



NUMBER 495

JUNE 12, 1946

OCCASIONAL PAPERS OF THE MUSEUM OF
ZOOLOGY

UNIVERSITY OF MICHIGAN

ANN ARBOR, MICHIGAN

UNIVERSITY OF MICHIGAN PRESS

A CONTRIBUTION TO THE TAXONOMY AND
ZOOGEOGRAPHY OF THE GOODEID FISHES

BY C. L. TURNER

THE taxonomy of the Goodeidae, a family of exclusively Mexican viviparous fishes, was thoroughly revised by Hubbs and Turner (1939). In the revision the following 4 subfamilies were set up: Ataeniobiinae, Goodeinae, Characodontinae, and Girardinichthyinae. Eighteen genera and 24 species were described. Analytical keys for both males and females were constructed, and all of the known distributional records of each species were included. A complete synonymy was presented, and outline drawings of ovarian and trophotaenial structures were introduced. De Buen (1940, 1941a, 1941b, 1941c) described a new genus, *Hubbsina*, and 2 new species, *Hubbsina turneri* and *Allotoca vivipara*. He also reviewed the classification of *Skiffia lermæ* and *Skiffia variegata* and furnished new distributional records of a number of species. In the revision of Hubbs and Turner the classification of the genus *Allodontichthys* was made with some hesitation, because females and embryos of this genus were not available for a study of the critical ovarian and trophotaenial structures.

In April, 1939, I made extensive collections in the streams of Colima, in the Río Purificación and some of its tributaries in the state of Jalisco, and in the Río Tamazula above the town

of Tuxpan. Females of *Allodontichthys zonistius* were secured and also specimens of a new species of *Allodontichthys*. A new genus and new species of the subfamily were taken in the Río Resolana, a tributary of the Río Purificación.

The present paper is intended as a brief supplement to the revision of Hubbs and Turner to present the following data and suggestions: a description of the character of the ovary and trophotaeniae of *Allodontichthys zonistius* and a correction of the taxonomic position of this genus, a description of a new species, *Allodontichthys tamazulae*, from the Tamazula River, a description of the characters of males, females, and embryos of a new genus and species, *Xenotaenia resolanae*, and some suggestions concerning the zoogeography and morphological evolution of the different genera of the subfamily Girardinichthyinae, particularly of those genera occurring outside of the plateau to the south and southwest.

CLASSIFICATION OF *Allodontichthys zonistius*

Allodontichthys zonistius was first described as *Zoonogoneticus zonistius* by Hubbs (1932) from a male specimen collected in a tributary of the Río Colima near the city of Colima. In the revision by Hubbs and Turner the new genus *Allodontichthys* was erected on the basis of certain external characters and peculiarities of the teeth, but the genus was retained in the subfamily Goodeinae because it possesses certain superficial characters common to this subfamily. The possibility that the genus might be closely related to *Balsadichthys* and *Ilyodon* was recognized. It was impossible to determine definitely the relationships of the genus because no females or embryos were available. It was stated in the revision (1939: 49) that "it would not be surprising, when females of *Allodontichthys* are obtained, to find that this genus possesses the ovarian and trophotaenial characters of the Girardinichthyinae rather than of the Goodeinae to which *Allophorus*, *Zoogoneticus*, and *Allotoca* are referred, and therefore that *Allodontichthys* may be regarded as ancestral to *Ilyodon*. Until these characters of the female and embryo are discovered, the position of *Allodontichthys* in the system will remain uncertain."

On April 2, 1939, I obtained 4 female specimens of *Allodontichthys* in the vicinity of Colima. One female which had been gravid recently, but contained no embryos, was collected in a stream tributary to the Río Tuxpan at Villa Alvarez; U.M.M.Z. No. 143020. Three mature females, 1 of which was gravid, were taken in the Río Colima about 300 yards from the Colima railway station; U.M.M.Z. No. 143021. The critical ovarian characters were observed in the nongravid females, and the diagnostic trophotaenial features were studied in the embryos dissected from the gravid female.

The study of the new material confirms the prediction of Hubbs and Turner that the genus possesses the ovarian and trophotaenial characters of the subfamily Girardinichthyinae. A cross section of the ovary (Pl. I, Fig. 1) shows that the ovary consists of a muscular wall surrounding an internal cavity which is divided by a single dorsoventral septum, except at the posterior end, and is partly filled by paired, folded masses attached to the walls of the ovary in dorsolateral positions. Oviparous tissue is confined to the folded masses. All other genera of the subfamily Girardinichthyinae possess these characters in the ovary. The trophotaeniae are much like those of *Balsadichthys*. The flattened ribbons are attached to the anal lip along the sides and posterior margin (Fig. 3). All are directed posteriorly. The ribbons are branched, and there are 9 to 13 termini. The longest trophotaeniae extend to the caudal end of the embryo.

There is a pronounced sexual dimorphism in the color markings. The females are like the males in having the part of the body above the lateral line spotted with dark brown, the scales blackened posteriorly, a black comma-shaped spot behind the opercle, and the black bars crossing the dorsal fin. All females have wide, dark, and fairly regular bars beginning well above the lateral line and extending well below the lateral line. There are 10 to 12 of these bars, the first just back of the eye and the last at the anterior end of the caudal fin. These bars are present in older females, but they are not as distinct as in younger specimens. In size there does not seem to be any

TABLE I

PROPORTIONS AND STRUCTURES IN TWO NEW SPECIES OF THE
GIRARDINICHTHYINAE AND IN CLOSELY RELATED SPECIES

The proportionate measurements and fin-ray counts for *Xenotaenia
resolanae* and *Allodontichthys tamazulae* are those of the holotypes.

	<i>Xeno- taenia resolanae</i>	<i>Allodont- ichthys tamazulae</i>	<i>Allodont- ichthys zonistius</i>	<i>Ilyodon furcoidens</i>
Total length	41 mm.	33 mm.	35 mm.	78 mm.
Length of head	12 mm.	8 mm.	8.2 mm.	16 mm.
Length of head in total length in per cent	28.8	24.2	23.4	20.5
Depth of body in total length in per cent	29.0	18.2	21.4	20.5
Predorsal length in total length in per cent	56.1	48.4	51.4	48.4
Preanal length in total length in per cent	58.5	50.2	52.7	52.8
Preventral length in total length in per cent	41.5	35.5	36.8	37.7
Length of caudal peduncle in total length in per cent	23.2	24.2	22.8	25.6
Height of caudal peduncle in total length in per cent	12.2	12.1	12.8	12.8
Width of body at opercle in total length in per cent	17.3	14.8	14.6	14.0
Length of gut in total length in per cent	85.1	66.6	70.1	141.0
Width of orbit in length of head in per cent	29.1	25.0	26.8	29.4
Interorbital distance in length of head in per cent	41.7	42.5	42.7	46.9
Gape of mouth in length of head in per cent	33.3	25.0	26.6	35.6
Length of snout in length of head in per cent	16.6	25.0	26.2	23.2
Base of dorsal in length of head in per cent	20.8	50.0	54.1	53.1
Base of anal in length of head in per cent	16.6	43.8	46.3	37.5

TABLE I—(Cont.)

	<i>Xenotaenia resolanae</i>	<i>Alloodontichthys tamazulae</i>	<i>Alloodontichthys zonistius</i>	<i>Ilyodon furcidens</i>
Base of pectoral in length of head in per cent	12.5	21.2	22.5	25.0
Base of pelvic in length of head in per cent	4.2	6.7	7.2	12.5
Scales in lateral line.....	36-40	40-43	40-43	50-54
No. of rays in dorsal fin	13	13	15	17
No. of rays in anal fin	16	15	16	14
No. of rays in pectoral fin	16	16	17	16
No. of rays in caudal fin	35	28	30	37

notable difference between males and females. For other external characteristics see Table I.

Allodontichthys tamazulae, new species

The holotype, U.M.M.Z. No. 143022, an adult female 33 mm. in total length (27 mm. in standard length) was collected on April 3, 1939, in the Río Tamazula, a tributary of the Río Tuxpan, just above the town of Tamazula, Jalisco, Mexico. Eight paratypes, 5 males and 3 females, U.M.M.Z. No. 143023, were taken with the holotype. The characters of the ovary were studied in the holotype which was mature, but, unfortunately, none of the females was gravid, and it was impossible to determine the character of the trophotaeniae. The size, body form, and other external characters, except for the coloration (Table I), indicate that the specimens belong to the genus *Allodontichthys*, and the characters of the teeth are decisively diagnostic. The species is named for the town of Tamazula.

In general the coloration of *A. tamazulae* is much lighter than that of *A. zonistius*, and the entire portion above the lateral line is more lightly mottled with dark brown. About 12 heavy, dark, vertical bars extend in the females of *A. zonistius*

from well above the lateral line to well below the lateral line, and a black comma-shaped patch is present just back of the pectoral fin. In *A. tamazulae* there are 18 to 22 very short dark bars along the lateral line. Only in the part anterior to the dorsal fin and behind the head is there any considerable extension of the bars below the lateral line. In this area 7 to 10 irregular bars extend downward upon the belly. The comma-shaped patch behind the pectoral fin is present in *A. tamazulae*, but is much lighter than it is in *A. zonistiuis*. Three light vertical bars occur upon the caudal fin in *A. tamazulae*. There are none in *A. zonistiuis*. All males are more heavily marked than the females, particularly in the vertical bars below the lateral line upon the belly.

The teeth of *A. tamazulae* resemble those of *A. zonistiuis* in being conical and shouldered instead of bifid. In *A. zonistiuis* there are 16 teeth in the main row of the upper jaw and 20 in the lower jaw. The teeth are long, fairly sharp, and firmly set in the jaws in a single, curved row, with smaller conical teeth forming a second irregular row behind. In *A. tamazulae* the teeth are definitely conical and shouldered, but they are shorter and more blunt than they are in *A. zonistiuis*. In both the upper and lower jaws there are 12 teeth in the main row. The teeth are crowded and somewhat uneven, but they are not in alternating rows. Only the middle half of each jaw is occupied, leaving the lateral part of each jaw toothless. In both jaws there is a second row of small, conical teeth, irregular in position and loosely set in the jaws. The teeth of this second row are larger than are those in *A. zonistiuis*.

The gut in both *A. zonistiuis* and *A. tamazulae* is two-thirds to three-fourths of the total body length. A carnivorous habit is indicated by the short gut and by the presence in the gut of some large (5 mm.) insect larvae.

Xenotaenia, new genus

Genotype, *Xenotaenia resolanae*, new species.

The genus *Xenotaenia* is distinguished from other genera of the Girardinichthyinae by a number of well-defined characters.

The trophotaeniae are in the form of a flattened rosette (Pl. I, Fig. 4) with 2 wide processes emerging from the posterior lip of the anus and a truncated mass attached to the anterior lip. The 2 posterior extensions are short and extend only to the posterior end of the anal fin of an embryo. All of the flattened processes have numerous small, bulbous masses upon the dorsal and ventral surfaces and the lateral margins. Since these trophotaeniae are unlike any others in the subfamily, the genus is named for the character.

Other distinguishing features of the genus are: (1) the great length and breadth of the head in relation to the total body length, 28.8 per cent (Table I), (2) the short and weak dorsal and anal fins, (3) the small number of scales in the lateral line, 36 to 40, (4) the small number of bifid teeth in the main row of the upper and lower jaws.

Xenotaenia resolanae, new species

The holotype of this species is a female 41 mm. in total length (34 mm. in standard length) taken in the Río Resolana, a tributary of the Río Purificación about 25 miles southwest of the town of Autlan in the state of Jalisco, Mexico, on March 29, 1939; U.M.M.Z. No. 143024. Two paratypes, a second and smaller female and a mature male, were taken in the same locality; U.M.M.Z. No. 143025. The holotype was gravid, and the character of the trophotaeniae was determined from embryos contained in her ovary.

Most of the measurements and numbers of rays in the fins are listed in Table I, together with those of *Ilyodon furcoides* and of the 2 species of *Allodontichthys* for comparison.

It will be noted that the head is unusually long in proportion to the total length and that the caudal peduncle differs little from the other species in proportion to the length. These facts taken together indicate that the region of the body between the posterior end of the head and the anterior end of the caudal peduncle is much shorter than it is in other species. The predorsal and the preanal lengths are greater than in other species because of the relatively greater length of the

head in *Xenotaenia resolanae*. The height of the body in relation to the total length is much greater than in other species. The interorbital distance in relation to the length of the head is about the same as in *Allodontichthys*, but not as great as it is in *Ilyodon*. The head is thick, and though it becomes narrower anteriorly, it is not as pointed as it is in *Allodontichthys* nor as bluntly rounded as it is in *Ilyodon*. The snout is short, and the eye is relatively large. The gape of the mouth is relatively narrower than is that of *Ilyodon* and wider than is that of *Allodontichthys*.

All fins except the caudal are short and weak. The dorsal and the anal fins are set well back upon the body. The caudal fin is relatively high and contains fewer rays than does that of *Ilyodon* and more than does that of *Allodontichthys*.

There are 36 to 40 rows of scales on the lateral line of *X. resolanae*, considerably fewer than in *Allodontichthys* and many fewer than in *Ilyodon*.

The teeth are arranged in both jaws in an anterior row with several scattered rows behind. The teeth of the anterior (main) row are large, strong, bifid, and firmly set in the jaws. The gut is relatively short, about 85 per cent of the total body length. As in *Allodontichthys* the short gut is indicative of a carnivorous habit in contrast to the omnivorous food habit of *Ilyodon*, in which the gut is much longer than is the body.

The swollen area in the male between the anus and the genital pore is rather flat and is as wide as it is long. There is no extension of the swollen area upon the thin membrane which envelops the bases of the anterior rays of the anal fin. This backward extension of the swollen area is characteristic of the males of *Ilyodon*. The first 6 rays of the anal fin in the male are only slightly differentiated from the other rays of the anal fin in contrast to the condition in some other species of the Girardinichthyinae in which the first 6 rays are well separated from the other rays in the form of a lobe and are much shorter. In *X. resolanae* the margin of the fin is only slightly indented between the anterior and posterior parts of the fin, and the longest rays of the anterior group of 6 rays are 80 per cent as long as the longest ray of the posterior group.

In color, specimens of *X. resolanae* are much lighter than are those of *Ilyodon* or *Allodontichthys zonistius*. In younger specimens the posterior halves of the scales are darkened by brown and black pigment cells above the lateral line for the entire length of the body and in the belly region for some distance. Along the lateral line there are about 15 irregular patches. In older specimens these dark patches along the lateral line often become broken up or disappear, whereas the markings upon the individual scales dorsal to the lateral line become more conspicuous. There are 3 irregular, vertical brownish bars on the caudal fin. The posterior margin of the dorsal fin is edged sparsely with light brown.

ZOOGEOGRAPHY AND MORPHOLOGICAL EVOLUTION OF THE GENERA OF THE SUBFAMILY GIRARDINICHTHYINAE

A survey of the geographical distribution of the genera and species of the subfamily Girardinichthyinae and of the morphological differentiation in each brings one to the conclusion that there has been an ancient division in the subfamily and that the members of the 2 divisions have differentiated along somewhat different lines. The geographical barrier between the groups is the mountain range extending in an east-west axis from Mount Popocatepetl to Mount Colima. The evidence points to the region of Colima as the one in which the subfamily originated. After the origin of the subfamily, presumably there was some dispersal so that the range was increased. Some differentiation would have accompanied the dispersal. With the throwing up of the mountainous barrier, there was a separation of the group into that part of the subfamily included in the plateau and the other part excluded from the plateau and occurring south of the barrier. The part included within the plateau increased its range to the north and east, and at the same time new genera arose. The group excluded from the plateau and remaining in the Colima region increased its range in part by emigration up the coast to the northwest, northward up the rivers to the southern edge of the plateau and eastward and southeastward up the

Río Balsas to its headwaters. Those genera outside of the plateau usually retained primitive characters, whereas those within the plateau usually have become more differentiated.

The hypothetical ancestral form would have had viviparity already established. The ovary would have had the characteristic features of the subfamily, and the trophotaeniae of the embryos would have been finger- or ribbon-shaped, rather numerous and rather long. There would have been little sex differentiation in size or color, and in the male the anal fin would have been only slightly changed from the condition in the female in the direction of the extreme lobation and shortening of the 6 anterior rays present in some species within the plateau. The teeth would have been conical, at least not bifid, fairly few in number, and arranged in one or more complete rows.

The living species which most nearly resembles the ancestral form is *Allodontichthys zonistiis*. This species qualifies in all regards except for sex dimorphism in color. *Allodontichthys tamazulae* has emigrated northward from the ancestral site, going up the Río Tuxpan, but it has not yet passed the mountain barrier so as to reach the plateau. This species has changed somewhat in color markings, but in general it has retained the primitive characters of the ancestor, including the lack of sex dimorphism in color. There have been some changes in the teeth. The conical shape has been retained, but the number of teeth in the first row has been reduced by the dropping out of teeth at the outer margins of the jaws.

Balsadichthys xanthus and *Ilyodon furcidens* probably arose from the ancestral form while still in the Colima region. These 2 species hybridize readily, and it is likely that there was a common ancestor for them in fairly recent times. In producing these species the ancestral form would have developed a larger size, a bifid condition of the teeth, and in the male a reduction of the first 6 rays of the anal fin together with a greater thickening of the swollen region between the anus and the genital pore and of the membrane enveloping the bases of the first 6 rays of the anal fin. In *Balsadichthys* there has

been an increase in the number of teeth by the formation of a second main row, the teeth of which alternate roughly with those of the first main row. Both genera have increased their ranges so that they are present now not only in the Colima region in which they originated but also to the north in the upper Río Tamazula. *Balsadichthys* has emigrated also to the east and the southeast using the Río Balsas as a highway, and during the emigration it has given rise to the new species *Balsadichthys whitei*. This species is present in the headwaters of the Río Balsas at Cuautla and Yautepec southeast of Mexico City and at Tlapa in the eastern part of the state of Guerrero. *Xenotaenia resolanae* has arisen from another stock of the ancestral form during its emigration from the ancestral site northwestward up the coast. Few of the streams in this region have been explored, and it is likely that other species will be found. *Xenotaenia* has changed from the ancestral form in some important structures, but in some other characters it is very primitive. It has developed strong bifid teeth, suggesting that it has arisen from a stock closely related to the one which gave rise to *Ilyodon* and *Balsadichthys*. This, however, may have been an instance of independent and parallel evolution. The head has become longer and wider and the body deeper than they are in the ancestral form. The body color has become generally lighter. The trophotaeniae are shorter and fewer, and the membrane connecting them to the anal lip has become wider. It has retained a more primitive type of male anal fin than has any other species, and in this respect it probably resembles the ancestor closely.

The division of the subfamily which was cut off within the plateau, while retaining the basic characters of the subfamily, has become divided into 2 main stocks identified by the character of the trophotaeniae. One stock, including *Skiffia*, *Ollentodon*, and *Neotoca*, has 3 long posteriorly directed trophotaeniae, whereas the other, including *Lermichthys* and *Girardinichthys*, has a short pair anterior to the anus and a longer pair posterior to the anus. The first group has become differentiated in sexual dimorphism in size and color, the

climax being reached in *Neotoca*. Shortening of the first 6 rays of the anal fin of the male has become most extreme in *Skiffia*. *Lermichthys* and *Girardinichthys* probably represent geographically isolated genera which arose from a common ancestor no longer living. The withdrawal of water from the Mexican and Toluca basins has probably destroyed an old communication between the basins, and each of the isolated genera has evolved independently. In *Lermichthys* a very long dorsal fin has developed as the most conspicuous external feature. In *Girardinichthys* extreme sexual dimorphism in color has developed, and in the male there has arisen a thick straplike muscle just beneath the skin and lying in a vertical position, attached to the bases of the anterior rays of the dorsal and anal fins.

To recapitulate, it is assumed that the subfamily Girardinichthyinae originated in the Colima region and after a period of dispersal the members of the subfamily were divided into 2 groups by the rise of the mountain range on the southern edge of the plateau. Those excluded from the plateau increased their range by extensions up the Pacific coast to the northwest, up the Río Tuxpan to the northward and up the Río Balsas to the east. The genera *Balsadichthys*, *Allodontichthys*, *Ilyodon*, and *Xenotaenia* are the living representatives of this subdivision. The subdivision which was included within the plateau at its southwestern corner became divided into 2 stocks, each of which spread to the north and east through the waters of the plateau and in some instances became isolated within relatively small ranges by physiographic changes in the plateau. One of the stocks is represented at present by the genera *Lermichthys* and *Girardinichthys* and the other by *Skiffia*, *Ollentodon*, and *Neotoca*.

REFERENCES

BUEN, FERNANDO DE

- 1940 Sobre una coleccion de peces do los Lagos de Pátzcuaro y Cuitzeo. *Ciencia*, 7: 306-8.
- 1941a Uno nuevo genero de la familia Goodeidae perteneciente a la fauna ictiológica mexicana. *Sobr. Anal. Escuel. Nac. Cienc. Biol.*, 2, numo. 2-3: 133-40.

1941*b* Notas sobre ictología de aguas dulces de Mexico. II Adiciones a la lista de peces. Invest. Est. Limn. Pátzcuaro, 5: 1-8.

1941*c* Contribucion al estudio de la ictología mexicana. Trab. Est. Limn. Pátzcuaro, 4: 1-31.

HUBBS, CARL L.

1932 Studies of the Fishes of the Order Cyprinodontes. XI. *Zoogoneticus zonistius*, a New Species from Colima, Mexico. Copeia, 2: 68-71.

HUBBS, CARL L., and TURNER, C. L.

1939 Studies of the Fishes of the Order Cyprinodontes. XVI. A Revision of the Goodeidae. Misc. Publ. Mus. Zool. Univ. Mich., 42: 1-80.

PLATE I

- FIG. 1. Diagrammatic cross section of ovary of *Alloodontichthys zonistius*.
O. C., ovarian cavity.
O. S., ovarian septum.
OV. T., ovigerous tissue.
- FIG. 2. Diagrammatic cross section of ovary of *Xenotaenia resolanae*.
Abbreviations as in Fig. 1.
- FIG. 3. Trophotaeniae of *Alloodontichthys zonistius*.
- FIG. 4. Trophotaeniae of *Xenotaenia resolanae*.



