Ameca splendens, a New Genus and Species of Goodeid Fish from Western México, with Remarks on the Classification of the Goodeidae

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A new genus and species of goodeid fish is described from the Río Ameca basin, Pacific slope of western México. Distinctive traits of the family, including those associated with reproduction, are reviewed and the first karyotype is given. *Ameca* is shown to have $2n = 26$ chromosomes (mostly metacentric), an apparently distinctive hemoglobin pattern, and an inability to hybridize in the laboratory with any of five species of goodeids tested. Rather than placing undue reliance on a few highly correlated, intraspecifically variable characters pertaining to the structure of the ovary and trophotaeniae, utilization of a diversity of characters is emphasized in discussing the classification of the family. The following synonymies are proposed or supported: *Balsadichthys = Ilyodon*; *Lermichthys = Girardinichthys*; *Ollentodon* and *Neotoca = Skiffia*; and *Skiffia variegata = S. lermae*. We suggest that *Hubbsina* lies along an evolutionary sequence leading to the two species of *Girardinichthys* and hence should be removed from the Goodeinae.

THE Goodeidae, a family of viviparous cyprinodontoid fishes, is restricted to and probably originated in México. It is a small group (perhaps 35 or 40 species) of rather limited range that has flowered through adaptive radiation in a region characterized by paucity or absence of primary freshwater fishes. Its center of abundance lies in the Río Lerma basin of the cool, tropical highlands of western México, where the only other cyprinodontoid is *Poeciliopsis infans* (Woolman), a poeciliid. The Lerma fish fauna is dominated by the goodeids and by a parallel radiation of the freshwater atherinid genus *Chirostoma* (Barbour, 1966. The systematics and evolution of the genus *Chirostoma* [Pisces; Atherinidae]. Ph.D. thesis, Tulane Univ., 1966).

Viviparity is evident in goodeids from (1) the distinctive shortening and crowding of the anterior anal fin rays of the male (Figs. 1, 2) and the slight separation of these rays from the rest of the fin; (2) the development, in all but one species, of trophotaeniae (Fig. 5), transitory rectal processes of the embryo and newborn fish that are associated with nutrition and respiration (Hubbs and Tur-

ner, 1939, and references cited therein; Turner, 1946; Mendoza, 1956, 1965a); and (3) the presence of an organ presumed to be functional in copulation (see p. 8). These three features, and probably the rudimentary anteriormost anal ray (Turner et al., 1962: figs. 1–15, and fig. 2 herein) and the differential fusion of basal segments in anal rays 2–7 (Turner et al., 1962:575, figs. 6, 13), distinguish goodeids from all other livebearers of the suborder Cyprinodontoidei.

Most members of the family inhabit the highlands of the Mesa Central (West, 1964: 42–48, fig. 8), or live on disrupted segments of this plateau, at elevations between about 915 and 2130 m. However, in the faunally unsaturated waters of the Pacific slope in Jalisco and Colima the genus *Ilyodon* (sensu lato, see below) descends to as low as 180 m. Goodeids occupy a variety of habitats: warm springs, large and small lakes (warm or cold) that may be clear to turbid, swiftly-flowing to sluggish streams, alkaline ponds, marshes, roadside ditches, and canals. Most probably do not regularly inhabit depths greater than about half a meter and prefer quiet or slowly-moving water. The species vary in length
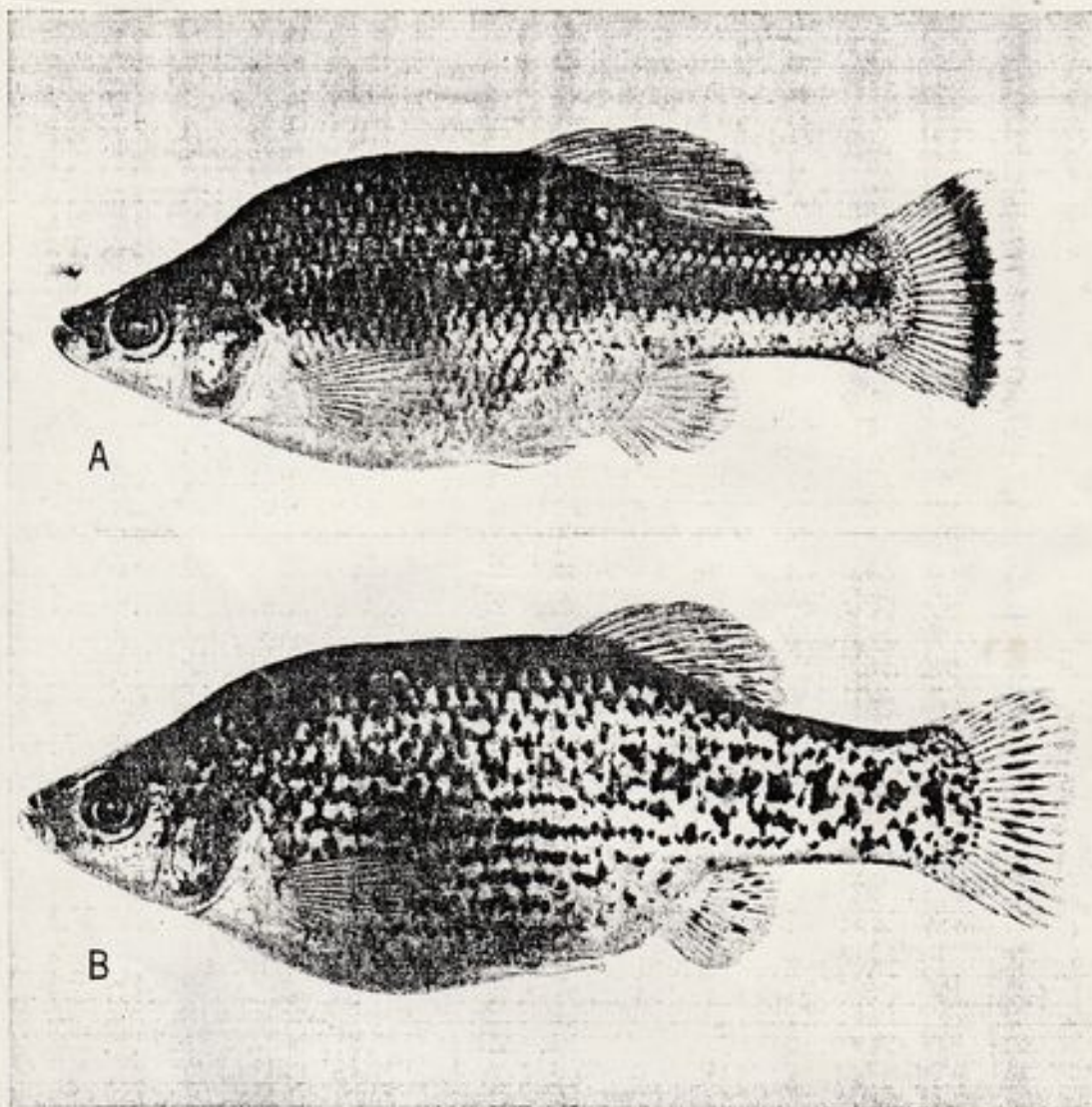
Fig. 1. *Ameca splendens*, new genus and species, photographed by W. L. Brudon. A, male para-topotype, UMMZ 172229, 73.0 mm SL; B, female paratopotype, UMMZ 172229, 81.5 mm.

from about 25 to 200 mm, but most are not much over 75–100 mm long.

A variety of trophic adaptations has produced a diversity of nutritional types, including filter feeders (*Goodea*), algal and ooze feeders (*Ilyodon*), carnivores (*Alloophorus*), and omnivores (*Xenotoca*). Correlated with these feeding habits are variations in the nature of the teeth, jaws, and length of intestine that formed the basis for early classifications of the group (*e.g.*, Meek, 1904). In the last general revision (Hubbs and Turner, 1939) major emphasis was on the structure of the ovary and trophoteniae. However, a recent intensive study of one species (Mendoza, 1965a) demonstrates considerable

intraspecific variability in these structures and indicates the need for a reappraisal of their importance in classification.

Evaluation of evidence from a diversity of sources—including behavioral traits, biochemistry, hybridization data, karyotype analysis, and comparative osteology—is needed to reach firmer conclusions about the origin and interrelationships of this remarkable family. We find these fishes to be admirably suited for experimental work, and studies involving comparative behavior, hybridization tests, isolating mechanisms, and karyology are being pursued in our experimental aquarium facility.

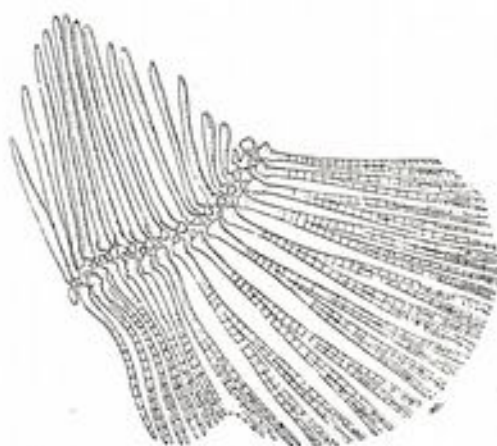In this contribution we describe a new

Fig. 2. Anal fin and supports of *Ameca splendens* male, from cleared and stained specimen (UMMZ 172229), 68.0 mm SL.
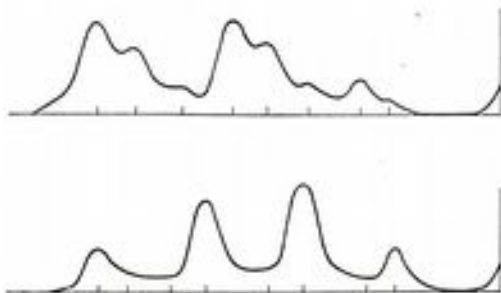

Fig. 3. Densitometer tracings of the hemoglobin patterns of *Ameca splendens* and *Xenoophorus captivus*. Anode at left, origin at extreme right. Graduations along horizontal axis indicate exact distances between protein bands; vertical axis represents the relative amounts of the proteins.

genus and species and comment on the classification of the goodeids, suggesting the consolidation of some genera. We also give the first chromosome count and karyotype for the family. The new taxon is based on specimens in The University of Michigan Museum of Zoology (UMMZ).

Ameca, n. gen.

Figs. 1–6

Type-species.—*Ameca splendens* sp. nov.

Diagnosis.—A large goodeid (to 90 mm SL) with bifid outer jaw teeth at all ages (inner teeth bifid except in newborn), a broad yellow, terminal band on the caudal fin of the male (Fig. 1), usually 30–36 (27–38) gill rakers, 13 or 14 dorsal and 15 or 16 anal rays (including rudimentary ray, Fig. 2), 37–39 lateral scales, 8 (7–9) preopercular pores, 35–38 vertebrae, 5 branchiostegals, a distinctive hemoglobin pattern (Fig. 3), a diploid chromosome number of 26 (Fig. 4), and 2–4 ribbon-like trophotaeniae (Fig. 5) that are attached to the ovarian septum.

Relationships.—In our present state of knowledge of the Goodeidae, we see little point in speculating on the generic relationships of *Ameca*. The reader is referred to the discussion given below on the classification of the family. *Ameca* is well differentiated from the other genera as presently recognized; a number of these may eventually be combined since we regard the current taxonomy of goodeids to be top-heavy at the generic level (see later).

Etymology.—The generic name *Ameca* is

from the name of the river to which the new genus is evidently confined. The gender is feminine.

Ameca splendens n. sp.

Types.—The holotype, a mature male 60.5 mm SL (UMMZ 172227), was collected by Robert R. Miller and John T. Greenbank on 25 March 1955, in the Río Teuchitlán just below Teuchitlán, near the road between Highway 70 (Ameca to Guadalajara) and Etzatlán, about 75 km W of Guadalajara, Jalisco. The allotype, an adult female 64.0 mm SL (UMMZ 172228), was taken with the holotype, as were 198 paratopotypes, 17–90 mm SL (UMMZ 172229), including three cleared and stained (male, female, and juvenile). There are 19 paratypes: nine juvenile to adult, 17–37 mm SL (UMMZ 160912), taken by Arthur A. Alcorn on 13 February 1949, about 2 km ESE of Teuchitlán, and 10 adults, 46–69 mm SL (UMMZ 173801), collected by James A. Peters and William B. McIntosh on 23 April 1949, in the Río Ameca about 12 km E of Ameca.

Description.—Most of the important specific characters of this species are given in the generic diagnosis. The form and coloration of large adults are portrayed in Fig. 1, the embryos in Fig. 5. Proportional measurements are given in Table 1. Methods of counting and measuring are those used by Miller (1948:9–13) except that the postorbital length of the head was measured to the upper angle of the opercle. For reasons given in the discussion of anal fin supports, the rudimentary (anteriormost) anal ray (Fig. 2) is included in the anal-ray count. The last two closely approximated rays in both dorsal and

Fig. 4. Metaphase chromosome spreads (A, female; B, male) and C, karyotype of female *Ameca splendens*.

anal fins are counted as a single ray rather than as two rays.

Dorsal rays: 13 (10), 14 (22), the first one unbranched in 7 fish and the first two unbranched in 25; anal rays: 15 (18), 16 (14), all rays except the first (rudimentary) branched in 2 (a male and a large female), the second ray unbranched in 27, and the second and third rays unbranched in 3 (see also pp. 6–7); pectoral rays (both fins): 14 (34), 15 (30); pelvic rays (both fins): 6 (63), 7 (1); principal caudal rays: 20 (1), 21 (6), 22 (18), 23 (6), 24 (1). The holotype has dorsal, i, 12; anal, ii, 14; pectorals, 14–14; pelvics, 6–6, and caudal, 22.

Scales in lateral series: 37 (8), 38 (15), 39 (9); scales between dorsal and anal fins: 14 (1), 15 (12), 16 (13), 17 (5); predorsal scales: 22 (1), 23 (2), 24 (9), 25 (9), 26 (6), 27 (4), 28 (1); scales around caudal peduncle: 19 (27), 20 (4); scales around body: 37 (1), 38 (4), 39 (5), 40 (16), 41 (1), 42 (2), 43 (0), 44 (1); and prepelvic scales (between pelvic insertion and isthmus on midline of abdomen): 21 (1), 22 (2), 23 (3), 24 (4), 25 (5), 26 (4), 27 (4), 28 (2). The holotype has 37 lateral scales, 16 from dorsal to anal, 25 predorsal, 19 (9 + 10) around peduncle, 40 around body, and 25 prepelvic scales.

Vertebral counts (including hypural complex), taken from radiographs, are: 35 (9), 36 (36), 37 (11), 38 (1), based on specimens from all localities. Of these, the precaudal vertebrae number 15 (5), 16 (47), 17 (1), 18 (1), and the caudal vertebrae are 19 (4), 20 (38), 21 (12). Holotype, 16 + 20 = 36.

Gill rakers: 27 (1), 28 (1), 29 (0), 30 (2), 31 (4), 32 (4), 33 (5), 34 (10), 35 (5), 36 (3), 37 (1), 38 (1). Fish less than 40 mm SL had 30 or fewer rakers (the smallest, 30.5 mm, had 27) and specimens 70–82 mm long had 36 to 38 rakers. Thus gill-raker number is correlated with size. The holotype has 34 gill rakers. All gill rakers on the first arch were counted, without distinction between upper and lower limbs.

The sensory pores and canals of the lateral-line system on the head (Fig. 6) vary as follows (both sides counted): mandibular, 2 (2), 3 (13), 4 (49); preopercular, 7 (3), 8 (58), 9 (3); lachrymal, 4 (64). The holotype has 3–4 mandibular and 8–8 preopercular pores. The arrangement of canals and pores on top of the head shows two main patterns (numbering is from Gosline, 1949:pl. I): one, in which the supraorbital system is disrupted between pores 2a–2b, and 4a–4b, hence with two breaks, and the other in which there is a third break between pores 6a–6b (these two variants are shown on the left side, Fig. 6B). A third, rare variant shows only one break, between pores 2a–2b (shown on right side, Fig. 6B). There is a tendency for the smaller fish to have three breaks and for the larger ones to show two, but there are frequent exceptions. The single break (noted only twice in 63 fish) occurred only in larger fish. All of the pores are small.
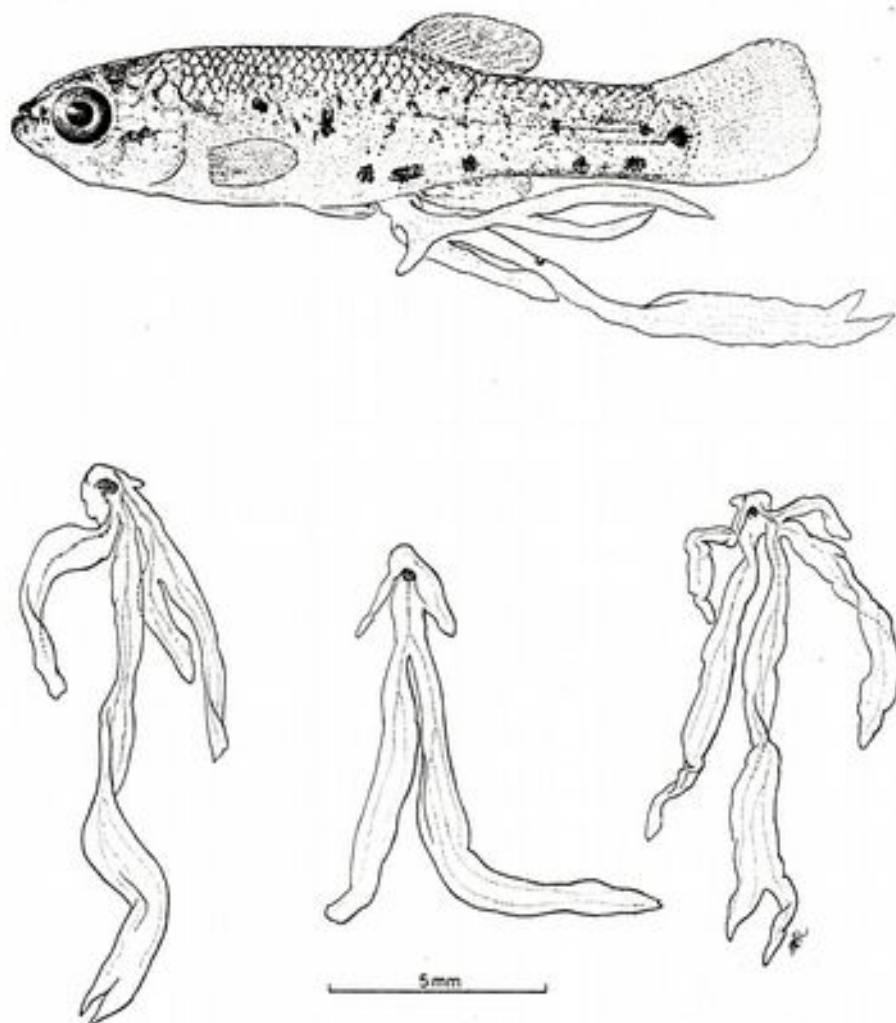
Fig. 5. Newborn young and trophotaeniae (aquarium reared) of *Ameca splendens*. Trophotaeniae dissected from embryos of a female 69 mm SL.

The branchiostegals numbered 5 in 24 specimens.

The jaw teeth of the evenly curved outer row are uniformly and strongly bifid, little compressed anteroposteriorly, curved backward, and number about 23–28 in the upper jaw and 21–26 in the lower jaw of adults. They are rather firmly attached to the strong jaws. The inner teeth are small, bifid at their tips (except in newborn, in which some or many are peg-shaped or weakly conic), and arranged in a rather broad, irregular, curved band.

Dimorphism and coloration.—Sexual dimorphism (Fig. 1, Table 1) is marked, especially in fin size (all fins larger in the male), body depth (deeper in large males), distance between anal-fin origin and caudal-fin base (greater in the male) and in the length of the caudal peduncle (longer in the male). The life colors of mature adults also readily distinguish the sexes. In the male the outer third of the caudal fin is brilliant yellow-orange to deep orange followed medially by a curving broad, black bar about equal to diameter of pupil, and with the basal part of the fin milky-white. The distal fourth of the anal fin is also yellow-orange to orange, as are the pectoral and pelvic fins. The dorsal fin is mostly dusky, but has a narrow to moderate yellow or orange margin. The sides show metallic bluish to turquoise reflections from the scales, and the head (except top) and abdomen are golden yellow. The back
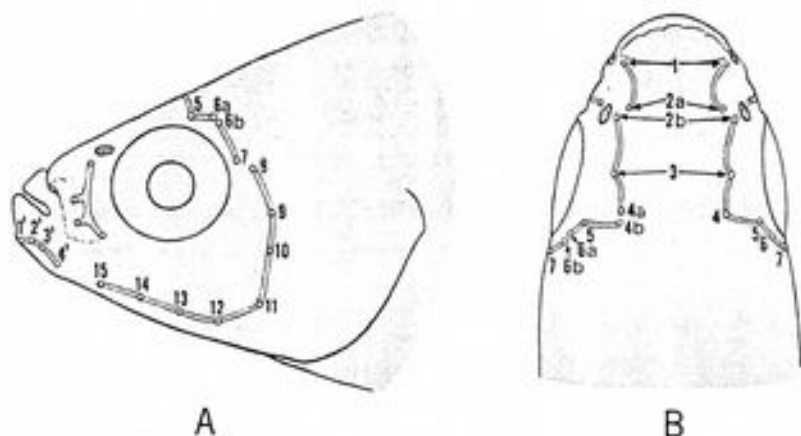
Fig. 6. Lateral-line system on the head of an adult *Ameca splendens*, showing (A) mandibular, lachrymal, and preopercular canals and pores and (B) the supraorbital system; semidiagrammatic.

is olivaceous brown. Females are greenish yellow over the caudal peduncle and entire venter and show pale bluish reflections from the scales over the sides; their fins are pale watery, with no bright colors.

In preservative (ethyl alcohol) the bright yellow to orange colors of the males and the more subtle yellow-greens of the females fade rapidly, leaving brownish-black pigment patterns overlying the light buff of the dermis. The brightly colored margins on the caudal, dorsal, and anal fins of live males are represented in preserved specimens by clear areas (see Fig. 1A). The subterminal black bar on the caudal fin remains distinct while the remainder of the caudal fin, as well as the other median fins, appears dusky (immature and young males) to very dark (large males). The paired fins are relatively pale in both sexes and in the young. In large males a midlateral concentration of pigment appears as a prominent dark band which extends posteriorly from the upper edge of the opercle to the base of the caudal fin; in small males this band is less distinct anteriorly where it is often broken up into a series of irregular, poorly defined spots. The body and median fins of females are conspicuously spotted (Fig. 1B). Spots on large females are arranged in 7–11 fairly distinct rows on the side of the body and in one or more bands on the membranes of the median fins, but such a pattern is not always apparent in small females. There are 8–16 large blotches on the side of the caudal peduncle in females of all ages and also in small males; certain of these spots have doubtless persisted from birth. We readily

distinguish the young of *Ameca splendens* from those of 15 other goodeid species by the pattern of spotting (Fig. 5). A large spot at the base of the caudal fin and the conspicuous row of from two to seven (usually four or five) spots below the midside of the caudal peduncle forward to above the pelvic fins are characteristic for newborn young of this species.

Anal fin rays and supports.—As mentioned earlier, the first anal ray of goodeids is typically rudimentary in males and often so in females. There is a one-to-one correspondence between the rays and the basal supports —the typical condition in teleosts (Lindsey, 1955:38)—with the rudimentary anteriormost ray of the adult male (Fig. 2) unsegmented (but the ray is segmented, as well as bilateral though unbranched, in the juvenile). This element would ordinarily be missed in recording anal rays because it can only be seen by careful dissection, clearing and staining, or on radiographs. For this reason, anal ray counts in goodeids, especially of males, have probably been recorded as 1 fewer than the actual number of rays (following the method of counting recommended by Hubbs and Lagler, 1958:21). We include this rudimentary ray in our counts of *A. splendens*.

The first 4 pterygiophores (in both sexes) lack medial radials—*i.e.*, these apparently are basals (= fused proximal and medial radials). The next 10 pterygiophores (numbers 5–14) have medial radials. The penultimate pterygiophore is a basal, and the last one (number 16) is apparently a highly modified basal. Each pterygiophore has a distal radial which (except for the anteriormost ray) fits into

TABLE 1. PROPORTIONAL MEASUREMENTS, IN THOUSANDTHS OF STANDARD LENGTH, OF *Ameca splendens*. (Holotype and Allotype Included with the 18 Larger Adults. Based on UMMZ 122278–122279.)

Measurement	Holotype ♂	Larger Adults		Smaller Adults	
		9 Males	9 Females	5 Males	5 Females
Standard length, mm	60.5	46.5–69.7 (58.1)	50.2–81.4 (62.9)	29.1–42.2 (35.3)	30.0–45.3 (37.8)
Predorsal length	592	568–602 (580)	576–615 (597)	571–583 (576)	567–580 (575)
Prepelvic length	514	494–517 (507)	501–532 (513)	494–505 (501)	499–503 (501)
Anal origin to caudal base	393	380–402 (390)	360–390 (372)	385–392 (388)	375–397 (388)
Body, greatest depth	392	363–410 (387)	339–366 (358)	310–341 (324)	309–338 (322)
Width	188	171–189 (182)	167–198 (178)	151–166 (160)	150–160 (156)
Head length	288	270–290 (283)	271–284 (277)	273–295 (286)	281–290 (284)
Depth	218	198–218 (210)	195–212 (205)	201–214 (206)	197–207 (201)
Width	180	172–181 (177)	163–179 (171)	166–176 (171)	160–168 (163)
Caudal peduncle length	289	280–300 (290)	267–291 (277)	280–291 (287)	282–293 (287)
Least depth	149	142–154 (149)	137–154 (144)	137–142 (139)	131–141 (136)
Interorbital, least bony width	114	110–119 (114)	107–113 (109)	110–114 (111)	105–110 (107)
Preorbital width	45	41–46 (43)	36–44 (41)	37–41 (39)	33–40 (36)
Postorbital length	122	118–126 (122)	107–118 (114)	111–120 (116)	110–121 (114)
Snout length	94	82–94 (89)	80–91 (87)	81–86 (84)	76–86 (81)
Orbit length	84	80–84 (83)	70–77 (75)	85–93 (90)	82–97 (88)
Mouth width	91	77–92 (85)	75–90 (79)	75–82 (80)	76–82 (80)
Mandible length	79	67–79 (73)	66–81 (73)	60–76 (66)	54–66 (61)
Dorsal fin, basal length	205	196–213 (203)	161–176 (169)	163–192 (173)	158–181 (165)
Depressed length	344	329–364 (344)	241–253 (247)	250–299 (272)	228–249 (239)
Anal fin, basal length	102	102–117 (108)	92–102 (96)	103–110 (106)	94–104 (98)
Depressed length	193	186–200 (191)	146–170 (156)	163–181 (172)	152–163 (158)
Middle caudal rays, length	179	174–185 (181)	161–178 (170)	192–204 (199)	181–203 (191)
Pectoral length	218	208–221 (215)	190–202 (197)	196–213 (204)	192–203 (197)
Pelvic length	154	139–154 (147)	131–145 (138)	139–154 (146)	137–148 (141)

the base between the two halves of the corresponding ray. All but the first two rays of the male anal fin are typically branched. However, branching varies from that in which all but the anteriormost ray are branched to that in which rays 1–3 are unbranched. The branched condition may be primitive (Turner et al., 1962:576).

With respect to bifurcation of anal fin rays and consolidation of basal segments (Fig. 2), this species may be regarded as rather generalized, for it typically has all but rays 2 and 3 branched (occasionally all but the rudimentary one, or all but rays 1–3) and there is little segment consolidation. In these characters, *Ameca* rather closely resembles *Ataeniobius* (Turner et al., 1962:fig. 1), considered by most students of the family to be the most primitive genus.

Reproductive biology.—Unlike their viviparous relatives, the Poeciliidae, male goodeids lack spermatophores and the females do not store sperm for the fertilization of more than one brood. Thus each new complement of developing eggs must be fertilized separately.

The eggs are extremely small and contain very little yolk, and the embryos are retained in the ovarian follicles until the yolk is virtually absorbed. They are then evacuated into the intra-ovarian cavity, where they remain for several weeks. The ovary functions as a nutritive organ, producing secretions that are discharged into the intra-ovarian cavity and absorbed by the embryo (Turner, 1933).

Brood intervals average about 50% longer in goodeids than in poeciliids—approximately 45–55 versus 25–35 days. In *A. splendens*, under the less than optimal conditions of aquarium life, the average brood interval has been 54 days (range 44–78) and the average brood size 7 young (range 1–17), as based on 37 broods from 12 females. Sixty-nine young, representing 10 broods from 5 females, average 14 mm in total length at birth (range 11–17 mm).

Attempts to hybridize *A. splendens* by forced reciprocal matings (18 pairs) with five species of goodeids (*Characodon lateralis*, *Xenotoca variata*, *X. eiseni*, *X.* sp., *Xeno-*

ophorus captivus) have consistently failed, plausibly because of differences in chromosome number and morphology but possibly also because of behavioral blocks. Artificial insemination was not attempted.

In the male, the swollen area between the anus and the genital opening is much wider than long, turgid basally and constricted distally, with the posterior margin concave; the structure is weakly to moderately scaled laterally, the scales scarcely encroaching on the ventral surface anterolaterally.

Mohsen (1961a, b) described and figured a copulatory organ in *Skiffia lermae* Meek that also occurs in all four of the recognized subfamilies of the Goodeidae (Mohsen, 1965). It is not yet known just how this internal muscular organ operates, but Mohsen believes that it may eject a jet of semen or be everted and applied to the genital pore of the female. Dr. Guillermo Mendoza advises us that he is attempting to determine how the organ functions.

In view of the above and our general lack of knowledge of the method of insemination in goodeids, we feel that the term gonopodium, as applied to poeciliids and some other livebearers, may not be applicable to the male anal fin in this family.

Ovary.—As in other goodeids the single, median ovary of *A. splendens* is formed by the union of right and left organs whose fused walls are represented by a prominent septum. The dual origin of the ovary is apparent since the two halves are not completely united anteriorly, thereby giving the entire structure a slightly bilobed appearance. Eggs may be found throughout the length of the ovary in juvenile females or in females with embryos less than 2 mm long. However, in adult females with embryos well beyond the tail-bud stage, the ovigerous tissue occurs primarily in the anterior one-third of the ovarian septum and wall. The septum remains thickened posteriorly but contains a large number of longitudinal blood vessels rather than ova. Since the trophotaeniae are attached to the highly vascular, posterior two-thirds of the septum, it is assumed that this section of the septum is the site of circulatory exchange that takes place between the female and the developing young throughout their embryogeny. Because it is much thinner than the septum, the ovarian wall is sufficiently transparent to render visible the encased ova and embryos.

The greatly thickened septum is entire and attached dorsally and ventrally except at the posterior end, where the two lateral compartments merge into a common birth canal. The septum may be highly convoluted, moderately folded, or vertical, depending on the volume occupied by the embryos. The septum of an ovary containing tail-bud stage embryos that are 1–2 mm long is folded extensively; however, the septum may be practically straight in an ovary bearing near-term embryos 14–16 mm long. Evidently the septal folds disappear as the ovary is stretched by the growing embryos.

Trophotaeniae.—In *A. splendens* the trophotaeniae consist of 2–5 (usually four) flattened, ribbon-like structures extending posteriorly from a common base around the perianal lip (Fig. 5). Termini number from two to 10 but counts between four and seven are most frequent. Similarly, the length of the trophotaeniae varies; they may be fairly short in tail-bud stage embryos, reaching maximum length in half-developed embryos, and short again in young nearing birth. A conspicuous sheath which separates the internal vascularized tissue from the external epithelium is present in the trophotaeniae of young embryos, present or absent in half-grown ones, and usually absent in those near birth.

Taxonomic criteria for phylogenetic assessment in the Goodeidae erected by Hubbs and Turner (1939) on the basis of the structure of the ovary and trophotaeniae indicate that *A. splendens* belongs to the subfamily Goodeinae, since the ovigerous tissue is primarily confined to the ovarian wall and septum. However, other characters related to the nature of the median septum and the number, length, and histological type of trophotaeniae are much too variable to permit the assignment of this species to any one of the seven phyletic lines proposed for the subfamily by the above authors. Its position in the family must await the accumulation of data from diverse disciplines from all members of the Goodeidae.

Karyology.—Teruya Uyeno, of Nippon Luther Shingaku Daigaku, Tokyo, Japan, and the second author recently initiated a study of chromosomes in the Goodeidae which helps to corroborate the validity of *Ameca*. Karyotype analyses of 35 species, representing all of the currently recognized genera, have revealed a distinctive chromosome number and configuration for *Ameca splendens* (Fig. 4). The diploid number is

26, comprising 22 large metacentric, 2 small submetacentric, and 2 small acrocentric chromosomes, a karyotype thus far not observed in any other goodeid. Diploid numbers in other species include 24 (1), 26 (2), 28 (1), 30 (2), 36 (1), 46 (2), and 48 (25).

Biochemistry.—Comparison of the multiple hemoglobins of a number of cyprinodontoid fishes (48 poeciliids, 8 goodeids, 7 cyprinodontids) by Huddle (1967, Multiple hemoglobins in the systematics and genetics of poeciliid fishes. Ph.D. thesis, Univ. Mich., 1967.) showed the Goodeidae to have more fractions (8) than the other two families (5–7). Among the goodeids tested by Huddle, only *Ameca* displayed a variance from the high uniformity found among the other seven species (Fig. 3). Electrophoresis was a modification of the Ornstein-Davis technique (unpubl. paper entitled "Disc Electrophoresis," available from Distillation Products Inc., Rochester, N. Y.) in acrylamide tubes at a pH of 9.0.

Feeding adaptations and habits.—The intestine is long and greatly convoluted. Within the anterior two-thirds of its length it is coiled counter-clockwise, followed by reverse (clockwise) coiling. In a female, 73 mm SL, there were four complete counterclockwise coils and three complete clockwise coils. In this specimen, and in a male 69 mm long, the intestine measured about 4.5 times the standard length of the fish.

A long, coiled gut and lack of a discrete stomach in the embryos, juveniles, and adults suggest that *A. splendens* is herbivorous. Gut contents of field-preserved specimens revealed a predominance of pennate diatoms and filamentous algae, mostly Ulotrichales, Zygnematales, and Oedogoniales. The sparse animal material included such items as mosquito larvae, copepods, and oligochaetes. Although these may have been adventitiously ingested along with vegetation, laboratory stocks of *A. splendens* readily feed on live brine shrimp, *Daphnia*, worms, and small insects. These observations could indicate that *A. splendens* is an omnivore; however, the gut contents of fishes with similar gut morphology often merely reflect the relative abundance of available plant and animal food.

Habitat.—The Río Teuchitlán, the type locality of the new species, rises in large springs near Teuchitlán and, shortly below, forms a stream that averages 6 m wide and up to 1.2 m (but generally less than 1 m)

deep, flowing over a bottom that is mostly deep mud and silt but with some sand, gravel, volcanic rocks, and boulders. It is heavily utilized for irrigation, drinking water, and washing, with much pollution by man and livestock. Fishes were extraordinarily prolific, a short haul readily filling a 4.5 m seine. Vegetation comprised a broad-leaved *Potamogeton* (locally abundant), water hyacinth, and *Ceratophyllum*, with green alga on the rocks. In the main channel the current was moderate; where the stream expands below a stone bridge to form a pool about 21.5 × 18 m in major dimensions, it becomes more pond-like, open and shallow, with no or little current. When the type collection was made the water was almost continuously muddied by cattle, pigs, and horses wading or being bathed in the stream. At 1100 hr on 25 March 1955, the air and water were 26.1° C; on 8 April 1965, at 1700 hr they were 32.2° and 29°, respectively; and on 5 May 1966, air and water were 27° and 28° C at noon. Where sampled, the river is perhaps 15 km above its confluence with the Río Ameca; the latter flows to the Pacific, north of Puerto Vallarta, after descending into a deep barranca perhaps 90 km below the town of Ameca (as seen from the air on 3 March 1957). The elevation at Teuchitlán read 1311 m on our altimeter.

Specimens of *Ameca* have been seen by us from only one other locality, the Río Ameca about 12 km east of Ameca, where James A. Peters and William B. McIntosh obtained 10 adults in 1949 with a 1.8 × 1.2 m seine. The water was described as muddy, the vegetation water hyacinths and rushes, the bottom sand and mud, the current slow, and the water depth 1.2 m.

Associates.—Eleven species representing five families have been taken with the new genus. Cyprinidae: *Algansea, Hybopsis,* and *Notropis*; Ictaluridae: *Ictalurus dugesi* (Bean); Goodeidae: *Chapalichthys, Goodea, Skiffia, Zoogoneticus quitzeoensis* (Bean), and *Xenotoca*; Poeciliidae: *Poeciliopsis infans*; and Atherinidae: *Chirostoma jordani* Woolman. The fish fauna of the Río Ameca basin in the plateau region (generally above 914 m), which extends below Ameca, Jalisco, at least as far as Los Mesquites (31.4 km S of Ahuacatlán), Nayarit, is very different from that below the barranca, where, to our knowledge, no cyprinids, goodeids, or atherinids (*Chirostoma*) have been taken. Apparently only the genus *Poeciliopsis* occurs

in both areas, with *P. infans* above and *P. viriosa* Miller both above and below (Miller, 1960), the latter not sympatric with *infans*. At Los Mesquites Clyde Barbour (in 1969) obtained two minnows (*Algansea, Hybopsis*) and two cyprinodontoids (*P. infans* and *Xenotoca*). The plateau segment of the fish fauna is derived from that of the Río Lerma basin, just to the east; hydrographic connections between these two drainages were probably broken during Pleistocene time.

Etymology.—The specific name, of Latin derivation, means bright (shining) or glowing, in reference to the striking life colors of the new species.

CLASSIFICATION OF THE GOODEIDAE

Although much remains to be learned regarding the interrelationships of the goodeids, some consolidation of currently recognized genera and species seems definitely called for in the light of recent work, especially the penetrating study by Mendoza (1965a) of the ovary and trophotaeniae of "*Characodon*" *eiseni*. Convergent adaptiveness, in particular, has clouded the interpretation of phyletic lines.

Currently, 20 genera and 32 species are recognized in the taxonomic literature (Hubbs and Turner, 1939; de Buen, 1941, 1942; Turner, 1946; Alvarez and Navarro, 1957; Alvarez, 1959, 1963; Alvarez and Cortés, 1962; Romero, 1967). Hubbs and Turner delimited four phyletic lines, of which two, the Ataeniobinae and the Characodontinae, are monotypic: *Ataeniobius toweri* (Meek) is regarded as the most primitive goodeid by Hubbs and Turner, and *Characodon lateralis* Günther is probably rather specialized as indicated particularly by the few chromosomes (24), all of which are metacentric. These two genera are the most removed, geographically, from the main range of the family, the Río Lerma basin. *Ataeniobius* lives off the eastern edge of the Mexican Plateau in headwaters of the Atlantic-draining Río Pánuco, in San Luis Potosí (Gregg, 1956, A distributional survey of the fishes of San Luis Potosí, México. Ph.D. thesis, La. State Univ.; Miller, 1956); *Characodon* is isolated by a broad expanse of arid highlands far to the north of the Río Lerma where it lives in streams and springs near the city of Durango and, formerly, in springs of the enclosed basin of Parras, Coahuila (Miller, 1961:388). The remainder of the goodeids are assigned to two other phyletic lines, the Goodeinae and the Girardinichthyinae. To what extent the subfamily classification of Hubbs and Turner is natural needs further study.

Generic consolidation.—In recommending the following consolidation of genera we are not trying to compensate for our erection of a new one. Nearly 20 years ago the senior author had the opportunity to identify the large collection of goodeids taken by the late C. L. Turner in 1939, and most of the following proposals stem from a systematic survey of the family made then.

Balsadichthys, type-species *Goodea whitei* Meek, was compared originally (Hubbs, 1926: 19) only with *Goodea*, from which we agree it should be separated generically. However, in their family revision, Hubbs and Turner (1939:63) showed that *Balsadichthys* is intimately related to *Ilyodon*, not only on morphological grounds but because *B. xantusi* Hubbs and Turner and *I. furcidens* (Jordan and Gilbert) readily and frequently hybridize in nature. Hubbs and Turner concluded that "It is not at all improbable that it will be found expedient to synonymize *Balsadichthys* with *Ilyodon.* . . ." We concur and herewith formally propose that *Balsadichthys* be placed in the synonymy of *Ilyodon*. To separate these species generically on the basis of differences in the number and strength of implantation of the jaw teeth, and hence on adaptations for feeding, would be to return to the demonstrably outmoded earlier classifications of the Goodeidae (see Hubbs and Turner, 1939:10–11).

Lermichthys was originally compared only with the very different genus *Characodon* (Hubbs, 1926:18). Subsequently, it was shown that *Lermichthys* is a close relative of, and perhaps derived from, *Girardinichthys* (Hubbs and Turner, 1939:34–36, 68–69). Both are monotypic. We feel that the many resemblances between the two species (see Alvarez and Navarro, 1957, regarding the name *G. viviparus*) justify synonymizing *Lermichthys* with *Girardinichthys*. Both show striking sexual dimorphism in dorsal and anal fin rays and in number of vertebrae, and the pores of the supraorbital, mandibular, preopercular, and lachrymal canals are entirely replaced by pit organs (Gosline, 1949:9, and observations by us).

In their account of the genus *Skiffia*, Hubbs and Turner (1939:69) wrote: "Largely on the basis of superficial characters, we set 2 species of *Skiffia* apart in distinct genera,

Ollentodon and *Neotoca*. . . ." Their separation of *Ollentodon* (p. 70) is based on the nature of the inner jaw teeth, larger dorsal fin, relative length of the median posterior trophotaenia, and coloration. In our judgment, strongly influenced by Mendoza's recent work, these are not adequate differences for generic separation. *Neotoca* is recognized generically (p. 71) on the basis of the development and nature of the jaw teeth, less transverse mouth, a shorter intestine, length of the median trophotaenia, nature of the inner pelvic rays, relative development of the anal pouch and anterior anal lobe of the male, convex versus concave (medially) genital opening of the male, and strikingly different coloration. We regard these to be excellent specific characters but feel that more fundamental differences are needed for generic separation. Consequently we propose that *Ollentodon* and *Neotoca* be regarded as synonyms of *Skiffia* Meek. An interesting similarity between *Ollentodon* and *Skiffia*, first pointed out by Mendoza (1965b), is the striking sexual dimorphism of the dorsal fin, which, in the male, has the anterior rays shortened and thickened and separated from the remainder of the fin by a notch. Also the species currently placed in these genera have the supraorbital canal system replaced by neuromasts and lack mandibular pores (as do *Hubbsina* and *Girardinichthys*), and *Ollentodon* and *Skiffia* are further degenerate in having the preopercular and lachrymal canals undeveloped.

Position of *Hubbsina*.—The monotypic goodeid, *Hubbsina turneri* de Buen (1941), is known only from the basin of Río Grande de Morelia which terminates in Lago de Cuitzeo north of Morelia, Michoacán. It was assigned by de Buen to the subfamily Goodeinae on the basis of ovarian structure. In his study of the gestational adaptations of this fish, Mendoza (1956:82–83) showed that the structure of the ovary of *Hubbsina* agrees with that regarded by Hubbs and Turner as characterizing the Goodeinae, whereas the trophotaeniae (not studied by de Buen) are most similar to those of *Characodon*, of the Characodontinae, and *Girardinichthys* (sensu lato), of the Girardinichthyinae. He concluded that the taxonomic position of *Hubbsina* is uncertain. It is our view, based on the following considerations, that *Hubbsina* should be disassociated from the genera currently placed in the Goodeinae and aligned closely with *Girardinichthys*, currently as-

signed to the Girardinichthyinae. The members of these genera share the following: (1) a long dorsal fin, with 18–38 rays (31–38 in *Hubbsina*, 18–24 in *G. viviparus*, 25–31 in *G. multiradiatus*); (2) few gill rakers, 10–16; (3) a cephalic sensory system lacking developed canals or pores in the mandibular, lachrymal, preopercular, and supraorbital canals, all of which are represented solely by neuromasts. *Hubbsina* may represent the basal part of the line along which the three species evolved.

Status of *Skiffia variegata*.—This species, described by Meek (1902:104–05, pl. 25) from Lago de Zirahuén in the same paper in which he proposed the genus *Skiffia* (type, *S. lermae* Meek), was synonymized with *Skiffia lermae* (type locality, Lago de Pátzcuaro) by Regan (1907:92), an action we feel is justified at our present level of knowledge. Meristic and morphometric data overlap widely between samples from Zirahuén and the Pátzcuaro basin (UMMZ 65225, 173507; 65230, 154342, 173962; including paratypes of each). Meek (1902:104) believed that *variegata* could be distinguished from *lermae* by the absence of the black caudal bar (and other details of coloration) and in being slenderer. These characters were used by Hubbs and Turner (1939:37) who also noted a difference in the configuration of the trophotaeniae. We find the black bar at the caudal base to be variably developed, as are other features of coloration, and fail to confirm that body depth will reliably separate the two forms at the specific level. We have not examined the trophotaeniae. Further study may indicate subspecific separation, and it is conceivable that determination of karyotypes may lead to a reversal of our action.

The large amount of morphological overlap between species and the fact that they have not diverged greatly from one another to form sharply segregated groups may suggest that differentiation within the Goodeidae has occurred recently, perhaps mostly since the Pliocene. Another factor is our ignorance of the variability of the various taxa, for few of these have been studied in sufficient detail to determine limits of variation and additional species recognized in 1939 may eventually be combined (Hubbs and Turner, 1939:8), as in *Xenoophorus*. An example of dental variation is shown by our examination of the outer row of jaw teeth of 30 specimens of *Characodon lateralis*, which gave the following results: conic in

both jaws in five fish, 11–18 mm SL; upper conic and lower bifid in six, 22–36 mm long; and bifid in both jaws in 19, 36–50 mm long. Probably all adults have the outer teeth bifid in both jaws and evidently all the young have these teeth conic. However, the teeth have been described as uniformly bifid, except at the sides of the jaw (Hubbs and Turner, 1939:32, item 7j in key). Again, the outer teeth are conic (not bifid) in the young of *Chapalichthys encaustus* (20 mm or less, SL) and the inner teeth may be bifid (not only conic) in *Xenoophorus erro*. It is reasonable to believe that bifid teeth have been derived from conic ones and therefore to hypothesize that those species having forked teeth start out at birth with unicuspid teeth. *A. splendens* seems to show this only for the inner teeth, which may be conic or essentially so in newborn young, but we expect that when the embryology is known the outer jaw teeth will also be shown to begin development as unicuspid structures. Details such as this need to be worked out for many characters (including behavioral, biochemical, and cytological) before we will be in a position to form plausible hypotheses concerning the phylogeny of goodeids.

ACKNOWLEDGMENTS

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