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Allotoca maculata, a New Species of Goodeid Fish from Western México, with Comments on Allotoca dugesi

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A new species of Allotoca is described from an endorheic basin in west-central México. It differs from its only congener, A. dugesi, in position of dorsal fin and number of dorsal rays, number and character of embryonic trophotaeniae, diploid chromosome number and coloration. The occurrence of Allotoca and other fishes in the Laguna de Santa Magdalena suggests a former hydrographic connection between that basin and the Río Lerma system. Allotoca vivipara is synonymized with A. dugesi.

THE Goodeidae comprises about 35 species of viviparous cyprinodontoid fishes generally confined to the Mexican Mesa Central (West, 1964) and its periphery. Though small, the family is remarkably diverse, having undergone an adaptive radiation into virtually all permanent aquatic habitats accessible to fishes in this region. Our knowledge of goodeid diversity has recently been expanded by the descrip-

tions of several new taxa (Miller and Fitzsimons, 1971; Fitzsimons, 1972; Kingston, 1978). The purpose of this paper is to describe the second, very localized, known species of the genus *Allotoca* and to discuss its relationships.

The Mesa Central has been a region of intense volcanic and tectonic activity that began in the Miocene and still continues today (Maldonado-Koerdell, 1964). The evolutionary his-

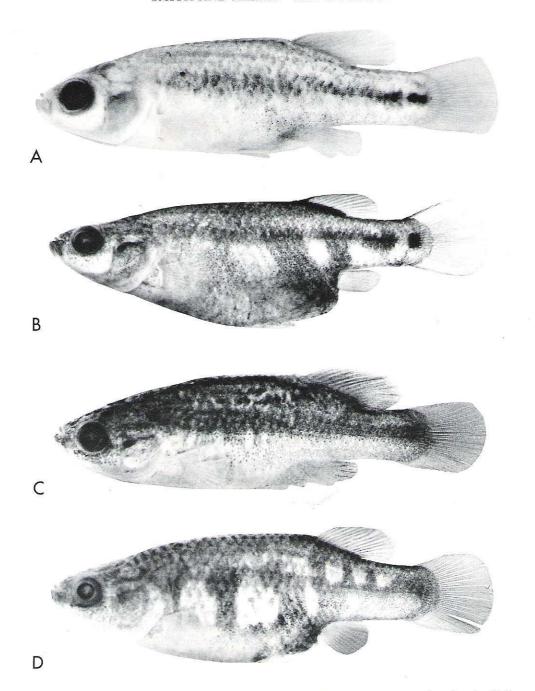


Fig. 1. A) Allotoca maculata male holotype, 27.2 mm, UMMZ 200250; B) A. maculata female, 35.0 mm, UMMZ 203851; C) A. dugesi male, 31.5 mm; D) A. dugesi female, 41.5 mm; C & D UMMZ 189620.

tory of the fishes of this region is closely tied in with geological events which have altered its surface configuration (Smith et al., 1975). Repeated disruption of hydrographic systems has provided multiple opportunities for allopatric speciation and may account for much of the endemism of the central Mexican fish fauna.

The new species is based on live and pre-

Table 1. Proportional Measurements in Thousandths of Standard Length of Adults of Allotoca maculata from the Type Locality. Based on UMMZ 178322 and 200250. Data for males include holotype.

		10 Males	10 Females			
Measurement	Holotype	Range	ž	Range	x	
Standard length, mm	27.2	19.7-32.0	25.3	22.6-35.9	26.2	
Predorsal length	654	643-684	665	643-684	662	
Prepelvic length	513	512-545	529	529-559	545	
Anal origin to caudal base	349	319-350	333	309-361	336	
Body depth	287	259-313	287	266-291	277	
Body width	169	135-169	146	135-156	146	
Head length	305	305-351	328	307-349	322	
Head depth	202	197-225	211	201-226	195	
Head width	184	177-194	185	181-196	190	
Caudal-peduncle length	272	247-282	269	236-299	263	
Least depth of caudal						
peduncle	140	127-145	136	124-158	137	
Interorbital width	125	106-125	115	101-134	113	
Preorbital width	11	11-24	18	13-23	17	
Snout length	66	61-83	71	61-78	69	
Orbit length	85	81-96	89	78-93	86	
Mouth width	73	68-88	82	77-97	85	
Mandible length	81	76-91	83	75-89	82	
Dorsal, basal length	158	158-187	174	137-168	149	
Dorsal, depressed length	279	162-334	236	156-243	205	
Anal, basal length	77	64-84	76	63-89	78	
Anal, depressed length	176	162-189	175	156-189	171	
Caudal length	206	206-236	221	200-243	219	
Pectoral length	169	132-169	149	103-167	146	
Pelvic length	95	95-130	117	96-115	105	
Upper-jaw length	40	29-59	42	31-56	45	
Opercle length	110	110-139	128	123-137	129	

served material in The University of Michigan Museum of Zoology (UMMZ).

Allotoca maculata n. sp. Figs. 1–4

Holotype.—UMMZ 200250, mature male, 27.2 mm SL; Laguna de Santa Magdalena, Jalisco, ca. 82 km W of Guadalajara by Hwy 15, 103°57'W long., 20°54'N lat., ca. 1210 m elevation; R. R. Miller and J. M. Fitz-simons, 22 February 1970 (maintained alive until 24 December 1970).

Paratopotypes.—UMMZ 178322, 48 specimens including mature males and females, 10-87 mm SL. UMMZ 203851, 51 newborn young to adults (9♂♂, 9♀♀), 10-48 mm SL, and USNM 219779 (2♂♂, 2♀♀), 21-38 mm SL, all maintained or reared in Ann Arbor.

Paratypes.—UMMZ 173553, 15 specimens including 5 cleared and stained, 18–35 mm SL, Hacienda San Sebastian about 2 km N of Etzatlán, Jalisco.

Diagnosis.—A small species of Allotoca (max. SL ca. 35 mm) with dorsal and anal fins set far back on body, but less posterior than in A. dugesi; predorsal length 64 to 68% SL; dorsal origin

slightly ahead of anal origin; dorsal rays usually 13 or 14, anal rays usually 11 to 13; scales in lateral series 28 to 32; mandibular pores absent; fins in adults dimorphic, longer in males which have dorsal and anal fins rounded and elevated; body deep and compressed; coloration distinctive, fins mostly clear, one or more irregular dark spots on caudal peduncle, females with three to six lateral blotches of iridescent blue, males with a lateral series of fine dark spots; diploid chromosome number 48 (no metacentrics).

Description.—Aspects of morphology and pigmentation are apparent in Fig. 1, morphometric data are given in Table 1, and frequency distributions of dorsal and anal rays appear in Table 2. The two species of Allotoca are compared in Table 3. Counts and measurements follow methods described by Miller (1948) as modified by Fitzsimons (1972). The rudimen-

		Dorsal rays					Anal rays						
Species and locality	12	13	14	15	16	17	ž	10	11	12	13	14	Ā
A. dugesi													
L. Zirahuén				6	2	2	15.6		5	5			11.5
L. Cuitzeo			4		1		14.4		2	3			11.6
R. Grande de Morelia				2	7	1	15.9		5	5			11.5
L. Yuriria			2	4	4		15.2		5 3	4	1		11.6
L. Pátzcuaro				4 3	2	1	15.7		3	3			11.5
Total			6	15	16	4	15.4		20	20	1		11.5
A. maculata													
L. Magdalena Basin	6	23	21	2			13.4	2	12	27	10	1	11.9

TABLE 2. Frequency Distribution of Dorsal and Anal Rays in Allotoca dugesi and A. maculata.

tary anterior anal ray of males is included in the anal-ray count, and the last two closely approximated rays of both dorsal and anal fins are counted as one ray. In the meristic data below the count for the holotype is indicated by an asterisk.

Body moderately deep and compressed. Median fins set far back, the dorsal origin well behind pelvic insertion and slightly in advance of anal origin. Predorsal length equals 64–68% SL.

Scales in lateral series 28(1 count), 29(6), 30(6), 31*(11), 32(1). Body circumference scale rows 26(6), 27(4), 28(9), 29(1), 30*(2), 31(1). Caudal peduncle scale rows 16*(23). Predorsal scales irregular, the diagonal rows numbering 20(2), 21(4), 22(5), 23*(4), 25(1). Caudal rays 16*(1), 19(6), 20(6), 21(4), 22(5), 23(2). Pectoral rays 13-13*(1), 13-15(2), 14-14(3), 14-15(5), 14-

16(1), 15-15(7), 15-16(6), 16-16(1). Pelvic rays 6-6*(21). Total gill rakers on the right anterior arch 10(1), 11*(16), 12(4). Total vertebrae 31(2), 32*(17), 33(11), 34(1). Precaudal vertebrae 13(26), 14*(5). Caudal vertebrae 18*(4), 19(17), 20(10). Branchiostegal rays 5-5*(21).

Jaw teeth conic, those in outer row larger and size-graded, largest ones near symphysis. Outer teeth in upper and lower jaws (both sides) number ca. 18 to 22; inner teeth (both jaws) arranged in single row or narrow band behind outer teeth. Lower jaw strong and heavy.

Sensory pores of acoustico-lateralis system on head (n = 10): mandibular 0; preopercular 3 to $10, \bar{x} = 7.2$; lacrimal 0 to $6, \bar{x} = 2.6$.

Karyotype.—A. maculata has a diploid number of 48 chromosomes in both sexes, consisting of 44 telocentrics and 4 subtelocentrics (Fig. 2). The

Table 3. Comparison Between Allotoca maculata and A. du	TABLE 3.	COMPARISON	BETWEEN	Allotoca	maculata	AND A .	duge	si.
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Character	A. maculata	A. dugesi			
Size	smaller; SL to 35 mm	larger; SL to 63 mm			
Dorsal fin rays	12-15; usually 13 or 14	14-17; usually 15 or 16			
Predorsal length	shorter; 64-68% of SL	longer; 69-73% of SL			
Lateral scales	fewer; 28-31	more; 30-35			
Mandibular pores	absent	usually 2-5; rarely absent			
Karyotype	2N = 48; no metacentrics	2N = 26; 22 metacentrics			
Lateral stripe (males)	less well-developed; diffuse anteriorly	prominent and continuous			
Yellow pigmentation	absent (sometimes faintly present in courting males)	well-developed in both sexes			
Basicaudal spot	present	absent			
Trophotaeniae	complex; lateral processes present; 8 termini	simple; lateral processes absent; 4 termini			

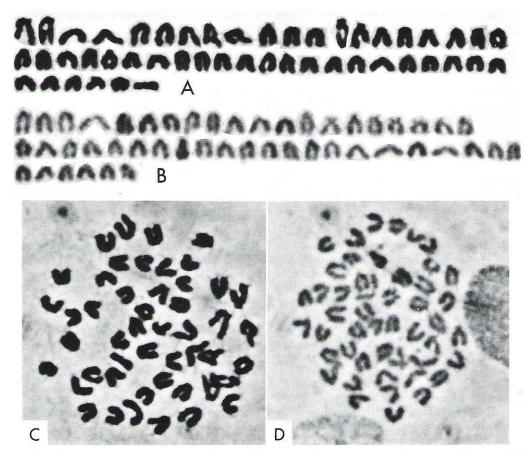


Fig. 2. Somatic chromosomes at metaphase of *Allotoca maculata* from the type locality. A, C) male; B, D) female.

karyotype was determined by Teruya Uyeno from gill epithelial cells of specimens from the type locality.

Reproductive biology.—In both species of Allotoca, the ovary is a single median structure formed by fusion of paired organs; the median septum is divided near the middle to form relatively thin dorsal and ventral flaps. Ovigerous tissue develops in the outer wall of the ovary and at the base of the septum. The ovary wall is thick, well supplied with blood vessels and folded to various degrees. The embryonic trophotaeniae are aligned against the wall. In A. dugesi the dorsal and ventral flaps are long and rolled together; in A. maculata they are also rolled, but they are shorter and independent of each other.

In 16 near-term and newly born young of A. maculata (UMMZ 203851) the unpigmented

trophotaeniae consist of a rosette of eight blunt, rounded processes of the perianal lip. Four of the projections (2 anterior and 2 posterior) are well-developed; the others are small and budlike, arising as lateral processes of the four main projections. Brood size ranged from 2 to 20 ($\bar{x} = 7.3$, n = 23) in an aquarium stock maintained at UMMZ (Kingston, 1979).

Sexual dimorphism and coloration.—As in all goodeids, the sexes of A. maculata are distinguished by structural modifications of the male anal fin to form an organ presumably involved in intromission (Mohsen, 1961a, b; Miller and Fitzsimons, 1971; Nelson, 1975). The fins of males, particularly the dorsal, are generally longer than those of females. The prepelvic length is greater in females. Coloration, especially the vertical bars of females, also distinguishes the sexes.



Fig. 3. Somatic chromosomes at metaphase of *Allotoca dugesi* from Lago de Zirahuén, Michoacán. A, C) male; B, D) female.

In life, adults are light gray-green dorsally, silvery below. The gray-green color of the backs of females extends onto the sides in 3 to 6 vertical bars separated by 4 to 7 prominent blotches of light iridescent blue. These dark vertical or obliquely directed bars are weak and diffuse anteriorly, most prominent above vent and anal fin, and typically number only one posterior to base of anal fin (Fig. 1). Females bear 1 to 3 irregular spots at caudal base. Males are distinctively marked with a lateral series of fine dark spots beginning behind opercle and becoming denser posteriorly, the spots usually coalescing to form a diffuse lateral stripe on caudal peduncle that ends in a dense spot, the size of the pupil, at caudal base. Many males bear

a dark lateral spot below or slightly in advance of dorsal origin. Backs and sides of males are generally gray-green with flecks of iridescent blue showing through on lower sides, especially during courtship. The preopercle and opercle in both sexes are metallic blue, the cornea is golden. The perianal region is often dusky, sometimes heavily so in females. The fins are mostly clear, but with a dusky color on interradial membranes. The caudal fin may take on a light yellow color in courting males.

In ethyl alcohol blues and gray-greens disappear, leaving a yellow-brown pattern dorsally with gray or buff below. As other colors fade, a light brown speckled pattern becomes prominent on back, each scale bearing a central spot of melanin. The lateral bars of females become faint, and most of the dusky color of the fins disappears. The lateral speckles of males largely disappear, remaining evident only on caudal peduncle. The spot at base of caudal fin remains distinct in both sexes.

Habitat.-Allotoca maculata is an inhabitant of shallow lake margins and adjacent marshes. It has been taken in rather clear to muddy water over soft mud substrates which are easily roiled. The species is found near shore or in shallow marshes in water generally less than 0.5 m deep. As the long dry season progresses, it survives well in the very shallow, well vegetated water of shrinking lakes and can then be collected by dipnet. A. maculata has been taken in areas bare of vegetation, but the margin of Laguna de Santa Magdalena, the type locality, was choked with Eichornia when collections were made there in 1957 and 1970; some Hydrocotyle was also present. Late afternoon water temperatures at the lake on 27 February 1957 and 22 February 1970 were 15.5 and 16.2 C, respectively.

Associated fish species at Laguna de Santa Magdalena were a cyprinid, Algansea tincella; a poeciliid, Poeciliopsis infans; and the goodeids, Xenotoca eiseni and X. melanosoma. Additional fish associates at Etzatlán were a catostomid. Moxostoma mascotae, and a goodeid, Goodea cf. G. atripinnis. In 1900, Laguna de Santa Magdalena supported a commercial fishery for an atherinid, Chirostoma sp. (Tamayo, 1964), that probably was C. jordani. Even as late as 1957 one of us (RRM) was told by boys that "pescado blanco" or "charal," local names for Chirostoma spp., were present well out in the main body of the laguna and were small, adults being only about 75 to 200 mm TL or less. In 1961, 5 specimens of Chirostoma jordani (UMMZ 179702) were collected in an irrigation ditch in the Magdalena basin 4 km north of Etzatlán

Distribution.—A. maculata has been taken at two localities, Laguna de Santa Magdalena and a reservoir near Etzatlán, both within the isolated Magdalena basin in western Jalisco (Fig. 4).

Relationships.—The species is closely allied with A. dugesi with which it shares conic teeth, posterior insertion of dorsal fin and structural characters of the ovary and trophotaeniae. A. maculata is presumably the more primitive of the two species as it has the basic diploid good-

eid chromosome number (48, with no metacentrics), whereas *A. dugesi* has a derived karyotype: 2N = 26, with 22 metacentrics. This genus provides an example of rather extensive chromosomal change which has been accompanied by relatively little morphological evolution within the genus, whereas closely related species of *Xenotoca* that are as morphologically distinct as *X. eiseni* and *X. variata* show only small differences in chromosomal evolution (Fitzsimons, 1972; Patton and Baker, 1979).

Etymology.—The adjective maculata is from the Latin macula, spot, in reference to the black basicaudal spot. Allotoca, of Greek origin (Hubbs and Turner, 1939), is feminine because the transliterated Latin terminal part of the compound name (tocus) was changed to toca (Int. Code Zool. Nomen., 1961:31, example 3).

Allotoca dugesi (Bean) Figs. 1-4

Despite its early description, *Allotoca dugesi* has remained poorly known. The ovaries and trophotaeniae of this species were described by Hubbs and Turner (1939), but most references have been based on the original description (Bean, 1887).

Frequency distributions of dorsal and anal rays are presented in Table 2 and the species is contrasted with *A. maculata* in Table 3. The observations below are based on examination of specimens from throughout the known range of the species.

A. dugesi reaches a maximum SL of ca. 63 mm and is robust, with a short caudal peduncle. Median fins set far back on body; predorsal distance 69–73% SL. Dorsal origin slightly ahead of anal origin. Total gill rakers on right anterior arch 10(14 counts), 11(20), 12(8), 13(2), 14(1). Lateral scales 30(4), 31(7), 32(12), 33(7), 34(3), 35(1). Branchiostegal rays 5-5(21). Total vertebrae 32(12), 33(8), 34(6), 35(1). Precaudal vertebrae 13(3), 14(11), 15(12), 16(1). Caudal vertebrae 17(6), 18(4), 19(16), 20(1).

Jaw teeth of outer row conic, firmly attached, numbering ca. 19 to 21 (total of both sides) in both upper and lower jaws. Teeth in a size-graded series, larger teeth nearer symphysis. Inner teeth are small, conic and arranged in single row or narrow band behind outer teeth. Lower jaw strong and heavy.

Sensory pores of acoustico-lateralis system of head as follows (UMMZ 172119, n = 10): man-

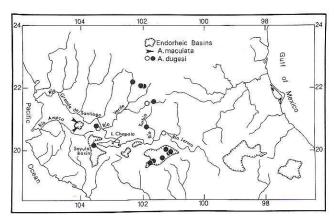


Fig. 4. Distribution of species of *Allotoca*. Not all collections at a given locality are shown. Open circles indicate literature records; solid circles are based on material examined. Boundaries of endorheic basins are from Tamayo and West (1964).

dibular 0 to 5; $\bar{x} = 2.6$; preopercular 8 to 10, $\bar{x} = 9.1$; lacrimal 4 or 5, $\bar{x} = 4.8$.

A. dugesi has a diploid number of 26 chromosomes consisting of 22 metacentrics of graded sizes, 2 large subtelocentrics and 2 small subtelocentrics (Fig. 3). Chromosomal sexual dimorphism has not been detected. The karyotype was determined by Teruya Uyeno from gill epithelial cells of specimens from Presa El Jigante, Aguascalientes (UMMZ 189071), Laguna de Yuriria, Guanajuato (UMMZ 189620), and Lago de Zirahuén, Michoacán (UMMZ 189613).

Trophotaeniae were examined in 22 newborn young from an aquarium stock from Lago de Zirahuén, Michoacán, and in 37 near-term young from Lago de Yuriria, Guanajuato. The trophotaeniae consist of two pairs of blunt, unbranched processes arising from the perianal lip. The members of a pair are equal in length, but the posterior pair is 2 to 3 times as long as the anterior pair. The processes lack pigmentation.

In life, the body of A. dugesi is olive above to silvery on abdomen. A dark lateral stripe, about as wide as orbit, extends from posterior margin of eye to caudal base. The stripe is solid and prominent in males, irregularly broken in females. Median fins yellow to orange at base, becoming clear toward margins. Females bear 4 to 11 lateral bars of olive or light brown separated by narrow streaks of metallic blue. The dominant pigment feature of males is an orange region which begins at pelvic insertion and extends across lower abdomen and caudal

peduncle (below the lateral stripe) to caudal fin. The periproct is stippled with fine points of dark brown. The most prominent features of preserved specimens are the vertical barring of females and the lateral stripe in both sexes.

Distribution.—A. dugesi is known from lakes and streams of the Mesa Central, now or formerly connected with the Río Lerma system (Fig. 4).

Locality records.—Jalisco: Laguna de San Marcos (UMMZ 160919); Presa Copalita (UMMZ 172119); near Guadalajara (Pellegrin, 1901); trib. Río Verde at Cuarenta Jalisco (UMMZ 172198); trib. Río Verde at Lagos (Meck, 1902); Hacienda La Punta (UMMZ 189056); Los Vergeles (UMMZ 189061). Aguascalientes: Presa El Jigante (UMMZ 189071). Guanajuato: Laguna de Yuriria (UMMZ 189074, 189620, 192349, 192364); Río Lerma at Salamanca (Hubbs, 1926); trib. Río Turbio near Cuerámaro (UMMZ 192322). Michoacán: Lago de Cuitzeo (UMMZ 172185, 192356); Tzinzimeo (UMMZ 191692); Alvaro Obregón (UMMZ 192402, 192407); Río Grande de Morelia (UMMZ 190858, 178586, 173966; De Buen, 1941); Lago de Pátzcuaro (UMMZ 191045, 143303; De Buen, 1940, 1941; Meck, 1902); trib. Lago de Pátzcuaro (UMMZ 202416); Lago de Zirahuén (UMMZ 189613, 198814).

Status of Allotoca vivipara.—De Buen (1940) described A. vivipara on the basis of a specimen (UMMZ 143303) from Lago de Pátzcuaro, Michoacán. He later improperly designated paratypes from Lago de Pátzcuaro and described additional material from Río Grande de Morelia, Michoacán (De Buen, 1941). The holotype has fin-ray counts as follows: dorsal 16, anal 12, pectorals 15-15, pelvics 6-6, caudal 22. It is a large (49.3 mm SL), pale adult female with only a faint suggestion of the vertical barring typical of the female of A. dugesi. Such barring tends to become obsolete in large females. We find no significant meristic or morphomet-

Table 4. Distributions of Fishes Occurring in the Magdalena Basin. Tributaries on the Mesa Central are not included in the Río Santiago.

	L. Magdalena	Río Ameca	Río Lerma	Río Santiago
Allotoca maculata	X			
Moxostoma mascotae	X	X		
Xenotoca eiseni	X	\mathbf{X}		
Xenotoca melanosoma	X	X	X	
Goodea cf. G. atripinnis	X	X	X	
Algansea tincella	X	X	X	
Chirostoma jordani	X	\mathbf{X}	X	
Poeciliopsis infans	X	\mathbf{X}	X	X

ric differences between the two species and therefore agree with Aurelio Solórzano (pers. comm., 1967) that A. vivipara is a synonym of A. dugesi.

ZOOGEOGRAPHY OF THE MAGDALENA BASIN

Laguna de Santa Magdalena occupies a small basin of interior drainage that lies between the Río Ameca and Río Grande de Santiago. It is the western-most of a series of endorheic basins that span central México at approximately 20°N latitude (Fig. 4). Tamayo and West (1964) believed this system of isolated basins, which coincides with the Neovolcanic Axis of México, was formed when normal exterior drainage was disrupted by volcanic activity. This is clearly so in some instances (L. Zirahuén, dammed by a lava flow), but the extensive playas of the Magdalena and Sayula basins suggest that increasing aridity and/or piracy of tributaries by stream capture have also contributed to disruption of drainages at least in the western basins. Laguna de Santa Magdalena was, in June 1892, "several miles wide and about twenty miles long" (Goldman, 1951:171); today little surface water remains.

On the basis of fish distributions, Meek (1904) inferred the former connection of the Río Lerma with the endorheic basins of Michoacán. The ranges of Allotoca (Fig. 4) and other fishes of Laguna de Santa Magdalena suggest that this lake also has been connected with the Lerma system. A former westwardflowing outlet of Laka Chapala is indicated by stream-deposited sediments at Jocotepec Quarry on the western end of that lake (Smith et al.,

1975). That this outlet continued westward to drain the Lerma basin through the present Ameca system is supported by the fact that the Río Lerma shares more fish taxa with the Río Ameca than it does with the Río Grande de Santiago (below the Mesa Central), its present lower course (Table 4). We hypothesize that Laguna de Santa Magdalena has also been drained by the Río Ameca, possibly when the latter served as the outlet of the Lerma basin.

RESUMEN

Una nueva especie de *Allotoca* se describe de una cuenca interior cerca de 80 km al oeste de Guadalajara, Jalisco. Se distingue de *A. dugesi* en la posición de la aleta dorsal y el número de radios en ella, el carácter de la trofotenia de los embriones, el número de cromosomas (2N = 48), y la coloración. La presencia de *Allotoca* y otros peces en la Laguna de Santa Magdalena indica una anterior conexión hidrográfica entre la Cuenca de Magdalena y la Cuenca del Río Lerma. *A. vivipara* se considera como sinónimo de *A. dugesi*.

ACKNOWLEDGMENTS

The chromosome information is taken from an unpublished survey of goodeid karyology being conducted by Teruya Uyeno, John Michael Fitzsimons and one of us (RRM). The illustrations of *A. maculata* and *A. dugesi* were made by Edward C. Theriot. Permission to collect fish in México was kindly granted by the Dirección General de Regiones Pesqueras. Field work was supported by NSF GB-3271 and GB-6272X (to RRM).

LITERATURE CITED

Bean, T. H. 1887. Descriptions of five new species of fishes sent by Prof. A. Dugés from the Province of Guanajuato, Mexico. Proc. U.S. Natl. Mus. 10:370–375.

De Buen, F. 1940. Sobre una colección de peces de los lagos de Pátzcuaro y Cuitzeo. Ciencia 7:306–308.

——. 1941. Contribución al estudio de la ictiología mexicana. Trabajos Estac. Limnol. Pátzcuaro 4:1– 31.

FITZSIMONS, J. M. 1972. A revision of two genera of goodeid fishes (Cyprinodontiformes, Osteichthyes) from the Mexican Plateau. Copeia 1972:728–756. GOLDMAN, E. A. 1951. Biological investigations in Mexico. Smith. Misc. Coll. 115:1–476.

HUBBS, C. L. 1926. Studies of the fishes of the order Cyprinodontes. VI. Material for a revision of the American genera and species. Misc. Publ. Mus. Zool., Univ. Michigan 16:1–87.

, AND C. L. TURNER. 1939. Studies of the fishes of the order Cyprinodontes. XVI. A revision of

the Goodeidae. Ibid. 42:1-93.

KINGSTON, D. I. 1978. Skiffia francesae, a new species of goodeid fish from western México. Copeia 1978:503–508.

——. 1979. Behavioral and morphological studies of the goodeid genus *Ilyodon*, and comparative behavior of fishes of the family Goodeidae. Unpubl.

Ph.D. Thesis, University of Michigan.

- MALDONADO-KOERDELL, M. 1964. Geohistory and paleogeography of Middle America, p. 3–32. *In*: Handbook of Middle American Indians, vol. 1. R. Wauchope and R. C. West (eds.). Univ. Texas Press, Austin.
- MEEK, S. E. 1902. A contribution to the ichthyology of Mexico. Field Col. Mus. Publ. 65 (Zool.) 3:63– 128.
- . 1904. The freshwater fishes of Mexico north of the Isthmus of Tehuantepec. *Ibid.* 5:1–252.
- MILLER, R. R. 1948. The cyprinodont fishes of the Death Valley system of eastern California and southwestern Nevada. Misc. Publ. Mus. Zool., Univ. Michigan 68:1–155.
- ——, AND J. M. FITZSIMONS. 1971. Ameca splendens, a new genus and species of goodeid fish from western México, with remarks on the classification of the Goodeidae. Copeia 1971:1–13.
- Mohsen, T. 1961a. Sur la présence d'un organe copulateur interne, très évolué chez Skiffia lermae

- (Cyprinodonte, Goodeidae). Compt. Rend. Seanc. Acad. Sci., Univ. Dakar 252:3327–3329.
- . 1961b. Sur le dimorphisme sexuel et la présence d'un organe copulateur très évolué chez le cyprinodonte Goodeidae *Shiffia lermae* Meek. Ann. Fac. Sci., Univ. Dakar 6:163–180.
- Nelson, G. G. 1975. Anatomy of the male urogenital organs of *Goodea atripinnis* and *Characodon lateralis* (Atheriniformes: Cyprinodontoidei), and *G. atripinnis* courtship. Copeia 1975:475–482.
- PATTON, J. C., AND R. J. BAKER. 1979. Chromosomal homology and evolution of phyllostomatoid bats. Syst. Zool. 27:449–462.
- Pellegrin, J. 1901. Poissons recueillis par M.L. Diguet, dans l'état de Jalisco (Mexique). Bull. Mus. Hist. Nat. Paris 7:204–207.
- SMITH, M. L., T. M. CAVENDER AND R. R. MILLER. 1975. Climatic and biogeographic significance of a fish fauna from the late Pliocene-early Pleistocene of the Lake Chapala Basin (Jalisco, Mexico). Univ. Michigan Mus. Paleont., Papers Paleont. 12:29–38.
- Tamayo, J. L., and R. C. West. 1964. The hydrography of Middle America, p. 84–121. *In*: Handbook of Middle American Indians, vol. 1. R. Wauchope and R. C. West (eds.). Univ. Texas Press, Austin.
- WEST, R. C. 1964. Surface configuration and associated geology in Middle America, p. 33–83. *In: Ibid.*
- MUSEUM OF ZOOLOGY AND DIVISION OF BIOLOGICAL SCIENCES, THE UNIVERSITY OF MICHIGAN, ANN ARBOR, MICHIGAN 48109. Accepted 18 June 1979.