body with these pigments appear light buff in contrast to the darker olive-brown elsewhere, and fins are pale gray to clear where once brightly colored. Dark pigments which form the subterminal black band on the median fins of live males persist in preserved specimens; these markings are still visible in the syntype male which, at this writing, has been preserved for 115 years. In adults and immatures of both sexes, the upper and lower lips and top of the head are dark brown, with

a narrow stripe of the same color and intensity extending posteriorly from the top of the head along the middorsal line to the leading edge of the dorsal fin. Although the dorsal surface of the caudal peduncle is noticeably darker than the sides, the dark middorsal stripe does not continue onto it. Random speckling in neonates and immatures is replaced by large spots in mature fish. Fish of all sizes have a concentration of pigments along the midside in the form of speckling, spotting, or a general darkening which, when viewed from a distance, appears as a distinct stripe. Spotting was examined in 50 specimens each of males and females and found to be concentrated predominantly along the midside in variable amounts. In males and females between 20 and 35 mm SL, spots half an eye diameter or larger varied rather uniformly from 0 to 12. Spots on fish 20 to 30 mm SL were usually distributed throughout the length of the caudal peduncle and body forward to the posterior margin of the opercle, but in larger specimens, spots were often present only on the caudal peduncle. Females have a dark "pregnancy spot" (see discussion of life colors for X. eiseni females) on the belly anterior to the anal fin that is equal to or slightly smaller than twice an eye diameter; this spot or blotch is faint in live fish but becomes more noticeable when overlying pigments fade in preservative.

Embryology.—On the basis of ovarian and trophotaenial characters, Hubbs and Turner (1939) restricted the genus Characodon to the single species C. lateralis and placed it alone in the subfamily Characodontinae. The discussion below summarizes my re-examination of these embryological features in this species and assesses their value in its classification.

As in other goodeids, the single ovary of Characodon lateralis is a spindle-shaped partitioned sac whose median septum represents the fused walls of two organ rudiments. Hubbs and Turner reported that ovigerous tissue in this species is restricted to dorsolateral bands on the walls and in the dorsal part of the septum. I observed this distribution of oocytes in females with large embryos nearing birth but, in females with eggs or small embryos, I found ovigerous tissue most often restricted to a small patch at the apex of the ovary where the walls and septum merge anteriorly. Presence of ovigerous tissue in extensive dorsolateral bands is a periodic occurrence related to the proliferation

of new oocytes as developing embryos approach birth. In females of all reproductive stages, the anterior quarter or more of the ovigerous tissue often extends throughout the height of the septum and is rarely restricted to its dorsal half, as stated by Hubbs and Turner. The septum is entire, unbranched, and attached dorsally and ventrally, as indicated by those authors, but folding in the septum is variable in location and extent. Folding is seldom restricted to the dorsal half of the septum; it is extensive early in embryogeny but is reduced or absent in ovaries stretched by large embryos.

According to Hubbs and Turner (1939), the trophotaeniae of C. lateralis occur in pairs, are long to very long, and are of the sheathed type histologically. Trophotaeniae were counted in each of 125 embryos and neonates and were always two in number. Trophotaeniae vary in length. Reaching maximum development in near-term embryos, they may equal or exceed the embryo's total body length (not just the length of its caudal peduncle as observed by Hubbs and Turner). However, trophotaeniae are short (less than one-third total length) in young near birth and in small embryos whose yolk has not been resorbed. "Sheathed" trophotaeniae is a term applied to processes in which the central core or medulla of connective and vascular tissue is separated by a wide primary tissue space from the epithelial covering. My observations for this species indicate that sheathing, although usually prominent, may be absent in some embryos and variably developed even in a single trophotaenial process. In early tailbud embryos, or those near birth, the tissue space is greatly reduced or absent (= unsheathed). For midgestational embryos the tissue space is absent at the basal peduncle of a trophotaenia, welldeveloped along its mid-length, and absent again at the tip where the medulla is covered only by an outer epithelium.

Most of the characters Hubbs and Turner (1939) described for the ovary and trophotaeniae of *Characodon lateralis* are difficult or impossible to use in identifying this species because they are too variable. Unless large series of specimens are available for dissection, one might not be able to find a female of *C. lateralis* in which the location of ovigerous tissue could be distinguished from the locations described for other members of the family: "in dorsolateral bands

and in dorsal part of septum" versus "in outer wall and septum" and "in a pair of dorsolateral convoluted folds." Characters of the median septum confirmed by my observations (entire, unbranched, attached dorsally and ventrally) are shared by eight other genera representing, together with Characodon, three of the four subfamilies which Hubbs and Turner delineated for the family. The length and histological type of the trophotaeniae are sufficiently variable in C. lateralis to be indistinguishable from species in five other genera to which Characodon is not closely allied. Of all the ovarian and trophotaenial characters employed by Hubbs and Turner, only the number of trophotaeniae is species-specific. If the other characters cannot be used singly or in combination to distinguish Characodon lateralis from other members of the family, they also cannot be used alone to determine the relationships of the genus or subfamily of which this species is the sole member. Their use in assessing degrees of relatedness must be accompanied by characters from other sources.

Ecology.—Characodon lateralis has been most abundant in clear, probably spring-fed ponds or stream pools with little current, abundant submerged vegetation, grassy banks, and water temperatures between 18 and 27 C.

The species was herbivorous in the twoacre pond at Ojo de Agua de San Juan where large masses of filamentous green algae, mostly Spirogyra and lesser amounts of Ulothrix, formed a layer up to two meters thick where there was a supporting understructure of rooted Chara and Ceratophyllum. Spirogyra and Ulothrix constituted the bulk of the diet but other filamentous chlorophytes and cyanophytes and pennate diatoms were also common food items. Two large oligochaetes found in the gut of one fish may have been ingested fortuitously along with algal material, but, since these fish take live brine shrimp, Daphnia, and earthworms in the laboratory, it is likely that they will readily feed on suitable animal material when available.

Hybridization experiments.—In forced crosses Characodon lateralis failed completely to hybridize with allopatric stocks of Xenotoca variata (6 crosses), X. eiseni (3), X. melanosoma (3), Ameca splendens (2), Xenoophorus captivus (3), and Allotoca dugesi (3). Attempts at artificial insemination (1 to 4)

per species) were also unproductive. Ameca splendens and Allotoca dugesi were chosen for experimentation because of their proximity to C. lateralis in chromosome number. Both have a diploid number of 26, C. lateralis has 24, whereas species of Xenotoca and Xenoophorus have 48. Hybridization data support the distinction of C. lateralis from the species listed but have no value in estimating its relationships to them.

Courtship displays.-After orientation to the female, a male performed one or more Tilting-Sigmoid displays in which the body was tilted vertically, dorsal surface toward the female, and bent horizontally into a sigmoid or S-shape. The angle of tilt was not the same in all displays, and the Sigmoid Posture seen in the relatively deep-bodied males of Characodon (and Xenotoca) was much less pronounced than that described for the slenderer poeciliid males of Lebistes (Baerends et al., 1955), Xiphophorus (Clark et al., 1954), and Poecilia (Liley, 1966). Males of C. lateralis had six courtship displays: the Lateral T-formation, Lateral Tailbeating, Oblique, Lateral Head-Down, Lateral Head-Up, and Gliding.

The Lateral T-formation display (Fig. 3) was a common preliminary courtship posture a male assumed before a stationary female. Approaching from the right or left with its median fins fully expanded, the male stopped directly broadside about half a body length in front of the female, bent its body into a strong sigmoid shape, tilted the dorsal surface toward the female, and quivered rapidly. Tilting was often so extreme that the vertical axis of the male's body was nearly parallel to the horizontal axis of the female's body. The dorsal and anal fins were inclined toward the female.

In a variation of the Lateral T-formation display the male took up a position with extreme tilting directly over the head of the female and rapidly bent his body first to one side then the other, often striking the top of the head and snout of the female with the side of the caudal peduncle and body. The distinguishing feature of this Lateral Tailbeating display was the jerky side to side movement resembling exaggerated in-place swimming. Although executed in a different plane, this movement was quite similar to that reported by Barlow (1961) for a lateral agonistic display between two males of Cyprinodon macularius; his term "tailbeating" has been adopted in naming this unusual

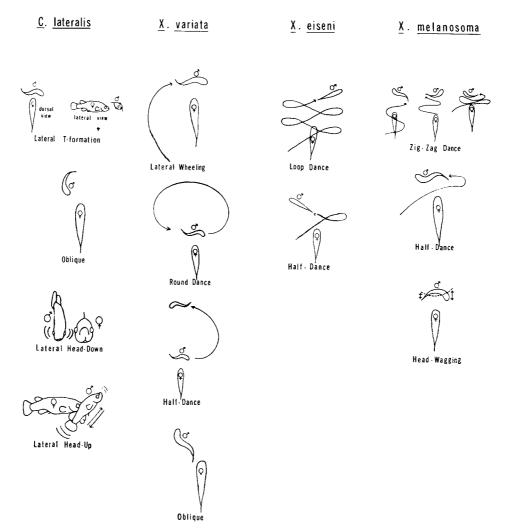


Fig. 3. Selected courtship displays of Characodon and Xenotoca.

courtship behavior of C. lateralis males. This Lateral Tailbeating display was presented to stationary females.

Males performed the Oblique display (Fig. 3) by facing the female from an angle 90° or less to her right or left at a distance of one to two body lengths while bending the caudal fin and peduncle toward her. This display was usually presented to a stationary female, but the male maintained his alignment with a slowly swimming female by sculling with the pectoral fins.

In the Lateral Head-Down display (Fig. 3) the male swam alongside a stationary female, braked suddenly with expanded pectoral fins, lowered his head, and quickly jerked it

from side to side. This Head-Jerking movement was similar to the Head-Flicking seen in many killifishes (Foster, 1967), but the amplitude of swing was greater and there was a conspicuous pause between lateral movements rather unlike the rapid twitching or shuddering of the anterior end of the body reported for cyprinodontids.

In another type of lateral display the male swam alongside the female, elevated his head, and swam slowly forward and upward, bringing his dorsal fin close to the female's eye. The slow forward movement was continued until the caudal fin was about opposite the female's eye; then the male backed slowly and repeated the forward movement. For-

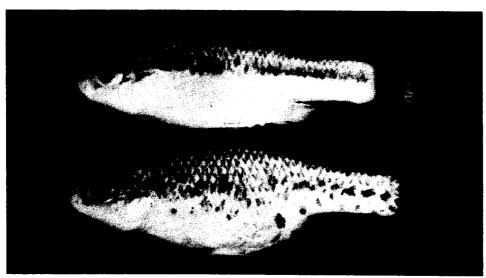


Fig. 4. Xenotoca variata male, 41.5 mm SL, and female, 45 mm SL, UMMZ 179760, Río de Aguascalientes, Aguascalientes.

ward and backward movements were executed several times (three to five), giving the display a smooth rocking appearance. Throughout the display the male tilted about 15°, quivered, and strongly curved its body, head and tail toward the female. This Lateral Head-Up display (Fig. 3) was presented to stationary females only.

A male sometimes darted alongside a female and glided by with its median fins fully expanded and body conspicuously S-curved and tilted. This Gliding display was given to stationary or swimming females.

Discrimination tests.—Mate selection by males and females of Characodon lateralis was always conspecific in tests with Xenotoca variata, X. eiseni, and X. melanosoma. A minimum number of experiments for each sex of C. lateralis was required for statistical significance, where P=0.9.

Xenotoca Hubbs and Turner Type species: Xenotoca variata (Bean)

Diagnosis.—Medium to large goodeids (75–85 mm SL with 3 to 6 nondeciduous ribbon-like trophotaeniae in embryos and neonates, a diploid chromosome number of 48 comprising 4, 6, or 8 subtelocentrics and the remainder telocentrics, the males with sexually dimorphic caudal fins that are solid black, or the black bordered by a terminal yellow band, or red to red-orange basally, the fin exhibited to mature females in elaborate dance displays during courtship.

Relationships.—The relationships of Xenotoca are obscure and will remain so until species and generic limits have been redefined throughout the family. Its closest relative is Chapalichthys, a genus it resembles in many characters (fin rays, scalation, body form, and coloration) other than karyotype (2n = 36 in Chapalichthys). The phenetic similarity of Xenotoca to Chapalichthys, Xenoophorus, Goodea Jordan, Allotoca, Zoogoneticus and Alloophorus indicate that it is well placed with these genera in the subfamily Goodeinae as suggested by Hubbs and Turner (1939). However, relatedness cannot be assessed objectively from ovarian and trophotaenial characters alone; these must be bolstered with comparative data from other sources.

Xenotoca variata (Bean) Fig. 4

Synonymy.—After examining the types of Characodon eiseni Rutter, Hubbs (1926) confirmed Regan's synonymy (1906–8) of this species with C. variatus. When Hubbs and Turner (1939) revised the family classification on the basis of ovarian and trophotaenial characters, variatus was placed in its own genus Xenotoca, with eiseni again listed as a synonym. At the suggestion of R. R. Miller, who recognized the specific distinctiveness of eiseni after seeing it alive in 1955, Mendoza (1965) examined specimens of it from Ma-

nantial El Sacristán, Nayarit (near the type locality), and found that the structure of the ovary and trophotaeniae did not agree with the description of these structures given for variata by Hubbs and Turner. My study based on both preserved and live specimens, leaves no doubt as to the specific distinction of both eiseni and variata. Most recently Romero (1967) has included eiseni as a synonym of variata, but this action was probably based on the literature rather than on a comparison of specimens of the two species.

Diagnosis.—A medium-sized goodeid (to 75 mm SL) with a dusky to black caudal fin terminated by a broad yellow band and with a dark stripe extending along the midside of the opercle, body, and caudal peduncle in breeding males (Fig. 4), usually 15 (14–16) pectoral rays in adults, 17 to 19 (16–21) scales around the caudal peduncle and 40 or 41 (36–43) around the body, usually 5 (4–6) ribbonlike trophotaeniae of the unsheathed histological type, a diploid chromosome number of 48 comprising four subtelocentrics and 44 telocentrics (Fig. 5), and four distinctive male courtship displays.

Distribution.-Xenotoca variata may be the most wide-ranging member of the family. Near the center of its range, the type locality includes streams and ponds around Guanajuato in the basin of the Río Lerma (Bean, 1887). Northern limit of distribution includes the Ríos Verde and Aguascalientes in the state of Aguascalientes and the Río Santa María in San Luis Potosí. It ranges in the west from the Río Grande de Santiago near Lago de Chapala (above the falls at Juanacatlán) in Jalisco and Michoacán, throughout the Río Lerma system of Guanajuato, and east to the Río de la Laja drainage near Querétaro. It has been collected as far south as Laguna de Zacapu and Balneario Cointzio (near Morelia) in Michoacán.

Material examined.—USNM 37809 (syntypes, one female 24.0 mm SL is Goodea sp.), 37810 (syntypes of Characodon ferrugineus), 2314, 37837, 37842, 37846, 38007, 41813. 43761, 55768, 161299, 161300, 161301, 161302, UMMZ 65217, 108554, 108648, 172188, 172200, 173514, 179760, 186284, 187398, 188802, 188803, 189025, 189037, 189042, 189051, 189073; LSUMZ 6271, 6293, 6309; TU 30689, 30808, 30810, 30827, 31885, 31947, 31980. Data were obtained from 338 specimens.

Description.-This species is most easily

distinguished from congenerics by the diagnostic characters given above.

Dorsal rays: 11-15 (12.67 \pm 0.78). Fish over 50 mm SL usually have only one unbranched ray in the dorsal fin; those between 40 and 50 mm SL most often have two unbranched rays; and fish between 18 and 30 mm SL commonly have three or four unbranched rays. The number of dorsal rays shows a slight clinal increase from north to south: $\bar{x} = 12.0$ for fish collected at or near Aguascalientes, Aguascalientes, $\bar{x} = 12.7$ for fish at or near Guanajuato, Guanajuato, $\bar{x} = 13.0$ for fish from Lago de Cuitzeo, Michoacán, $\bar{x} = 13.5$ for fish from Balneario Cointzio, Michoacán. Anal rays: (14.54 ± 0.63) . Males 45 mm SL and larger may have as few as two unbranched anal rays; those 35 mm SL and smaller usually have the first six anal rays unbranched. Females above 30 mm SL have three or fewer unbranched rays in the anal fin. Fish from Aguascalientes and Guanajuato averaged 14.3 anal rays; those from Lago de Cuitzeo and Balneario Cointzio averaged 15.0. Pectoral rays (both fins): 12-18 (15.19 ± 0.68). Pelvic rays (both fins): 4-7 (5.93 \pm 0.28). Principal caudal rays: $17-23 (20.3 \pm 1.09)$. Syntypes had 13 (1) dorsal rays and 14 (2) or 15 (1) anal rays.

Scales in lateral series: 32-39 (34.71 ± 1.75). A clinal variation in lateral series scales ranges from $\bar{x}=33.6$ for fish collected in Aguascalientes and Guanajuato to $\bar{x}=35.2$ and 37.5 for specimens from Lago de Cuitzeo and Balneario Cointzio, Michoacán, respectively. Predorsal scales: 18-29 (22.58 ± 2.17). Scales around body: 36-43 (40.00 ± 1.40). Scales around caudal peduncle: 16-21 (18.26 ± 1.02).

Vertebrae: 32-38 (34.27 ± 1.38). A north-south clinal increase in the number of vertebrae is apparent. Guanajuato fish averaged 33.8 vertebrae and Aguascalientes fish averaged 33.9, whereas the more southerly populations at Lago de Cuitzeo and Balneario Cointzio averaged 35.0 and 36.9 vertebrae.

Gill rakers: 12-23 (16.47 ± 2.42). Gill-raker number varies with size; fish 16 to 35 mm SL have 13 to 15 gill rakers, whereas larger fish usually have 16 to 20 gill rakers. Syntypes had 14 (1) and 17 (1) gill rakers.

Proportional measurements are summarized in Table 1.

Head pores were counted on both sides of the head. Lachrymal: 3 or 4 (3.98 \pm 0.12). Mandibular: 2–5 (3.9 \pm 0.22). Preopercular:

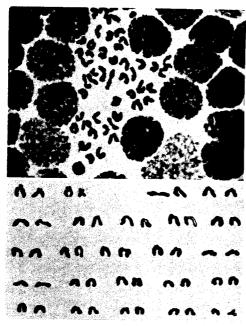


Fig. 5. Diploid chromosome complement of $Xenotoca\ variata$.

7-11 (8.70 \pm 0.71). The supraorbital canal system is type 11 in which there is a break in the canal between the second and third anteriormost pores (2a and 2b). In fish less than 40 mm SL, a second break frequently occurs between the fifth and sixth pores (4a and 4b). The supraorbital canal patterns for this species have the formula: 1-2a 2b-7 and 1-2a 2b-4a 4b-7.

Branchiostegal rays numbered five in 20 fish (10 males and 10 females).

Newborn and immatures, 15 mm SL or less, have flat-topped unicuspid teeth in the outer rows; in adults, 40 mm SL and larger, the outer teeth are mostly bifid, with only the lateralmost two to four (usually three) remaining unicuspid. Outer row teeth number from 18 to 24 in both jaws. Inner row teeth are conic in fish of all sizes, number from 19 to 75 (mostly 35 to 50), and are arranged in an irregular curved band paralleling the outer tooth rows.

Based on karyotypes of specimens from the Río Santa María, San Luis Potosí, Presa El Gigante, Aguascalientes, Ojo de Agua de Santiaguito, Guanajuato, Lago Yuriria, Guanajuato, and Lago de Cuitzeo, Michoacán, Xenotoca variata has a diploid chromosome complement of four subtelocentrics and 44 telocentrics (Fig. 5).

Dimorphism and coloration.-Fins, particularly the dorsal, are proportionately longer in males than in females (Table I). Adult males of X. variata are distinguished by a dark caudal fin with a bright yellow terminal band about an eye diameter in width. The yellow band occurs in fish as small as 25 mm SL, but the dark pigments appear gradually on the fin as the fish increase in size. This fin is often clear in males smaller than 30 mm SL, variably dusky in those beginning courtship, and often nearly jet-black in breeding males 60 mm SL and larger. The dorsal fin is dusky to black, darkest basally and paler toward the margin. As judged from field and aquarium observations of live males from five populations, the color of the anal fin is locally variable. In males 30 to 65 mm SL this fin may be completely colorless, slightly dusky, or bright yellowgold. In larger males the proximal third of the anal fin is usually dusky to black with the distal portion showing the range in coloration observed for smaller males. Paired fins are clear to pale yellow; the pelvic fins often have an iridescent sheen not seen in females. The chin, lips, cheek, and opercle above the lower margin of the orbit, the top of the head, and dorsal half of the body and caudal peduncle are dark brown. The ventral half of the body and caudal peduncle is pale yellow or yellow-gold. This striking contrast in coloration is even more marked in mature males by a dark stripe extending along the midside from the posterior margin of the orbit to the caudal fin base. Scattered gold reflections are seen on the dorsum and sides of the body and caudal peduncle. The cheek and opercle below the eye are similarly metallic golden. A faint dark blotch on the belly just anterior to the anal fin and approximately its width is seen in some males but may be obscured by yellow-gold pigments in the anal area of the belly in those fish with brightly colored anal fins. Males from Lago de Cuitzeo are uniformly pale silvery with an indistinct median stripe and scattered spots along the midside of the body and caudal peduncle; the pale coloration may reflect the muddy color of the water.

In preservative, males retain the dark pigmentation on the dorsal and caudal fins. The terminal yellow band on the caudal fin appears as a clear area. The stripe along the midside of the body and caudal peduncle persists in large males but is usually represented in small males by a series of irregular spots or by concentrated speckling. Males 40 mm SL and smaller are usually spotted above and below the midside as in females.

Median fins of live females are pale yellow to clear with the dorsal fin and proximal third of the caudal fin slightly dusky in fish larger than 50 mm SL. Paired fins are clear. Females are olive-brown dorsally and gradually pale down the sides to a vellowish silver, thus lacking the sharp delineation in color between the dorsal and ventral halves of the body as noted in males. A few scattered metallic gold reflections are seen on the top of the head, nape, and back. The chin, lips, cheek and opercle above the lower edge of the orbit are olive-brown and become pale yellow-gold below the orbit. A faint dark blotch or "pregnancy spot" (see discussion for X. eiseni females) occurs on the belly near the anal fin. Spotting is conspicuous in females of all sizes but becomes less distinct in large females because of a general increased darkening of the ground color. Females from Lago de Cuitzeo are pale silvery with very little dorsal darkening-perhaps a direct influence of the muddy water.

Spotting is more easily seen in preserved females. A midside row of 12 to 16 large spots extends from the upper edge of the opercle to the base of the caudal fin. Two other rows (six to nine spots each), one above and one below the midside row, run along the caudal peduncle forward onto the body just below the dorsal or just above the anal fin. The uppermost row is often obscured by dark basal pigmentation in large females. Newborn and immatures of both sexes are highly speckled on the head, nape, back, and dorsum of the caudal peduncle.

Embryology.—According to Hubbs and Turner (1939), the ovary of Xenotoca variata is characterized by the location of ovigerous tissue in the outer wall and septum, and by a median septum which is entire, attached dorsally and ventrally, and greatly folded.

My observations confirm the site of oocyte production on the ovarian walls and septum. The posterior extent of egg-producing tissue varies with the reproductive cycle of the female. Oocytes are usually restricted to the anteriormost quarter or less of ovaries in which early embryos are developing. As the embryos grow larger, new oocytes are produced more posteriorly until, in ovaries with near-term embryos, mature eggs often occur throughout the length of the walls and septum.

The ovarian septum is indeed attached dorsally and ventrally and greatly folded, but it is not always entire. In some females, particularly those less than 40 mm SL, the septum may be split partially or completely into unequal dorsal and ventral sections. I have never observed an ovarian septum which did not have several (three or more) perforations of various sizes.

Hubbs and Turner (1939) reported six to eight trophotaeniae, very long, and of the unsheathed type histologically. My counts on embryos from 14 females at three localities (Aguascalientes, Guanajuato, and San Luis Potosí), are 4 (12), 5 (62), 6 (26). Trophotaeniae increase in length allometrically in relation to body growth. They are of maximum length (about equal to body length) in embryos nearing birth but are partially resorbed just prior to birth. Whether the trophotaeniae are identified as short, medium, or long would depend on the degree of development of the brood of embryos examined. Trophotaeniae appear to be unsheathed in embryos of all sizes. I never observed a tissue space separating the vascular core from the outer epithelium in microslides of whole or sectioned trophotaeniae.

With the Hubbs and Turner criteria, the location of ovigerous tissue places Xenotoca variata in the subfamily Goodeinae, but the number and length of trophotaeniae, and variability in completeness of the ovarian septum do not permit the assignment of this species to any of the subfamily's six phyletic lines as the authors have defined them (1939, Table II).

Ecology.-Xenotoca variata has been collected most frequently in shallow water (to 1 m) from clear to murky rivers and lakes where the current was moderate to nil over bottoms ranging from deep mud to rock. Vegetation has usually been abundant. Emergent and floating plants often included pondweed (Potamogeton), water hyacinth (Eichornia), and cress (Armoracia). Conspicuous submerged plants were watermilfoil (probably Myriophyllum) and masses of attached or floating filamentous green algae. Water temperatures have ranged from 20 to 27 C. The shores of collection sites were typically gently sloping and grass-covered, sometimes with scattered cottonwoods or cypress.

Fish of this species are omnivorous. Food habits, ranging from almost completely

herbivorous to carnivorous at different localities, probably reflect differences in the relative abundance of available plant and animal foods rather than interpopulational differences in food preference.

Hybridization experiments.—Forced crosses and artificial inseminations involving Xenotoca variata were unsuccessful with allopatric congenerics eiseni (8 crosses) and melanosoma (7), and with allopatric stocks of Characodon lateralis (8), Ameca splendens (4), and Xenophorus captivus (1), but the two populations of variata from the Atlantic and Pacific slopes interbred freely, producing close to a one-to-one sex ratio among the 46 offspring from seven broods of four pairs.

Courtship displays.—Males exhibited seven displays: Lateral T-formation, Lateral Tilting, Lateral Wheeling, Head-Flicking, Round Dance, Half-Dance, and Oblique.

In the Lateral T-formation display a male approached a stationary female from her right or left, stopped broadside about one body length or less in front of her, and spread his median fins. The body was held straight and the caudal fin was flicked or jerked conspicuously.

In another type of Lateral display, extreme tilting and S-curving were seen. In this Lateral Tilting display the male also quivered his body, causing the fins, particularly the dorsal and anal, to flutter markedly.

A male performed the Lateral Wheeling display (Fig. 3) in response to an actively swimming female. He swam forward from the rear of the female, arched around in front of her from the right or left, braked with expanded pectorals, Tilted, S-curved, and quivered his body and fins as in the Lateral Tilting display. This display effectively blocked the path of the swimming female.

Head-Flicking was a common display presented to both stationary and swimming females; it was similar to or identical with the courtship display reported for males of many killifishes (Foster, 1967). The male rapidly twitched the anterior end of his body in a manner reminiscent of female receptive behavior (Head-Wagging), but the arc described by the right and left lateral movements was much smaller and more quickly executed than in Head-Wagging. Head-Flicking consisted of a single lateral movement, a burst of three or four at a time, or a continuous series up to six seconds duration. The male Head-Flicked while stationary in front of

and broadside to the female, oblique and head-on, lateral and parallel, or while swimming actively in any of these positions.

In the Round Dance (Fig. 3) a male briefly assumed the posture seen in the Lateral Tilting display, quickly circled in front of the female, and again resumed the lateral presentation with strong S-curving, tilting, quivering, and with the anal fin inclined toward the female. Circling was often repeated several times (two to six, usually three) but each circuit was separated by the stationary posture held briefly before the female.

In the Half-Dance display (Fig.3) the male postured as in the Lateral Tilting or Round Dance, immediately swam a half circle, and again postured. If the female was receptive (Head-Wagged), the male usually continued into the Round Dance.

Males performed the Oblique display (Fig. 3) by facing away from the female on an oblique angle less than one body length in front of her while Tilting and S-curving; the caudal fin was brought close to her head. In this position the male quivered its body rapidly causing the semi-erected median fins, especially the dorsal and caudal, to flutter violently.

Discrimination tests.—Fish from two populations of Xenotoca variata were tested against Characodon lateralis, X. eiseni, and X. melanosoma. The conspecific partner was always chosen. Intraspecific tests between the two populations of variata indicated no discrimination; a member of one population responded to an individual of the opposite sex from the other population as readily as to one from its own.

Relationships.-Meristic, proportional, and chromosome data indicate a high degree of similarity between Xenotoca variata and its congenerics, X. eiseni and X. melanosoma, but it is not possible to state with which species it has greater affinity. Meristic data, for example, indicate that variata more closely resembles eiseni in number of dorsal rays and mandibular pores, but in anal and caudal-ray counts it is closer to melanosoma. In other meristic characters, variata often shows no trend toward either species (e.g., number of scales around caudal peduncle) or has values that include the ranges of both (pectoral ray number). The greater genetic similarity between eiseni and melanosoma than between either species and variata is indicated by their morphology, behavior, and, particularly,

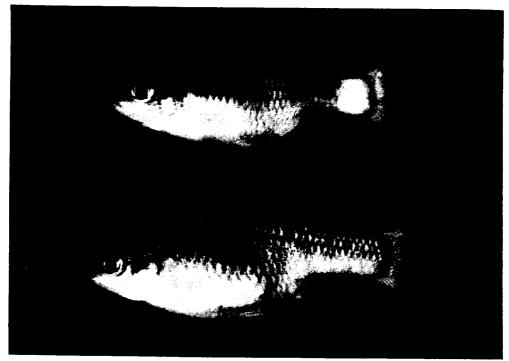


Fig. 6. Xenotoca eiseni male, 33 mm SL, and female, 38.5 mm SL, from Río Tamazula, Jalisco.

their ability to hybridize. With the assumption that the three species arose from a common ancestor, the stock which eventually diverged into eiseni and melanosoma probably became geographically isolated later than, and/or was subjected to less intensive and diverse selective pressures than, the stock from which variata evolved. If the monophyletic origin and mode of evolution for members of the genus are correct as outlined above, the difficulty in allying variata with either congeneric species should be expected.

Xenotoca eiseni (Rutter) Fig. 6

Synonymy.—Rutter's original description (1896) is good; the meristic and proportional data presented here agree with his observations. Unfortunately, Rutter did not have the opportunity to observe the striking life colors that distinguish males of this species from all other goodeids. Most of the characters used by Rutter have values close to, or overlapped by, those in certain populations of Xenotoca variata, and this may be the reason that Regan (1906–08), Hubbs (1926), Hubbs and Turner (1939), and Romero (1967) included eiseni as a synonym of vari-

ata. However, it is surprising that Turner coauthored a family revision confirming the synonymy of eiseni with variata after collecting a large series of eiseni (with many mature males) near the type locality seven months earlier in the same year. Questioning the synonymy of eiseni and variata, R. R. Miller studied the syntypes of eiseni at Stanford University in 1955 and has allowed me to include his data in the following account. Miller also sent specimens of eiseni to G. Mendoza, Grinnell College, for study of the ovarian and trophotaenial anatomy. Mendoza (1965) concluded that the structure of the ovary and trophotaeniae of eiseni does not agree with that described for variata by Hubbs and Turner (see below). My studies confirm Miller's and Mendoza's opinion of the specific integrity of eiseni. On the basis of the data reported herein, I propose that eiseni be withdrawn from synonymy with Xenotoca variata and be reinstated as Xeno-

Diagnosis.—A medium-sized goodeid (to 75 mm SL) with the posterior half of the caudal peduncle (and often the caudal fin) of the male bright orange to red-orange, usually 13 (12–14) anal and 13 or 14 (12–16) pectoral

rays, commonly 30 to 32 (29–33) lateral series scales, 30 or 31 (29–33) scales around the body and 16 to 18 (14–19) around the caudal peduncle, 20 or 21 (18–23) gill rakers in fish 40 mm SL and larger, usually 31 or 32 (29–34) vertebrae, inner conic teeth arranged in lateral triangular patches behind outer bifid teeth, 4 ribbon-like trophotaeniae, a diploid chromosome number of 48 including 6 subtelocentrics and 42 telocentrics (Fig. 7), and a unique male courtship display.

Distribution.-Xenotoca eiseni was described from a tributary of the Río Grande de Santiago near Tepic, Nayarit. It is now known in this state also from the Ríos Tepic and Compostela. Its distribution in the Río Grande de Santiago basin extends southeastward into Jalisco at least to Magdalena, 77 km northwest of Guadalajara. It is abundant in the Ríos Tamazula and Tuxpán in southern Jalisco where it ranges south to Atenquique in the Río Tuxpán. The species is absent from the basins of the Río Ameca and Río Armería which lie between its northwestern population in the Río Grande de Santiago and its southeastern population in the Río Tuxpan.

Material examined.—SU 5008 (syntypes, examined by R. R. Miller, 18 May 1955); UMMZ 138687, 172113, 172157, 172164, 172232, 172239, 172243, 173555, 173558, 173609, 173612, 173614, 178312, 178320, 179700, 184845, 184901, 186290, uncataloged laboratory-raised fish. Two hundred and twenty-nine specimens were examined.

Description.—Dorsal rays: 11-14 (12.45 \pm 0.58). Anterior unbranched dorsal rays: 1-5 (3.04 ± 0.85) . One or two unbranched rays are most common in fish above 40 mm SL; four or more unbranched rays occur mostly in fish 30 mm SL and smaller. Anal rays: 11-15 (13.09 ± 0.60). Unbranched anal rays: 4-6 (5.51 \pm 0.65) in males and 1-4 (1.79 \pm 0.74) in females. Fewer than six unbranched anal rays were seen only in large males (40 mm SL and larger). One unbranched ray was common in females 45 mm SL and larger; three or four unbranched rays occurred most frequently in smaller females (32.0 mm SL and smaller). Pectoral rays (both fins): 12-16 (13.99 ± 0.83) . Pelvic rays (both fins): 5-7 (5.96 ± 0.29) . Principal caudal rays: 15-22 (18.70 ± 1.19) . The syntypes examined by R. R. Miller have 12 (3) and 13 (1) dorsal, 13 (4) anal, 14-14 (4) pectoral, 6-6 (3) pelvic, and 19 (3) principal caudal rays.

Scales in lateral series: 29–33 (31.28 \pm

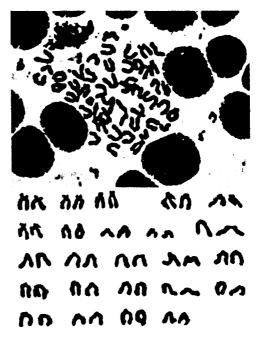


Fig. 7. Diploid chromosome complement of Xenotoca eiseni.

0.88). Predorsal scales: $18-27~(21.47\pm1.65)$. Scales around body: $29-33~(30.70\pm0.96)$. Scales around caudal peduncle: $14-19~(16.82\pm1.12)$. The four syntypes have 31~lateral scales each (although possibly 32~in two).

Vertebral counts: 29-34 (31.60 ± 0.90). Gill rakers: 17-23 (20.38 ± 1.29).

Proportional measurements are summarized in Table 1.

Head pores were counted on both sides of the head. Lachrymal: 2-5 (3.97 ± 0.26). Mandibular: 2-4 (3.40 ± 0.56). Preopercular: 6-11 (8.18 ± 0.57). Syntypes have 4-4 (1) and 3-3 (1) lachrymal, 3-3 (2) mandibular, and 9-8 (1), 9-9 (1), and 10-9 (1) preopercular pores. The supraorbital canal system is type 11 (Gosline, 1949, Pl. I) with two patterns: 1-2a 2b-4a 4b-7 (18 fish averaging 41.8 mm SL) and 1-2a 2b-4a 4b-6a 6b-7 (15 fish averaging 32.8 mm SL). Eight fish 31 to 43.5 mm SL had both patterns.

Branchiostegal rays numbered five in 20 fish (10 males and 10 females).

Outer row teeth are unicuspid in neonates and immatures less than about 15 mm SL but, except for 2 or 3 lateralmost teeth, are strongly bifid in adults larger than 40 mm SL; they number from 18 to 22 in the upper jaw

and from 17 to 22 in the lower jaw. Inner row teeth are conic and number from 16 to 31 (mostly 16 to 20) in both jaws and are arranged in a triangular patch on each side of both jaws behind the lateralmost five or six teeth of the outer rows.

Specimens of Xenotoca eiseni from Manantial El Sacristán and Río San Leonel, Nayarit, and Río Tamazula, Jalisco, had a karyotype of 6 subtelocentrics and 42 telocentrics in the diploid complement (Fig. 7).

Dimorphism and coloration.—Sexual dimorphism is evident in the lengths of the fins, especially the dorsal and anal (Table 1), which are longer in the male. However, the most striking sexual differences are in life colors.

In males the posterior half of the caudal peduncle is orange to red-orange. This bright color continues well onto the membranes of the caudal fin or at least persists as a pale yellow-orange zone at the fin base. The anal fin is similarly colored except for the shortened anterior six rays which remain clear. The dorsal may be dusky to dark in some populations and pale yellow to yelloworange in others. In large males a narrow median dark stripe runs through the dorsal fin. Paired fins are pale yellow (large mature males) or clear (immatures). A bluish-black band, equal to or slightly larger than an eye diameter, extends from the upper edge of the opercle posteriorly along the midside, becoming indistinct near the midlength of the pectoral fin. A similar dark band, beginning below the midlength of the dorsal fin base and running back onto the caudal peduncle, occurs in males 40 mm SL and larger. The top of the head, nape, and back are olivebrown to dusky; these colors grade into lighter shades ventrally. The sides of the posterior third of the body and anterior half of the caudal peduncle range in color from dull blue-black to iridescent turquoise. The chin, throat, and belly are pale yellow to off-white.

Ground color in females, as in males, is olive-brown. Pigmentation is most dense dorsally and fades out down the sides to the venter. Scattered gold reflections are sometimes seen on the head, nape, and dorsal surface of the caudal peduncle in large females. Inconspicuous wedge-shaped brown bars occur above and below the midside of the caudal peduncle and above the midside of the body from the anal origin forward to slightly anterior to the dorsal origin. The abdomen is pale white to yellow-white. Ma-

ture females have an iridescent blue-black bar behind the eye on the upper part of the opercle. A prominent black blotch on the lower abdomen begins at the anal fin and extends forward about halfway to the base of the pelvic fin. This is the same as the "pregnancy spot" described by aquarists for poeciliid fishes. Pigment forming the spot lies in the tissue lining the peritoneal cavity and shows through the thin, relatively unpigmented dermal and epidermal layers overlying it. The blotch enlarges as the belly swells during gestation and, although it is largest in females with near-term embryos, the mark can also be seen in immatures of both sexes. Paired and median fins are usually clear or pale yellow but in at least one population red-orange pigments are present on basal membranes of the caudal fin of mature females.

The distribution and intensity of colors show considerable populational differences and may vary in members of a single population. For example, on 14 March 1970, R. R. Miller and F. de Lachica collected a live stock of *X. eiseni* at the Río San Leonel, 26 km southeast of Tepic, Nayarit, in which bright colors were completely lacking in both males and females. When the fish arrived in Ann Arbor five days later, only a very dull red was visible on the caudal peduncle of males. However, after several weeks in an aquarium the fish developed nearly typical coloration.

In preservative, the bright red to redorange of males is represented by a pale area on the caudal peduncle and fin. The sides of the body and anterior caudal peduncle are olive-brown with a median dark bar discontinuous at the midlength of the body. The dorsum is dark olive-brown, and the cheek and opercle below the eye and the chin, throat, breast, and belly are pale buff in both sexes. The wedge or triangular-shaped spots or blotches on the sides of the body and caudal peduncle of females are conspicuous in preserved specimens. These same markings distinguish newborn and immatures of this species whether alive or preserved.

Embryology.—Mendoza (1965) studied the ovary and trophotaeniae of Xenotoca eiseni in great detail. The discussion and conclusions below are abstracted from his report.

Ovigerous tissue is varied in distribution. Although eggs always occur in the anterior half of the ovary, they may extend nearly throughout its length in immature females.

Eggs are most common on anterior ventral and lateral walls but frequently they occur anywhere along the ventral edge of the septum.

The median septum of the ovary is variable; it may be complete, partially complete anteriorly, or divided into dorsal and ventral portions throughout its length. The dorsal and ventral parts of a divided septum may be equal or unequal in size. Complete septa are sometimes, but not always, perforated by one or more holes of various sizes at the posterior end. The septum is branched and variably folded, depending on the volume occupied by eggs and embryos in the ovary.

Trophotaeniae include four basic processes of which any one can be reduced, absent, or divided into two or three branches anywhere along its length. Members of a single set of trophotaeniae are never equal in length; the anterior ones remain much shorter throughout development than the posterior median or lateral processes. Trophotaeniae increase in length during embryogeny, reaching maximum size in near-term embryos, but becoming partially resorbed just before birth. Trophotaeniae are sheathed in developing embryos and often unsheathed in those near birth.

Mendoza found that the characters of the ovary and trophotaeniae of Xenotoca eiseni disagree with the description given for Xenotoca variata by Hubbs and Turner (1939), thus invalidating their placement of eiseni as a synonym of variata. According to the Hubbs and Turner criteria based on ovarian and trophotaenial characters (1939, Table II), Xenotoca eiseni is similar to three of the six phyletic lines proposed for the subfamily Goodeinae but cannot with certainty be assigned to any one of them. Mendoza concluded that the relationship of X. eiseni cannot be determined from the nature of ovarian and trophotaenial structures alone.

Ecology.—Xenotoca eiseni has been collected from a variety of habitats, ranging from clear spring-fed pools to turbid road-side streams heavily polluted with effluents from sugarcane factories. Bottom types have been described as bouldery, sand and rubble, silt, or deep mud. Varying from one locality to another, emergent or floating vegetation has been entirely absent, limited to a few clumps of rushes (Scirpus) or cattails (Typha), or very dense with water hyacinths (Eichhornia) or duckweed (Lemna and Wolffia) forming extensive floating mats. Algae and

submergent vascular plants have also been absent, sparse, or abundant from one locality to another. The banks of streams and ponds containing these fish are described as either long, sloping, and grassy, low and rocky, or steep, muddy, and greatly eroded. Water temperatures at collection sites ranged from 15 to nearly 32 C. The only marked similarity between collection localities is the predominance of fish in ponds or stream pools where the depth was less than three feet and the current slight or nil.

Although plant material forms the greater volume of food for *Xenotoca eiseni*, members of this species are omnivorous.

Hybridization experiments.-No hybrids were obtained in forced crosses of Xenotoca eiseni with X. variata (6 crosses), Characodon lateralis (3), Ameca splendens (3), and Xenoophorus captivus (8). Four attempts each at artificial insemination were also unsuccessful with X. variata and C. lateralis. Forced crosses between X. eiseni and X. melanosoma produced hybrids in all combinations of their two sympatric and allopatric stocks. The F₁ hybrids were completely fertile, breeding among themselves to produce F₂ young or backcrossing to both parental species. From 118 pairs 3,084 hybrid offspring were born in 317 broods. In choice crosses (Table 3), hybrids were produced only from combinations of allopatric stocks. No natural hybrids were found in large collections from Jalisco where the species eiseni and melanosoma are sympatric.

Courtship displays.—Displays included the Lateral T-formation, Lateral Wheeling, Loop Dance, Half-Dance, and Oblique.

Although the displays of males from Manantial El Sacristán were basically similar to those observed for Río Tamazula males, there were certain interpopulational differences that were unmistakable: at El Sacristán Sigmoid Posturing was absent, Tilting was rarely seen and never exceeded an angle of 15° from the vertical, and the Oblique display was never observed. These differences, not treated here in detail, are attributable to the reinforcement of premating isolating mechanisms where X. eiseni and melanosoma are sympatric; except for these differences, the descriptions below apply to males of both populations.

The simplest display was the Lateral Tformation where the male swam across in front of the female, braked with expanded pectoral fins, assumed a slight sigmoid shape,

Table 3. Results of "Choice" Hybrid Crosses between Sympatric and Allopatric Populations of Xenotoca eiseni and X. melanosoma. Six females and four males of each species were placed in a 250 gallon tank.

		Number of births	Number offsprin	
	A. Sympatric experiment			***
	X. eiseni	10	101	••
	X. melanosoma	12 9	191	all conspecifi
		3	75	all conspecifi
	B. Allopatric			
	experiment			
	X. eiseni	8	84	75 conspecific
				9 hybrids (1
	X. melanosoma	۲		brood)
	A. metanosoma	5	31	28 conspecific
				3 hybrids (I brood)
I.	Fish undisturbed for 117 days.			
		N	Number of offspring	Identity of offspring
	A. Sympatric experiment		64	41 X. eiseni
				23 X. melanosoma
	D A11.			0 hybrids
	B. Allopatric experiment		42	19 X. eiseni
				16 X. melanosoma
				7 hybrids
I.	Fish undisturbed for 90 days.			
			lumber of offspring	Identity of offspring
	A. Sympatric experiment		56	31 X. eiseni
				25 X. melanosoma
	D Allamatic			0 hybrids
	B. Allopatric experiment		16	12 X. eiseni
				0 X. melanosoma
				4 hybrids

head toward and caudal fin away from the female, dorsal and mainly anal fins conspicuously bent toward her, and the dorsum of the body tilted toward her. The male often quivered slightly. This display was presented to a stationary or very slowly swimming female.

If the female were actively swimming forward, the male approached from the rear, tilted, wheeled around in front of her from the right or left, stopped, and assumed the posture seen in the Lateral T-formation. This is the Lateral Wheeling display.

The most elaborate display was the Loop

Dance (Fig. 3), in which the male executed a series (one to six, usually four) of figure-eight movements slightly above (about half a body length) and one to two body lengths ahead of a swimming female. In this display the male often tilted so much that the vertical plane of his body became nearly horizontal. The dorsal and especially the anal fins were inclined toward the female as the male Quivered violently. If the female were swimming rapidly, the forward progression of the male approximated her swimming speed so the Dance appeared more like a series of stretched-out loops than smooth figure-eights.

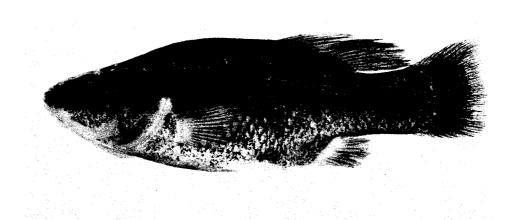


Fig. 8. Xenotoca melanosoma new species, male holotype, UMMZ 189077, 66.5 mm SL, Río Tamazula, Jalisco.

At the end of each leg of the Dance, the male turned back to describe a loop before continuing.

The Half-Dance display (Fig. 3) consisted of the male swimming the first leg of the Dance, but, rather than continuing to complete a figure-eight, he stopped short in the second run, tilted, and quivered rapidly. This display was presented to a stationary or slowly swimming female.

In the Oblique display the male faced the female from an angle less than 90° on her right or left, assumed a head-down posture with the body at an approximate 45° angle to the horizontal, and bent the caudal fin and peduncle toward her. The dorsal and anal fins were strongly inclined toward the female. This display was presented only to a stationary female.

Discrimination tests.—Xenotoca eiseni from Nayarit and Jalisco populations required a minimum number of tests to indicate discrimination against Characodon lateralis and Xenotoca variata. Extensive tests were conducted for sympatric and allopatric populations of eiseni and melanosoma, the only species studied which readily produced hybrids in the laboratory from parents of both sympatric and allopatric stocks. X. eiseni males and females from sympatric stocks always chose the conspecific partner. Individuals raised in complete isolation chose their own species at first exposure as unerringly as fish

raised in large stock tanks (conspecific experience). Even fish set up in hybrid crosses, in which they were associated since birth only with members of the other species (heterospecific experience), readily responded to the conspecific partner when a choice was available. When X. eiseni, sympatric to X. melanosoma, were tested against their conspecific heterosex and the F1 hybrid, the conspecific mate was chosen, but, when given the choice of the hybrid and a heterospecific mate, the hybrid was selected. Members of the allopatric stock of X. eiseni discriminated against the potential heterospecific mate but more test fish and more trials per fish were required for statistical significance. Allopatric females rejected F, hybrid males, but males courted equally the females of their own species and the hybrid. Tests between populations of X. eiseni, one allopatric and the other sympatric to X. melanosoma, showed that sympatric fish directed significantly more courtship behavior toward members of their own population. Allopatric females preferred sympatric males but allopatric males readily displayed to females of either population.

Relationships.—Similarities in morphology and behavior and the ability to hybridize readily in the laboratory indicate that Xenotoca eiseni is more closely related to X. melanosoma than to its other congeneric, X. variata.

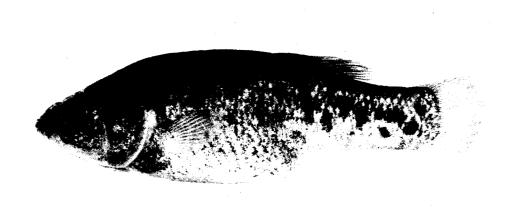


Fig. 9. Xenotoca melanosoma new species, female allotype, UMMZ 189078, 76 mm SL, Río Tamazula, Jalisco.

Xenotoca melanosoma new sp. Figs. 8, 9

Types.-Holotype, a mature male 65.5 mm SL (UMMZ 189077), was collected by Robert R. Miller and Howard L. Huddle on 3 April 1968, in the Río Tamazula just below Highway 110 bridge, 5 km S of the Ciudad Guzmán turnoff, Jalisco. Farther downstream this river is called the Río Tuxpán, and it eventually joins the Río Coahuayana along the Colima-Michoacán border. The allotype, an adult female 76 mm SL (UMMZ 189078), was taken with the holotype as were 21 paratopotypes (UMMZ 189079; three males and 18 females, of which one male and one female are cleared and stained), 49 to 78.5 mm SL. Fourteen additional paratopotypes (UMMZ 186292; seven males and seven females), 22 to 41 mm SL, were taken earlier (3 May 1966) by Miller and Huddle.

Etymology.—The specific epithet melanosoma means dark body, a diagnostic feature of this species; the name is treated as a substantive.

Diagnosis.—A large dark-bodied goodeid (to 85 mm SL) with a long dusky to black dorsal fin, reaching, when depressed, to the caudal fin in males 50 mm SL and larger (Fig. 8), usually 14 to 16 (13–17) dorsal rays, 34 or 35 (31–38) scales around the body, and 19 or 20 (18–21) around the caudal peduncle, 14 or 15 (13–16) gill rakers, outer row teeth all strongly bifid in fish larger than 40 mm

SL, 5 mandibular sensory pores, 3 or 4 (rarely 5) trophotaeniae in embryos and newborn, a diploid chromosome number of 48 including 8 subtelocentrics and 40 telocentrics (Fig. 10), and 3 distinguishing male courtship displays.

Distribution.—The known range of Xenotoca melanosoma is limited to the state of Jalisco. The type locality is in the Río Tamazula about 16 km by highway south of the town of Tamazula, and the new species has been collected in the same drainage system (Río Tuxpán) as far south as Atenquique. Lago de Chapala forms the eastern limit of the species, and from there it ranges north in streams and ponds to within 30 km of Guadalajara. The western part of its distribution includes Lago Atotonilco, the Río Ameca to Etzatlán, and the basin of the Río Grande de Santiago to La Quemada near the Jalisco-Nayarit border. It may have dispersed via the series of lake basins and troughs extending southward from Atotonilco to Ciudad Guzmán.

Other material examined.—UMMZ 160907, 160914, 160918, 160921, 172123, 172128, 172162, 172225, 173535, 173564, 173571, 173576, 173602, 173803, 178321, 178325, 179699, 184902, uncataloged laboratory-raised fish; UU CDB69-28. One hundred and seventy-eight specimens were examined.

Description.—A summary of the most important specific characters is given in the diagnosis above.

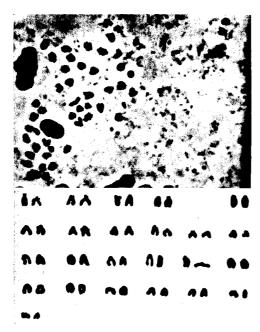


Fig. 10. Diploid chromosome complement of Xenotoca melanosoma.

Dorsal rays: $13-17 (14.90 \pm 0.74)$. Anterior unbranched dorsal rays: 1-6 (3.20 \pm 1.04). Although there were many exceptions, fish with only one or two unbranched dorsal rays were 49 mm SL and larger, those with three or four unbranched rays ranged down to 23 mm SL, and smaller ones had five or six unbranched rays in the anterior part of the dorsal fin. Anal rays: 13–16 (15.15 \pm 0.45). Branching in the anal fin varies with sex and size. For males, the numbers of anterior unbranched anal rays were 3-6 (5.27 ± 0.91) . Males about 46.0 mm SL and larger had three or four unbranched anal rays whereas smaller ones had five or six of them unbranched. For females, unbranched anal rays were 1–7 (2.80 \pm 1.24). Females 45 mm SL and larger usually had only one or two unbranched rays, those down to 25 mm SL generally had three or four, and those smaller, five to seven. Pectoral rays (both fins): 14-17 (15.82 \pm 0.53). Pelvic rays (both fins): 5-7 (6.02 \pm 0.34). Principal caudal rays: $17-23 (20.34 \pm 1.11)$. The holotype male has dorsal, i, 15; anal, iv, 12; pectorals, 16-16; pelvics, 6-6; and caudal, 21. The allotype female has dorsal, iii, 13; anal, ii, 13; pectorals, 16-16; pelvics, 6-5; and caudal, 21. Scales in lateral series: 31-35 ($32.73 \pm$

0.77). Predorsal scales: 19-26 (22.57 ± 1.63). Scales around body: 31-38 (34.80 ± 1.39). Scales around caudal peduncle: 18-21 (19.3 ± 0.75). The holotype has 32 lateral scales, 26 predorsal, 35 around the body, and 20 around the caudal peduncle. The allotype has 32 lateral scales, 25 predorsal, 35 around the body, and 20 around the caudal peduncle.

Vertebral counts: 31-34 (33.08 ± 0.61). The holotype has 34 vertebrae, the allotype, 33

Gill rakers: 12-17 (14.13 ± 0.91). Gill-raker number is correlated with size; fish above 40.0 mm SL usually have 14 or 15 gill rakers. The holotype and allotype each have 15 gill rakers.

Proportional measurements are summarized in Table 1.

Sensory pores were counted on both sides of the head. Lachrymal: 3 or 4 (4.00 \pm 0.05): mandibular 3-6 (4.99 \pm 0.31); preopercular: $8-12 (9.85 \pm 0.69)$. Both the holotype and allotype have 4-4 lachrymal, 5-5 mandibular. and 9-10 preopercular pores. The supraorbital canal pattern fits Gosline's (1949, Pl. 1) type II in which a break occurs between the second and third anteriormost pores (Gosline's 2a and 2b). Continuing posteriorly, the canal of this species is also discontinuous between the fifth and sixth pores (4a and 4b) and sometimes between the penultimate pore and the one just anterior to it (6a and 6b). The two patterns are written: 1-2a 2b-4a 4b-7 and 1-2a 2b-4a 4b-6a 6b-7, according to Gosline's numbering. The second pattern is most common in fish 30 mm SL or less; both types are seen in larger fish, but for those 50 mm SL or greater the first pattern with two breaks predomi-

Branchiostegal rays numbered five in 20 fish (10 males and 10 females).

Newborn young have unicuspid outer teeth but the median ones are flat-topped, a condition precursory to the development of bifid teeth. In immatures 30 mm SL the teeth are predominantly bifid and in adults 50 mm SL or larger the outer row teeth are all strongly bifid, numbering from 15 to 21 (mostly 19–21) in the upper jaw and from 19 to 29 (mostly 19–21) in the lower jaw. Inner row teeth are conic in both jaws of fish of all sizes. Upper jaw inner row teeth number from 13 to 34 (mostly 20–25) and are arranged in a more or less even row paralleling the outer row teeth. Inner row teeth of the lower jaw number from 32 to 53 (mostly 35–

40) and are distributed in an irregular curved band.

Karyotypes of X. melanosoma from the Río Tamazula and Presa de la Vega, Jalisco, revealed a diploid chromosome number of 48, 8 subtelocentrics and 40 telocentrics (Fig. 10).

Dimorphism and coloration.—In addition to the shortened anterior anal fin rays of the male, a characteristic shared by all goodeids, sexual dimorphism in this species is marked in the lengths of the dorsal and anal fins (Table 1; Figs. 8 and 9); they are longer in the male. The most striking feature of the adult male is the long, showy dorsal fin. Growth in the male dorsal fin is allometric. In immature males 25 mm SL or less, it approximates the female condition, reaching, when depressed, less than halfway along the length of the caudal peduncle; in males 50 mm SL or larger, the depressed dorsal fin touches the caudal fin.

Against a dark background, adult males may be nearly jet-black, with only the cheek below the eye, and the chin, throat, and breast region remaining slightly paler. Immature males or mature males against a light background are uniformly gray along the sides and somewhat darker, with an irregular pattern of small, indistinct spots, on the head, nape, and back. The chin, breast, and abdomen are light gray to grayish white. Depending on the background and size of the fish, the dorsal fin is dusky to black. In large males over 60 mm SL the caudal fin may be almost uniformly black. In males approximately 40 to 55 mm SL, a concentration of pigment at the base of the principal caudal rays may appear as a poorly defined curved bar or blotch approximately the width of the orbit; in males less than 25 mm SL, the basal dark blotch is lacking and the fin appears pale gray to clear. The anal fin is dusky to black but with the membranes of the first six rays, and a narrow marginal band on the membranes of the remaining rays, relatively pigment-free. The paired fins are pale gray to dusky. The dark coloration of males fades considerably in preservative.

Females are also dark-bodied but their fins lack the heavy pigmentation seen in males; paired and median fins are pale gray to clear. The opercle is pale silvery. The chin, throat, and breast are pale gray-white and, in larger females, often lightly speckled. Barring and spotting on the sides of the body and caudal peduncle are conspicuous in immatures and adults against a light back-

ground and can be seen even in very large, dark females after preservation. Three to eight scattered vertical bars, varying in length from one to three times an eye diameter, occur on the sides of the body between the pectoral base and the anal origin. In some females they are evenly distributed but in others they may occur in three or more clumps. They are best developed in females 40 to 60 mm SL but are less distinct in larger and darker females. An irregular row of five to eight (mostly six) dark spots extends along the midlateral line from the caudal base forward onto the body above the anal origin. Viewed from a distance, the spots often appear as a vague stripe about an eye diameter in width. Speckling is pronounced on the sides and venter of the caudal peduncle but is largely obliterated dorsally by countershading. The venter of courted, sexually responsive females is a brilliant iridescent blue. This color is transient; it is seen only in the presence of males and quickly fades to an inconspicuous blue- or gray-white when females are disturbed. The venter of immature or sexually unresponsive females is pale white to graywhite.

Newborn are spotted on the sides of the caudal peduncle and along the body behind the tip of the pectoral fin. Two rows of five to nine (mostly six) spots above and below the midside and a single spot at the structural base of the caudal fin on the midline are characteristic for this species.

Embryology.—The single elongate ovary of Xenotoca melanosoma is divided into two approximately equal lateral halves by a vertical median septum. Attached dorsally and ventrally, the septum may be entire, divided longitudinally into equal or unequal portions, or variably perforated by scattered small holes or longitudinal splits sometimes half its length. The septum may be branched throughout its length or, most frequently, only in its anterior quarter; it is always folded, but maximum folding occurs in ovaries with a small volume of eggs or embryos.

The location of ovigerous tissue is variable. Developing oocytes or mature eggs are found only on the ventral half of the septum and lateral and ventral walls of the anterior half of some ovaries, throughout the length and height of the septum and walls in other specimens, or restricted to a small patch on the septum and walls in the anteriormost

part of the ovary in others. Location and extent of ovigerous tissue is related to the female reproductive cycle. In females with small embryos or cleaving eggs, oocytes are restricted to the anterior section of the ovary; as the embryos gradually develop and approach birth, there is a concomitant proliferation of oocytes throughout the length of the ovarian wall and septum preparatory to fertilization and production of a new brood once the present one is evacuated.

Three or four trophotaeniae, rarely five, are characteristic. They are sheathed or unsheathed in fin-fold stage embryos, usually sheathed in advanced embryos, and most often unsheathed in ones just prior to birth. Trophotaeniae are mere stubs in tailbud embryos, about half the body length of fin-fold embryos, almost equal to the body length in nearly fully developed embryos, and variably shorter in those near birth.

The structure of the ovary and trophotaeniae indicates that *Xenotoca melanosoma* belongs with congenerics in the subfamily Goodeinae of Hubbs and Turner (1939) but if only these characters are employed it cannot be assigned to any of the subfamily's six phyletic lines which they proposed.

Ecology.-Xenotoca melanosoma has been taken from ponds and streams where the water was very clear, variably murky, or badly polluted. Submerged vegetation, predominantly filamentous green algae, has been abundant at some localities and almost lacking at others. Also variably represented, standing vegetation has consisted largely of cress (Armoracia), sedges (Cyperus and Eleocharis), rushes (Scirpus and others), several types of pondweed (Potamogeton), and cattails (Typha). At certain localities water hyacinths (Eichornia) have formed a solid mat across the surface of the water. Bottom types have ranged from deep mud to bedrock, and shorelines have been grassy to muddy and open to well-shaded by willows or acacias. Water temperatures ranged from 21 to 29 C. The fish were usually netted in shallow water (to one m) where there was little or no current.

Omnivorous in trophic habits, the fish feed predominantly on aquatic animals and lesser amounts of algae.

Hybridization experiments.—Xenotoca melanosoma hybridized only with allopatric and sympatric stocks of X. eiseni (see above). Forced crosses with allopatric stocks of X. variata (6 crosses), Characodon lateralis (3), Ameca splendens (3), and Xenoophorus captivus (5) were unproductive as were three attempts each at artificial insemination with X. variata and G. lateralis.

Courtship displays.—As with X. eiseni, interpopulational differences in courtship of X. melanosoma are believed caused by a modification of behavior where the two potentially hybridizable species are sympatric; these differences, along with others, are to be evaluated in another report.

Males from Presa de la Vega exhibited six courtship displays: the Lateral T-formation, Lateral Wheeling, Zig-zag Dance, Half-Dance, Oblique, and Head-Wagging. In addition to these, Río Tamazula males showed the Lateral Sidling and Dart displays.

The male courtship displays of fish from the Río Tamazula lacked Sigmoid Posturing; Tilting was rare and never exceeded 10°.

In the Lateral T-formation display a male approached the female from her right or left and paused while broadside in front of her. The male from Presa de la Vega quivered rapidly in the display, bent his body into a strong sigmoid posture, with the head toward and tail away from the female, and tilted, dorsum away from her. The semi-erected dorsal and anal fins were strongly inclined toward her. A Río Tamazula male held its body straight, the dorsal fin erect, and the anal fin straight (usually) or slightly inclined toward the female. The Lateral T-formation display was presented to stationary or slowly swimming females.

Two other types of lateral displays were the Lateral Wheeling and Lateral Sidling. The male approached the swimming female from the rear, wheeled around in front of her, and assumed the stationary posture described above for the Lateral T-formation display; this is the Lateral Wheeling display. At Presa de la Vega, tilting occurred throughout the male's display; it was slightest (10° or less) during wheeling and greatest (up to about 25°) during frontal presentation. The Lateral Wheeling display was presented to actively swimming females and, less often, to stationary ones. In the Lateral Sidling display of Río Tamazula fish, the male moved alongside the stationary or slowly swimming female with his dorsal fin inclined so that it brushed, or nearly so, the back and head of the female and, once past her, he turned in and assumed the posture seen in the other lateral displays.

The Zig-zag Dance of the Presa de la Vega

male (Fig. 3) consisted of a series (two to six, usually three) of to-and-fro movements during which the male swam one to two body lengths in front of, and at the same swimming depth, as the female. As the male went through each turn, S-Curving was extreme; in the transverse portion of the Dance, Quivering and inclination of the dorsal and anal fins toward the female were marked. Restricted to the transverse legs of the dance, tilting was infrequent and never exceeded an angle of 10°. The amplitude of the lateral movements was one to two body lengths, and the pattern traced as the male moved forward appeared as a series of meanders if the female were actively swimming forward or it was compressed into sharper cornered zig-zag movements if the female were stationary or swimming very slowly. In the shortened Zig-zag Dance of Río Tamazula fish the male swam slowly across from the right or left in front of the female, turned back to complete a second leg, stopped, and spread his median fin as in the Lateral T-formation display. The Dance rarely extended to the beginning of a third leg. The Dance was presented to stationary or very slowly swimming females.

In the Half-Dance display, the male from Presa de la Vega (Fig. 3) swam the first leg of the Dance, stopped abruptly in the second leg, and assumed a pronounced sigmoid posture while quivering and tilting (dorsum away from the female) with the dorsal and particularly the anal fins erected and bent toward the female. If the female were responsive, the male usually continued into the dance. In the Half-Dance display of Río Tamazula fish, the male approached from the rear or side of a stationary female, quickly swam in front of her, braked with pectoral fins, and backed slowly with his dorsal and anal fins fully expanded. If the female were not receptive, the male held the backed position for several (one to five) seconds, conspicuously twitching his dorsal and caudal fins before repeating the forward movement of the display. If the female were responsive, the male usually repeated the forward darting movement and continued into the short Zig-zag Dance.

In the Oblique display a male took up a position at an angle less than 90° to the right or left in front of a female. In Presa de Vega fish, the male faced away from the female and held his body in a strong sigmoid flexure, head toward and tail away from the

female, while quivering rapidly with the dorsal and especially the anal fins inclined toward her. The Río Tamazula male held his body at an oblique angle to the female and presented his right or left side and median fins, fully expanded but not inclined.

A male from the Río Tamazula stock sometimes approached the female from the front or rear, right or left, and performed the Dart display in which he quickly sprang across in front of the female with the dorsal and anal fins lowered, stopped suddenly with expanded pectorals, and sculled backward while erecting the dorsal fin and inclining the anal fin toward her. The forward movement of the Dart ceased when the trailing edge of the dorsal fin was directly in front of the female, and backing stopped when the leading edge of the fin was about in the same position. The Dart display consisted of two to six such forward and backward movements in rapid succession with the raising and lowering of the dorsal fin its most conspicuous feature. Although similar to the Half-Dance in general pattern of movements, the Dart display had a much smaller amplitude and quicker repetition of the backward and forward components so that a striking to-and-fro or seesaw-like movement was produced. The dart display was presented to stationary females.

A male from either population sometimes approached a female from the side or front, turned broadside to her, and rapidly bent his body into a series of horizontal C-shapes. Moving through a greater arc than the rest of the body, the head was jerked erratically right and left while sculling movements of the pectoral fins offset the propulsive force of the flexing caudal peduncle and fin. The dorsal fin was alternately raised and lowered as in the Dart display (Río Tamazula males) or only slightly expanded so that the movements of the body caused it to flutter conspicuously (males from both populations). The anal fin was inclined toward the female. Except for median fin movements, this display resembled receptive behavior in the female and, accordingly, is called the Head-Wagging display (Fig. 3). It was presented only to stationary females.

Discrimination tests.— Members of Xenotoca melanosoma stocks effectively discriminated against X. eiseni, X. variata, and Characodon lateralis. Fish sympatric with X. eiseni showed superior discrimination ability against this species. The conspecific heterosex was preferred over the melano-

soma-eiseni hybrid of sympatric parents but, when X. eiseni constituted the second choice, the hybrid was selected. Conspecific interpopulational tests did not indicate discrimination.

Relationships.--Morphological criteria indicate that Xenotoca melanosoma has a slightly greater phenetic resemblance to eiseni than to variata. However, a closer genetic similarity of melanosoma to eiseni is demonstrated by their ability to hybridize readily in the laboratory; neither species has interbred with variata.

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The Hawaiian Trunkfishes of the Genus Ostracion

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The trunkfish genus Ostracion is represented in the Hawaiian Islands by the common O. meleagris camurum Jenkins, the rare O. whitleyi Fowler (new name for ornatus Guichenot; here recorded for the first time from Hawaii, Tahiti, and the Tuamotus), and the wide-ranging O. cubicus Linnaeus (only one specimen reported from Hawaii—a record which should be substantiated with further material from the islands). All but cubicus display marked sexual dichromatism. The Hawaiian O. meleagris camurum it differentiated from the Indo-Pacific O. meleagris meleagris only by color; the females of camurum have fewer white spots at any specific length, and the males usually have numerous blackish dots on the sides instead of larger yellow spots.

Introduction

THE Indo-Pacific trunkfish (or boxfish) genus Ostracion (family Ostraciontidae) is readily distinguished by its bony carapace of hexagonal plates which is quadrangular in cross section, the dorsal and broader ventral surfaces usually convex and the sides slightly concave. The carapace is closed behind the anal fin, and there are no preocular or pelvic spines. There is a single dorsal fin of 9 rays;

the anal fin, the origin of which lies below or posterior to the rear base of the dorsal fin, also has 9 rays.

The status of Ostracion in Hawaii has been confused since the first specimens were recorded from the islands. Jenkins (1901) described Ostracion camurum from six specimens from Honolulu. In 1903 he stated that these specimens were 89 to 114 mm long and also recorded two specimens of O. len-