issued

by the

SMITHSONIAN INSTITUTION
U. S. NATIONAL MUSEUM

Vol. 100

Washington : 1950

No. 3267

A REVIEW OF THE AMERICAN CLUPEID FISHES OF THE GENUS *DOROSOMA*

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THE clupeid fishes of the genus *Dorosoma* Rafinesque, or gizzard shads, range from Nebraska, Minnesota, and the Great Lakes-St. Lawrence River drainages, and from about latitude 40° on the Atlantic seaboard of New Jersey and Pennsylvania, southward along the mainland of North America to Nicaragua, with a single representative in the Pacific drainage of northwestern Mexico. They comprise four known species: *D. cepedianum*, of Canada, Eastern United States, and northeastern Mexico; *D. anale*, of southeastern Mexico and northern Guatemala; *D. chavesi*, of the Great Lakes of Nicaragua; and *D. smithi*, of Sonora and Sinaloa, northwestern Mexico.

The gizzard shads are essentially fresh-water fishes, although *D. cepedianum* frequents brackish water and, rarely, salt water. They receive their common name from the short, muscular stomach, which resembles the gizzard of a fowl. Their feeding habits are correlated with this structure and with the extremely fine gill rakers, the long, convoluted small intestine, and the accessory pharyngeal pockets. Although held in low regard as a food fish, *Dorosoma* serves admirably in nature by utilizing food derived largely from muddy bottoms and thereby converting this waste material into a food supply for game fishes. Its value in this respect, however, appears to be limited largely to the young stages (Lagler and Applegate, 1943).

The present study was undertaken to determine the more precise systematic characters and variation within the genus, to provide preliminary data on changes with growth, and to cast further light upon the origin and relationships of the species. All the type material of the three southern species (*anale*, *chavesi*, and *smithi*) was carefully

reexamined. Eleven counts were made on all the species and, in addition, 24 proportional measurements were made on each of the three southern species. Material for an adequate study of body proportions in *D. cepedianum* was not available, but preliminary study demonstrated that the so-called slender subspecies, *D. c. exile* (Jordan and Gilbert, 1883), described from Texas, cannot be reliably distinguished on the basis of body depth.

In examining the number of scales and vertebrae in *Dorosoma* I found a negative correlation. The scale numbers of the southern species are greatly increased, whereas the vertebrae show a significant decrease. Thus *D. cepedianum*, with 52 to 70 scales in the lateral series, has 48 to 51 vertebrae, whereas the three southern species, with 70 to 83 scales, have only 43 to 48 vertebrae (tables 3 and 4). Study of much new material of the Pacific species, *Dorosoma smithi*, has demonstrated that the number of anal rays increases from north to south (table 9), a gradient reversed from the usual variation in fishes.

The following abbreviations are used in this paper: C.N.H.M.=Chicago Natural History Museum; S.N.H.M.=Stanford Natural History Museum; U.M.M.Z.=University of Michigan Museum of Zoology; and U.S.N.M.=United States National Museum.

METHODS OF COUNTING AND MEASURING

In counting the fin rays I have followed the procedure recommended by Hubbs and Lagler (1947, pp. 9-10). The count for the dorsal and anal rays is of the principal rays, the branched rays plus one unbranched ray. This unbranched ray is usually the first ray reaching to or near the tip of the fin. In advance of this ray are three, occasionally two, rudimentary rays in the dorsal fin and two, rarely one, in the anal fin. Occasionally the higher variant for the number of dorsal rays is combined with the lower number (2) of rudimentary rays; thus the third ray (usually a rudiment) is elongated to become the first full-length unbranched ray. The last ray of the dorsal and anal fins was always regarded as split to the base and counted as one ray. In the caudal fin the count was made of the principal rays, which are the branched rays plus two. All rays of both pectoral and pelvic fins were counted.

In the enumeration of the scales of the lateral series, the first scale counted was the first one lying above the uppermost corner of the gill opening. With the exception of the scales along the throat region, this is the anteriormost scale on the body. By this method my counts are somewhat greater than those usually given for *Dorosoma*, but I believe that a more precise enumeration was obtained. The number of scales between the dorsal and anal fins was counted along an oblique line joining the origins of these fins. The scale count around

the body began with the first scale just in front of the base of the left pelvic fin, counting upward in zigzag fashion over the back and down the right side over the belly to the starting point. The scale number around the peduncle was also made in zigzag fashion around the slenderest part.

The count of ventral scutes was divided into two parts, prepelvic and postpelvic. The tip of the last prepelvic scute counted extended to or close to the insertion of the pelvics. Thus my counts are in agreement with those of most workers except Hubbs and Miller (1941), who regarded the last prepelvic scute as always extending beyond the pelvic insertions. Their prepelvic counts should therefore be decreased by one and their postpelvic counts increased by one (e. g., $19+11=18+12$) to agree with general practice. In enumerating the vertebrae, the hypural was always included. Whenever any count was in doubt, the maximum possible figure was always recorded.

In measuring head length I always included the opercular membrane. Head depth was measured vertically over the posterior end of the isthmus. The dorsal filament was measured from its tip to the posterior face of its contact with the back.

THE GENERA DOROSOMA AND SIGNALOSA

Jordan and Evermann (1896–1898, pp. 415, 2809–2810) and others placed the closely related genera *Dorosoma* and *Signalosa* in a separate family, the Dorosomidae (more properly, the Dorosomatidae). Later students, adopting a more conservative view, generally have referred these genera and their Old World relatives, *Nematalosa*, *Gonialosa*, *Anodontostoma*, *Konosirus*, and *Clupanodon*, to the Clupeidae.¹ The describers of *Signalosa*, Evermann and Kendall (1898, p. 127), also referred that genus to the Clupeidae, and in the most recent general classification of fishes by Berg (1940, p. 421) *Dorosoma* and its allies are given subfamily recognition only.

The generic status of *Dorosoma* has been reviewed recently in detail by Hubbs and Miller (1941, pp. 233–234). In addition to structural characters that differentiate *Dorosoma* and *Signalosa*, I now find that *Signalosa* has only 40 to 45 vertebrae, in contrast to 43 to 51 in *Dorosoma* (table 1). In the areas where the two genera are known to occur together, from Florida to northern Guatemala, the vertebral counts do not overlap. The fewer vertebrae were briefly noted by Regan (1917, p. 310) who gave 41 as the number in *Signalosa*. Thus the New World Dorosomatinae have 40 to 51 vertebrae, rather than 49 as stated by Jordan and Evermann (1896, p. 415).

Despite the review of *Signalosa* by Weed (1925), the members of this genus are still in need of clarification, as Gunter (1945, p. 31) has

¹ Among recent writers, Fowler (1945, p. 22) retained family recognition (Dorosomidae) for *Dorosoma* and *Signalosa*.

TABLE 1.—*Comparison of Dorosoma and Signalosa*

Character	<i>Dorosoma</i>	<i>Signalosa</i>
Mouth.....	Subterminal or inferior.	Terminal.
Ventral edge of upper jaw.....	With slight to pronounced notch.	Smooth.
Scales.....	More than 50 in lateral series, irregularly arranged.	Less than 50 in lateral series, regularly arranged.
Vertebrae.....	43 to 51 (47 to 51 where range overlaps that of <i>Signalosa</i>).	40 to 45. ¹
Anal rays.....	22 to 38, usually 29 to 35 (where range overlaps that of <i>Signalosa</i>).	17 to 27, usually 20 to 25.
Ventral scutes.....	Usually 17 to 18 + 10 to 12 (but only 16 + 11 or 17 + 11 in the Pacific species).	Usually 16 + 11 or 16 + 12 (or generally fewer prepelvic scutes). ²
Distribution.....	Atlantic and Pacific (Canada to Nicaragua; northwestern Mexico).	Atlantic (Florida to northern Guatemala and British Honduras).

¹ Counts based on 30 specimens in the U. S. National Museum as follows: Florida (2), Arkansas (2),¹ Alabama (1), Louisiana (4, one a cotype of *S. atchafalayae*, U.S.N.M. No. 48971), Tampico, Mexico (6), near Veracruz, Mexico (5), and Lake Petén, Guatemala (10, topotypes of *S. petenensis*).

² Where the two genera coexist, *Dorosoma* has 17 to 20 and *Signalosa* 14 to 17 (rarely 17) prepelvic scutes. The counts of anal rays and ventral scutes for *Signalosa* are based on 186 specimens from Florida to Lake Petén, Guatemala, all deposited in the U. S. National Museum.

recently emphasized. Part of the difficulty has been the lack of adequate material, particularly from Guatemala and Mexico.² Thus in the major division of his key, based on the number of abdominal scutes, Weed (1925, pp. 141–142) had to rely upon the published descriptions of *S. petenensis*, with the result that he widely separated *petenensis* and *atchafalayae*. An examination of 52 topotypes of *petenensis* from Lake Petén, Guatemala (U.S.N.M. No. 132269), demonstrates that, in this character at least, there is virtually no difference between these species. The total number of abdominal scutes in this sample varied from 26 to 29, and in 68 specimens in the National Museum from Louisiana to Florida (the range given by Weed for *atchafalayae*) the number varied from 25 to 29. Material from Mexico, however, shows far fewer scutes. In 38 specimens from El Hule = Papaloapán (U.S.N.M. No. 55739), Lake Catemaco (U.S.N.M. No. 48213), and Tampico (U.S.N.M. No. 62271) the scutes varied from 23 to 26, which agrees closely with the variation of 20 to 27 given by Weed (1925, p. 143) for his Mexican material (including a sample from Brownsville, Tex.). On the basis of this character, *S. mexicana* (Günther) appears to be very distinct from both *atchafalayae* and *petenensis*, but Hubbs, after study of much material, recognized (in Hubbs and Allen, 1943, p. 116) only a single species, *petenensis*. Fowler (1945, pp. 22, 266, 366, 372), without presenting data, followed Hubbs and Allen. A thorough revision is obviously needed.

² Fowler's record (1911, p. 211) of "*Dorosoma petenensis*" from Panama obviously represents an erroneous locality. *Signalosa* is not known to occur south of northern Guatemala and British Honduras (Río Belize; uncataloged material at U.M.M.Z.).

The characters used to distinguish *Dorosoma* and *Signalosa* are summarized in table 1.

The only other New World clupeid likely to be confused with either *Dorosoma* or *Signalosa* is the wholly marine genus *Opisthonema*. *Signalosa* appears to be more marine in its habitat preference than *Dorosoma*, but even so it would probably only rarely occur with *Opisthonema*. In all three genera the last ray of the dorsal fin is prolonged into a prominent filament. Beyond this the resemblance is not great, but a further comparison seems desirable. Some of the following characters were worked out in collaboration with the late Dr. S. F. Hildebrand while he was studying the Western Atlantic Clupeidae, exclusive of the gizzard shads. *Opisthonema* differs from both *Dorosoma* and *Signalosa* in having (1) the ridge of the back anterior to dorsal origin crossed by scales rather than naked; (2) a bilobed, dermal fold on the vertical anterior edge of the cleithrum; (3) a weak development of the paired pharyngeal pockets (Lagler and Kraatz, 1945) found above the branchial cavity of the gizzard shads; (4) a broader upper jaw, so that the maximum width near the distal portion is greater than (rather than less than) the diameter of the pupil; (5) no axillary scale, the pectoral fins folding into a groove; (6) the opercle and subopercle elongated and narrowed so that the maximum width of either bone enters the length of the opercle 1.6–2.4 (rather than 1.1 to 1.5, rarely 1.6) times; (7) the dorsal origin well in advance of the pelvic insertion (over or well behind in *Dorosoma*, very slightly in advance to behind in *Signalosa*); and (8) the gizzard is smaller and more elliptical. Atlantic material of *Opisthonema* was examined from North Carolina to Brazil, including Bermuda, the West Indies, and Panama; Pacific specimens studied came from Mazatlán to Peru, including the Galápagos Islands.

The following key will serve as a convenient means of rapid determination of the species of *Dorosoma*. Greater detail is given under the separate treatment of each species and in the tables.

KEY TO THE SPECIES OF *DOROSOMA*

- 1a. Lateral scales 52 to 70, usually 58 to 65; scales around body 36 to 45; vertebrae 48 to 51. Atlantic drainage of eastern North America south to Río Pánuco Basin, Mexico.....*cepedianum*
- 1b. Lateral scales 70 to 83, usually 73 to 78; scales around body 46 to 60; vertebrae 43 to 48.....2
- 2a. Dorsal filament long, its length as measured from dorsal origin 0.95 to 1.4, usually 1.1 to 1.3, in distance from pelvic insertion to tip of snout; anal base 1.1 to 1.4 in same distance; anal rays 29 to 38, usually 32 to 35. Atlantic slope of Mexico and northern Guatemala (Río Papaloapán to Río Usumacinta).....*anale*
- 2b. Dorsal filament short, its length as measured from dorsal origin 1.4 to 1.85, usually 1.5 to 1.8, in distance from pelvic insertion to tip of snout; anal base 1.6 to 2.2 in same distance; anal rays 22 to 31, usually 23 to 29...3

- 3a. Mandible long, nearly 1/2 length of head; scales around caudal peduncle 20 to 26; dorsal rays usually 13 (12-14). Atlantic drainage of Lakes Managua and Nicaragua, Nicaragua-----chavesi
- 3b. Mandible short, less than 1/3 length of head; scales around caudal peduncle 28 to 31; dorsal rays usually 11 or 12 (9-13, rarely 9, 10 or 13). Pacific slope of northwestern Mexico (Sonora and Sinaloa)----smithi

DOROSOMA CEPEDIANUM (LeSueur)

Megalops cepediana LESUEUR, 1818, pp. 361-363 (original description).

This wide-ranging species is a common inhabitant of the fresh and brackish waters of eastern North America. According to a recent study by Gunter (1945, pp. 30-31 and table 74), it spawns in fresh water, and often frequents brackish water, but only rarely enters the sea.

Diagnosis.—A *Dorosoma* with 48 to 51 (usually 50) vertebrae,³ 52 to 70 lateral scales, 36 to 45 scales around the body, usually 12 dorsal rays, 25 to 36 (usually 29 to 34) anal rays, preponderantly 18+12 ventral scutes, and with a long dorsal filament.

TABLE 2.—Fin-ray counts in four species of *Dorosoma*

[The figures in the first line for each count are the observed range and, in parentheses, the mean; the figure in the second line represents the number of specimens]

Species	Number of fin rays		
	Dorsal rays	Pectoral rays	Anal rays
cephedianum-----	{ 10-13 (11. 61) 197	{ 14-17 (15. 52) 288	{ 25-36 (31. 32) 195
anale-----	{ 10-13 (11. 25) 71	{ 14-16 (14. 97) 112	{ 29-38 (33. 34) 71
chavesi-----	{ 12-14 (12. 91) 35	{ 14-16 (15. 04) 72	{ 24-31 (27. 14) 35
smithi-----	{ 9-13 (11. 45) 185	{ 12-16 (14. 55) 319	{ 22-29 (25. 38) 185

Variation.—Counts of fin rays, scales, and ventral scutes were made on 51 to 200 specimens distributed from Michigan and Maryland southward and westward to Tamaulipas, San Luis Potosí, and Querétaro, Mexico (tables 2-4). There seems to be no correlation between the counts and geographic regions, but the material examined was so widely scattered and the number from any one locality so few (maximum 9, usually 2 to 5) that potential gradients may have been masked. A thorough study of variation in this species is needed.

As in the other species of the genus, the length of the dorsal filament varies greatly with age (see section on "Changes with Growth"). Statements regarding this structure are therefore meaningless unless accompanied by data on the size of the specimen.

³ In response to my query, Dr. Vladikov wrote that the number of vertebrae he recorded (1945, p. 35) for this species was a typographical error and should have read 51 (29+22).

Since 21 counts of the caudal rays were invariably 19, and 23 counts of the pelvic rays were 8-8 (with two exceptions, both 7-8), no further examination of these fins was made. As shown below, 19 caudal and 8 pelvic rays predominate in *Dorosoma*, and therefore counts of these fins are of no systematic value for distinguishing the species of this genus.

The possibility that examples of the southernmost populations of *D. cepedianum* from Mexico might more closely approach its nearest representative, *D. anale*, was dispelled by an examination of four specimens of *cepedianum* from the Río Pánuco Basin, Mexico, just to the north of the range of *anale*. Two of these fish were from Río Valles at Valles, San Luis Potosí (C.N.H.M. No. 4497); one was from Río Forlón at Forlón, Tamaulipas (C.N.H.M. No. 4481); and the fourth was from Río San Juan at San Juan del Río, Querétaro (S.N.H.M. No. 31996). All were recorded by Meek (1904, p. 94) as *D. exile*. The following critical counts on these specimens are typical of *cepedianum*: Lateral scales, 58, 60, 65?, 58; scales from dorsal to anal, 22, 23, 21, 20; scales around body, 41, 40, 41?, 40; scales around peduncle, 16, 18, missing, 16; ventral scutes, 18+12, 17+12, 18+12, 17+11; vertebrae 50 (Forlón specimen).

TABLE 3.—Number of scales in four species of *Dorosoma*

[The figures in the first line for each count are the observed range and, in parentheses, the mean; the figure in the second line represents the number of specimens]

Species	Number of scales			
	Lateral series	Dorsal to anal	Around body	Around caudal peduncle
<i>cepedianum</i>	{ 52-70 (61.06) 67	{ 19-24 (21.77) 52	{ 36-45 (41.03) 73	{ 16-20 (18.02) 53
<i>anale</i>	{ 70-82 (75.84) 32	{ 27-33 (29.76) 29	{ 46-54 (50.45) 29	{ 21-28 (23.90) 21
<i>chavesi</i>	{ 72-83 (77.33) 24	{ 28-33 (29.77) 22	{ 48-58 (52.93) 27	{ 20-26 (23.39) 23
<i>smithi</i>	{ 71-79 (74.61) 36	{ 28-35 (31.15) 47	{ 50-60 (55.23) 48	{ 28-31 (29.47) 19

The apparent uniformity in the meristic characters of *cepedianum* over such a vast range should not be accepted on the basis of the present data but should be thoroughly tested. No doubt Regan (1917, p. 311) correctly assigned Meek's material (identified as *D. exile*) to *cepedianum*, but whether *exile* is a valid subspecies of *cepedianum* has not been determined conclusively.⁴ Fowler (1945, pp. 22, 365-366), presenting data on body depth only for scanty material from

⁴ I have been unable to locate the types (two specimens) of *D. c. exile* Jordan and Gilbert (1882, p. 248; 1883, p. 585), which bear U.S.N.M. No. 30913. The catalog book records that they were "Distributed," that is, sent out to some institution.

South Carolina, Tennessee, and Louisiana, accorded *exile* subspecific status. My examination of 25 specimens (56 to 196 mm. in standard length) from Texas (none from Galveston, type locality of *exile*) and of 26 (61 to 211 mm. in standard length) taken at random from Maryland south to North Carolina gave the following ratios (of greatest body depth to standard length): Texas—2.45 to 2.9 (avg. 2.72); Maryland to North Carolina—2.3 to 2.95 (avg. 2.65).

These preliminary data indicate that body depth is very variable in *D. cepedianum* and that *exile* cannot be subspecifically distinguished on this basis. I did find that large adults from Atlantic-slope waters definitely tend to be deeper-bodied than do those from Texas waters—perhaps a racial characteristic. The proportionate length of the head and of the caudal peduncle in these specimens gave similarly variable results. Careful measurements of many individuals of various sizes from the entire range of *cepedianum* is obviously required before deciding if subspecies are to be recognized.

TABLE 4.—*Number of ventral scutes and vertebrae in four species of Dorosoma*
[The figures in the first line for each count are the observed range and, in parentheses, the mean; the figure in the second line represents the number of specimens]

Species	Number of scutes			Number of vertebrae
	Prepelvic	Postpelvic	Total	
<i>cepedianum</i>	{ 17-20 (17.99) 196	{ 10-14 (11.76) 197	{ 27-32 (29.74) 196	{ 48-51 (49.83) 42
<i>anale</i>	{ 17-20 (17.96) 71	{ 9-12 (10.23) 71	{ 26-31 (28.18) 71	{ 46-48 (46.91) 22
<i>chavesi</i>	{ 15-18 (16.91) 35	{ 10-12 (10.58) 36	{ 25-29 (27.51) 35	{ 44-47 (46.13) 15
<i>smithi</i>	{ 15-18 (16.84) 185	{ 9-12 (10.87) 185	{ 26-30 (27.71) 185	{ 43-47 (44.71) 34

Material examined.—In determining the range of variation in meristic characters for *D. cepedianum*, I used the data published by Hubbs and Miller (1941, p. 234, table 1) and in addition examined many collections of this species deposited in the U. S. National Museum. These included 33 specimens from 6 localities on the Atlantic Slope (Potomac River to Orlando, Fla.); 33 from 10 localities along the Gulf of Mexico (Florida to Texas); and 35 from 13 localities in the basins of the Mississippi Valley and the Great Lakes. Critical material from northeastern Mexico was examined both at Michigan and at Washington. In recording the number of vertebrae, I included the 26 specimens counted by Hubbs and Whitlock (1929, p. 463).

Range.—From Nebraska and Minnesota to the St. Lawrence River and the Ohio Valley in western Pennsylvania; south to the Gulf of Mexico and to the Río Pánuco Basin of eastern Mexico; coastwise northward to about latitude 40° N. in New Jersey and eastern Penn-

sylvania and rarely to Sandy Hook Bay, N. J. (Breder, 1933, pp. 23 and 28; Breder and Nigrelli, 1934, p. 194; Hubbs and Lagler, 1947, p. 34; and Vladykov, 1945, pp. 35-37; 1947, p. 201). I recently found a specimen of this species (U. S. N. M. No. 131346) collected by S. E. Meek in the fall of 1908 from Lake of the Woods, western Ontario, Canada. This may represent an introduction, or perhaps a misplaced specimen, for during the history of the extensive fisheries on that lake no further specimens of gizzard shad have been collected (Carlander, 1948).

The presence of *Dorosoma* in the Great Lakes-St. Lawrence Basin may have resulted from its transfer from the Mississippi Basin during the glacial or postglacial history of the region. Gerking (1945, p. 33) has suggested that the gizzard shad may have entered the Glacial Great Lakes during the Lake Maumee outlet stage. Vladykov (1945, p. 37) firmly believed that the presence of *D. cepedianum* in the St. Lawrence River resulted from its entrance by way of the Great Lakes rather than by migration up the St. Lawrence. The view that the gizzard shad entered the Great Lakes via canal connections seems now to be generally discounted, but I do not feel that this possibility should be eliminated entirely from consideration.⁵ Kirtland (1850, p. 2) definitely stated, "It has become evident that the species has found its way into the Lake [Erie] through either the Dayton and Maumee or the main Ohio canals, probably thro' the former, and it is likely from its prolificness that before many years it will become one of our most abundant fishes." Kirtland was impressed with the fact that fishermen had not recognized the gizzard shad in the vicinity of Cincinnati much before 1840 and that they considered it to be an emigrant from the south. Kirtland was perhaps overimpressed by the death of large numbers of *D. cepedianum* during a hard freeze in the Dayton Canal, for he cited this as supporting evidence for the supposition that the species "was a native of a warmer climate." He was very sure, however, that the species did not occur in the Lake Erie Basin in 1840. He wrote further, "In November 1848 four were taken near the mouth of the Cuyahoga, and brought to me as a curiosity by one familiar with the Lake fishes. In the course of the same month of the present year [1850], some thirty or forty specimens were caught in this vicinity by the same fisherman."

DOROSOMA ANALE Meek

Dorosoma anale MEEK, 1904, p. 93, fig. 26 (original description; type locality, El Hule=Papaloapán, Oaxaca, Mexico).

This close relative of *D. cepedianum* replaces that species in southern Veracruz, Mexico. To my knowledge it has been taken only in fresh water.

⁵ See also Radforth (1945, p. 58).

Diagnosis.—A *Dorosoma* with 46 to 48 vertebrae, 70 to 82 lateral scales, 46 to 54 scales around the body, 10 to 13 (most frequently 11) dorsal rays, 29 to 38 anal rays, usually 18+10 or 18+11 ventral scutes, and with a long dorsal filament.

Relationships.—*D. anale* differs from *cepedianum* principally in having smaller scales and fewer vertebrae (tables 3 and 4) and in the ratio of the length of the anal fin base to the distance between the pelvic insertion and the tip of the snout. This ratio varied from 1.1 to 1.4 (usually 1.2–1.3) in 23 specimens of *anale* 83 to 256 mm. long, and from 1.4 to 1.9 (usually 1.6–1.7) in 24 specimens of *cepedianum* 84 to 250 mm. long. It is sharply distinguished from both *smithi* and *chavesi* by the longer anal base and by the greater number of anal rays, the much longer dorsal filament, and the more anterior pelvics (tables 2 and 5). Its close relationship with *cepedianum* is indicated by the long dorsal filament, the high number of anal rays (25 to 36 in *cepedianum*), the similar number of prepelvic scutes (predominantly 18 in both), and the anterior position of the pelvics. It resembles both of the southern species in the fine scales and in the number of postpelvic scutes (tables 3 and 4).

Variation.—Counts of fin rays, scales, and ventral scutes were recorded for 21 to 71 specimens from Veracruz and Tabasco, Mexico, and from Petén, Guatemala (tables 2–4). In addition, 24 measurements were made on each of 35 specimens (table 6). With the exception of the number of vertebrae, the meristic characters and the proportional measurements of this material were rather consistent. The southernmost stocks from Petén, Guatemala, yielded a lower vertebral number: 46 in 8 specimens, 47 in 2 specimens, and 48 in 1 specimen, rather than 47 (in 6) or 48 (in 5) for the 11 specimens from the basin of the Río Papaloapán, Mexico, which were examined for this character. This decrease in number southward is in line with the gradient noted for vertebral number in the species of *Dorosoma*.

The caudal rays of 26 specimens were 19 except for a single 18. The pelvic rays of 27 were 8–8 except for one 7–8.

Material examined.—In the following collections, all from the basin of the Río Papaloapán in Veracruz, Mexico, all but C.N.H.M. No. 3787 and C.N.H.M. Nos. 14621–28, were collected by Meek and are types. These two lots were taken later by Heller and Barbour:

C.N.H.M. No. 3787: 2 specimens, 67 and 133 mm. long, from Achotal.

C.N.H.M. No. 4681: 7 paratypes, 52 to 171 mm. long, from Pérez.

C.N.H.M. No. 4606: 2 paratypes, 98 and 131 mm. long, from Veracruz.

C.N.H.M. No. 4637: holotype, 145 mm. long, from El Hule (now renamed Papaloapán).

C. N. H. M. No. 4708: 2 paratypes, 187 and 188 mm. long, from San Juan Evangelista.

C.N.H.M. Nos. 14621–28: 8 specimens, 83 to 149 mm. long, from Achotal.

C.N.H.M. 43148: 2 paratypes, 130 and 133 mm. long, from El Hule, listed by Hubbs and Miller (1941, p. 235) as F. M. Nos. 4190 and 4191 (see Grey, 1947, p. 140).

U.S.N.M. No. 55738: 1 paratype, 121 mm. long, from Pérez.

S.N.H.M. No. 9349: 1 paratype from Pérez.

TABLE 5.—*Diagnostic differences in proportional measurements between three species of Dorosoma, expressed in thousandths of the standard length*

[Summarized from tables 6-8. The superscripts indicate the number of specimens]

Measurement	anale		charesi		smithi	
	Range	Average	Range	Average	Range	Average
Standard length, in mm.	92-149	²² 124	84-142	²¹ 124	82-134	²⁷ 107
Dorsal origin to tip of snout.....	486-529	510	535-588	557	475-528	502
Pelvic insertion to tip of snout.....	409-454	432	454-549	489	455-494	476
Anal origin to caudal base.....	399-445	424	320-407	²⁰ 379	362-397	376
Head: Length.....	253-294	270	306-405	336	278-321	297
Depth.....	200-245	223	236-307	262	215-255	235
Interorbital, least fleshy width.....	65-85	75	77-94	88	66-93	75
Snout, length.....	41-58	49	51-84	64	39-61	49
Eye, length.....	61-76	70	77-102	90	62-77	70
Snout+eye.....	113-130	119	136-178	153	115-136	125
Dorsal filament, length.....	252-319	²¹ 285	129-192	¹⁸ 157	131-239	186
Anal fin, basal length.....	318-363	338	235-305	²⁰ 281	247-309	272
Mandible, length.....	82-99	88	110-165	128	90-104	96
Upper jaw, length.....	61-76	69	91-130	106	72-89	79

The following specimens are all from the Río Usumacinta Basin in Guatemala and along the Mexican-Guatemalan border. The localities for the Guatemalan material are shown on a map by Hubbs and van der Schalie (Goodrich and van der Schalie, 1937).

U.S.N.M. No. 61252: 1 specimen, about 256 mm. long, collected in 1900 by E. W. Nelson and E. A. Goldman at Monte Cristo, Tabasco, Mexico (see Evermann and Goldsborough, 1902, p. 149).

U.M.M.Z. No. 143377 and U.S.N.M. No. 133097: 8 specimens, 28 to 190 mm. long, collected on April 23, 1935, by Carl L. Hubbs and party, about 2 miles above Sayaxché, Petén, Guatemala.

U.M.M.Z. No. 143378: 27 specimens collected April 19, 1935, by Hubbs and party, in the flooded mouth of the Arroyito Jolomáx, opposite El Cambio, Petén; this stream is tributary to the Río de la Pasión.

U.M.M.Z. No. 143379: 2 specimens, 118 and 125 mm. long, collected on April 22, 1935, by Hubbs, van der Schalie, and Taintor in Arroyo San Martín, near its mouth in Río de la Pasión, Petén.

U.M.M.Z. No. 144256: 5 specimens, 233 to 254 mm. long, collected March 17, 1935, by Hubbs and van der Schalie in Laguna de Yalác, in course of Río San Pedro, about 6 leagues by river eastward from El Paso Caballos, Petén.

U.M.M.Z. No. 144257: 2 specimens from same locality as preceding.

Range.—From the Río Papaloapán in southern Veracruz and Oaxaca southward in the Atlantic drainage to the Río Usumacinta Basin, northern Guatemala, from which it had been recorded previously by

Hubbs and Miller (1941, p. 234). The single, large adult from the Río Usumacinta at Monte Cristo (U.S.N.M. No. 61252), Tabasco, was misidentified by Evermann and Goldsborough (1902, p. 149) as *D. cepedianum exile*, but was properly referred to *anale* by Meek (1904, p. 93).

TABLE 6.—*Proportional measurements of Dorosoma anale, expressed in thousandths of the standard length*

[Superscripts preceding measurements indicate the number of specimens. For convenience, measurements of the holotype are given separately but are included in the range and average of the 22 adults]

Measurement	Holo- type, C. N. H. M. 4637	Large adults (8) ¹		Adults (22) ²		Young (5) ³	
		Range	Aver- age	Range	Aver- age	Range	Aver- age
Standard length, in mm.....	145	154-190	174	92-149	124	28- 83	62
Dorsal origin to tip of snout.....	529	499-526	510	486-529	510	488-565	526
Pelvic insertion to tip of snout.....	445	402-423	413	409-454	432	447-525	477
Anal origin to caudal base.....	427	415-457	435	399-445	424	318-465	398
Body:							
Greatest depth.....	394	339-386	358	347-405	366	308-387	348
Greatest width.....	101	86-113	93	84-116	99	⁴ 82-104	94
Head:							
Length.....	284	231-261	248	253-294	270	281-357	311
Depth.....	230	189-222	220	200-245	223	229-289	256
Width.....	125	99-116	109	107-131	115	114-151	126
Interorbital, least fleshy width.....	82	64- 78	70	65- 85	75	68- 86	76
Snout, length.....	41	39- 51	46	41- 58	49	46- 63	54
Eye, length.....	69	56- 69	63	61- 76	70	79-103	90
Snout + eye.....	120	100-114	108	113-130	119	132-168	148
Dorsal filament, length.....	307	⁷ 278-314	293	252-319	285	⁴ 89-233	185
Dorsal fin:							
Basal length.....	121	114-133	122	111-134	124	106-125	115
Depressed height.....	227	208-241	228	214-247	230	189-229	215
Anal fin:							
Basal length.....	334	329-369	348	318-363	338	257-345	296
Height.....	115	95-111	106	¹⁸ 102-118	111	⁴ 107-121	115
Pectoral fin, length.....	208	195-211	203	194-223	207	202-220	211
Pelvic fin, length.....	126	109-123	118	115-130	125	122-136	131
Lower caudal lobe, length.....	—	⁵ 272-295	289	¹⁵ 277-331	304	³ 294-313	304
Caudal peduncle, least depth.....	103	96-107	101	89-109	102	83-103	93
Mandible, length.....	90	74- 84	80	82- 99	88	98-143	116
Upper jaw, length.....	71	61- 69	65	61- 76	69	75-100	85

¹ Based on C.N.H.M. Nos. 4681 and 4708; U.M.M.Z. No. 143377; and U.S.N.M. No. 133097—from Mexico and Guatemala.

² Based on material from throughout the range of the species.

³ Based on C.N.H.M. Nos. 3787, 4681, and 14628; and U.M.M.Z. No. 143377—from Mexico and Guatemala.

DOROSOMA CHAVESI Meek

Dorosoma chavesi MEEK, 1907, p. 112 (original description; type locality, Laguna Jenicero, between Lake Managua and Lake Nicaragua, Nicaragua).

This is the southernmost species of the genus in the Atlantic drainage and is known only from the basins of Lakes Managua and Nicaragua, Nicaragua.

Diagnosis.—A *Dorosoma* with 44 to 47 (usually 46) vertebrae, 72 to 83 lateral scales, 48 to 58 scales around the body, 12 to 14 (usually

13) dorsal rays, 24 to 31 anal rays, usually 17+10 or 17+11 ventral scutes, and with a short dorsal filament. It is exceptional for the genus in having a very large mouth.

TABLE 7.—*Proportional measurements of 21 specimens of Dorosoma chavesi, expressed in thousandths of the standard length*

[Superscripts indicate the number of specimens]

Measurement	Laguna Jenf- cero C.N.H.M. Nos. 5928; 14632-36		Laguna San Francisco C.N.H.M. No. 5927		Lake Managua C.N.H.M. No. 5926		Species total	
	Range	Aver- age	Range	Aver- age	Range	Aver- age	Range	Aver- age
Standard length, in mm.....	123-142	¹⁰ 136	110-125	⁶ 117	84-137	⁵ 108	84-142	²¹ 124
Dorsal origin to tip of snout.....	535-561	547	545-564	557	568-588	579	535-588	557
Pelvic insertion to tip of snout.....	454-485	471	472-492	483	497-549	530	454-549	489
Anal origin to caudal base.....	385-407	395	369-406	⁵ 384	320-353	341	320-407	²⁰ 379
Body:								
Greatest depth.....	345-386	366	359-386	373	366-403?	384?	345-403?	372?
Great width.....	101-116	107	106-119	111	119-140	132	101-140	114
Head:								
Length.....	306-327	319	331-343	337	347-405	371	306-405	336
Depth.....	236-260	249	259-265	262	273-307	286	236-307	262
Width.....	121-136	127	123-139	131	136-147	143	121-147	132
Interorbital, least fleshy width.....	77- 94	86	85- 92	89	82- 94	90	77- 94	88
Snout, length.....	51- 64	56	59- 69	66	71- 84	77	51- 84	64
Eye, length.....	77- 95	87	86- 96	91	83-102	95	77-102	90
Snout+eye.....	136-152	144	151-156	154	154-178	171	136-178	153
Dorsal filament, length.....	129-160	147	160-179	⁵ 170	150?-192	³ 171	129-192	¹⁸ 157
Dorsal fin:								
Basal length.....	123-138	129	129-139	134	123-136	129	123-139	131
Depressed height.....	207-236	217	232-250	243	219-242	³ 232	207-250	¹⁹ 228
Anal fin:								
Basal length.....	285-305	294	271-300	⁵ 287	235-265	251	235-305	²⁰ 281
Height.....	100-112	105	87-121	107	103-136	⁴ 119	87-136	²⁰ 108
Pectoral fin, length.....	201-223	213	215-230	224	208-245	234	201-245	221
Pelvic fin, length.....	120-130	124	123-134	128	124-146	131	120-146	127
Lower caudal lobe, length.....	282-327	297	294-347	319	Fins broken		282-347	¹⁶ 305
Caudal peduncle, least depth.....	105-115	111	110-115	113	100-108	104	100-115	110
Mandible, length.....	110-124	118	125-140	133	122-165	144	110-165	128
Upper jaw, length.....	91-105	99	99-114	104	112-130	121	91-130	106

Relationships.—As indicated in the diagnosis, and as shown in table 5, the mandible and upper jaw are much elongated in *chavesi*. These structural features are so distinctive that the relationships of *chavesi* are not readily discerned. It might even be justifiably set apart in a distinct subgenus. In addition, *chavesi* is distinguished by its large head and eye, the posterior position of the dorsal, the broad interorbital (table 5), and also by the reversal in growth pattern of the dorsal filament (see section on "Changes with Growth"). As demonstrated in tables 5, 7, 10, and 11, all these distinctive traits are those of the juvenile gizzard shad. Thus these specific characters of *D. chavesi* represent the retention in the adult of juvenile characters and tend further to mask the relationships of this species. In the

short dorsal filament, posterior position of the pelvics, short basal length of the anal fin, and few anal rays *chavesi* agrees rather closely with *smithi* (tables 2 and 5). The number of vertebrae, usually 46, is somewhat intermediate between that recorded for *anale* and *smithi* (table 4). On the basis of present knowledge, it may be hypothesized that the similarities between *chavesi* and *smithi* suggest that the two arose from a common ancestral stock. The fact that Lake Nicaragua was at one time a Pacific tributary (Hayes, 1899; Durham, 1944; and Marden, 1944) might help to explain these resemblances. An alternate hypothesis, however, is proposed under the account of *Dorosoma smithi*.

Variation.—Counts of fin rays, scales, and ventral scutes were made on 22 to 36 specimens (tables 2–4). In addition, 24 measurements were recorded for 21 specimens (table 7). Although no correlation was noted between the samples from the two lakes and their meristic characters, unmistakable differences were observed in certain measurements. Thus five specimens from Lake Managua differed prominently from five of comparable size taken in the basin of Lake Nicaragua in having (1) a more posteriorly placed anal fin, as expressed by the shorter distance between anal origin and caudal base; (2) a longer and deeper head; (3) a longer snout + eye (the eye is only slightly larger but the snout is much longer); (4) a shorter anal fin base; (5) a longer upper jaw; (6) a more posterior dorsal fin; (7) more posteriorly inserted pelvic fins; (8) a broader body; and (9) a narrower caudal peduncle (table 7). Since only five specimens of comparable size were available from the basins of the two lakes, and since it has been shown that body form in the gizzard shad is subject to environmental modification (Hubbs and Whitlock, 1929), I hesitate to give nomenclatorial recognition to the Lake Managua form. If and when large samples from these lakes become available and the differences shown are further tested and found to be valid, then I would regard *chavesi* as comprising two subspecies. There are falls between Lakes Managua and Nicaragua which seem to prevent the migration into Lake Managua of certain species found in Lake Nicaragua (Meek, 1907, p. 99; Marden, 1944, pp. 178–179). According to Marden, the stream connecting the two lakes is normally subterranean.

The caudal rays of 27 specimens were 19, except for two with 18 and one with 17 rays. The pelvic rays of 29 specimens were 8–8, except for one with 7–8.

*Material examined.*⁶—In the following list of specimens all but U.S.N.M. Nos. 16882 and 22138 represent paratype material collected by S. E. Meek in March, 1906.

⁶ U.S.N.M. No. 30965, an adult collected by Capt. J. M. Dow, reportedly in Panama, represents *D. chavesi* and obviously was not taken in Panama but probably came from Nicaragua, where Dow also collected.

C.N.H.M. No. 5925: 6 young from Lake Managua.

C.N.H.M. No. 5926: 6 specimens, 53 to 137 mm. long, from Lake Managua.

C.N.H.M. No. 5927: 6 specimens, 110 to 125 mm. long, from Laguna San Francisco.

C.N.H.M. No. 5928: 5 specimens, 123 to 142 mm. long, from Laguna Jenícero.

C.N.H.M. Nos. 14631-36: 6 specimens, 135 to 162 mm. long, from Laguna Jenícero.

U.S.N.M. No. 78100: 2 specimens, 88 and 171 mm. long, from Nicaragua.

U.S.N.M. No. 16882: 2 young in poor condition, 41 and 68 mm. long, collected by J. F. Bransford in Lake Nicaragua in March, 1876.

U.S.N.M. No. 22138: 3 adults, 145 to 186 mm. long, collected by Bransford in Nicaragua in 1877.

Range.—Known only from the basins of Lakes Managua and Nicaragua in Nicaragua.

DOROSOMA SMITHI Hubbs and Miller

Dorosoma smithi HUBBS and MILLER, 1941, pp. 232-238, fig. 1 (original description; type locality, Río Piaxtla near Piaxtla, Sinaloa, Mexico).

This is the only species of *Dorosoma* known from the Pacific drainage, and it has been taken thus far only in northwestern Mexico. Since *D. smithi* was described from only five type and three nontype specimens, its range of variation was imperfectly known. The examination of 177 additional specimens, along with renewed study of the original series, has brought to light new characters that further distinguish *smithi* and has eliminated most of the described differences between the types and the three variants.

All the additional series of *smithi* were generously collected by my father, the late Ralph G. Miller, from the state of Sinaloa: in the Río del Fuerte, the Río Sinaloa Basin, and in the Río de Mocerito. These three streams lie between the type locality, Río Piaxtla, also in Sinaloa, and Río Muerto, Sonora, where the variants discussed by Hubbs and Miller (1941, pp. 237-238) were taken. The new material agrees well with the original description.

Diagnosis.—A *Dorosoma* with 43 to 47 (usually 44 or 45) vertebrae, 71 to 79 lateral scales, 50 to 60 scales around the body, 28 to 31 scales around the caudal peduncle, 11 or 12 (rarely 9, 10, or 13) dorsal rays, 22 to 29 (24 to 27) anal rays, usually 17+11 ventral scutes, and with a short dorsal filament.

Relationships.—*D. smithi* is distinguished most significantly from the other members of the genus by the much fewer vertebrae, the reduced number of anal rays, and the greater number of scales around the caudal peduncle and around the body (tables 2-4). In having a short dorsal filament it closely approaches *D. chavesi* (table 5) and differs sharply from both *D. cepedianum* and *D. anale*. The number of prepelvic scutes, usually 17 and commonly 16, is also similar to that of *chavesi*, and the fewer anal rays is a further point of resemblance between these two species.

As previously stated under the account of *chavesi*, it is thought that these similarities may indicate a common ancestry. On the other hand, it is perhaps equally plausible to consider the resemblances between *smithi* and *chavesi* to be the result of parallel evolution. Under this alternate hypothesis it is suggested that the gizzard shad may have gained access to the Pacific drainage during Tertiary times, when a continuous waterway connected the Atlantic and Pacific across what is now the Isthmus of Tehuantepec. This idea is supported by the absence of any records of *Dorosoma* on the Pacific slope of Middle America south of the Isthmus of Tehuantepec. To the north of that region *Dorosoma* is known at present only as far south as Sinaloa, Mexico, though I venture to predict that thorough exploration along the Coastal Plain will reveal its occurrence much farther southward. Careful ichthyological surveys in El Salvador (Hildebrand, 1925) and

TABLE 8.—*Proportional measurements of 27 specimens of Dorosoma smithi, expressed in thousandths of the standard length*

[Superscripts indicate the number of specimens; averages are given in parentheses. Localities are arranged from northwest to southeast (see table 9)]

Measurement	Río Muerto	Río del Fuerte	Río Yecorato	Río de Mocorito	Río Piaxtla	Species total
Standard length, in mm.-----	³ 104-126 (117)	⁸ 85-122 (104)	⁶ 100-134 (117)	⁶ 82-91 (86)	⁴ 114-123 (119)	²⁷ 82-134 (107)
Dorsal origin to tip of snout-----	[*] 484 (484)	475-506 (484)	508-528 (518)	506-525 (512)	497-510 (505)	475-528 (502)
Body:						
Greatest depth-----	³ 339-371 (356)	319-399 (362)	356-370 (361)	334-361 (350)	364-398 (377)	319-399 (361)
Greatest width-----	⁹⁸ 98-103 (100)	124-135 (129)	100-110 (104)	107-122 (113)	115-126 (120)	98-135 (115)
Head:						
Length-----	²⁷⁸ 278-293 (284)	286-305 (295)	281-300 (293)	305-321 (312)	288-301 (294)	278-321 (297)
Depth-----	²¹⁸ 218-243 (231)	215-234 (224)	225-244 (234)	237-248 (243)	237-255 (248)	215-255 (235)
Width-----	¹⁰⁶ 106-124 (115)	124-138 (128)	116-127 (123)	127-134 (130)	125-135 (131)	106-138 (126)
Interorbital, least fleshy width-----	⁶⁶ 66- 81 (75)	71- 80 (75)	67- 77 (69)	72- 77 (76)	80- 93 (85)	66- 93 (75)
Eye, length-----	⁶² 62- 64 (63)	63- 69 (66)	70- 75 (73)	74- 77 (75)	69- 72 (71)	62- 77 (70)
Snout+eye-----	¹¹⁵ 115-121 (118)	116-125 (120)	121-132 (127)	128-136 (132)	127-131 (128)	115-136 (125)
Dorsal filament, length-----	¹⁴⁹ 149-176 (167)	131-174 (161)	199-239 (224)	168-197 (179)	188-229 (208)	131-239 (186)
Dorsal fin, basal length-----	¹²⁴ 124-130 (128)	122-137 (129)	121-138 (129)	123-139 (133)	132-141 (136)	121-141 (131)
Pectoral fin, length-----	¹⁹⁶ 196-217 (204)	191-209 (199)	201-222 (216)	207-215 (211)	212-230 (221)	191-230 (209)
Lower caudal lobe, length-----	³¹⁷ 317-328 (322)	288-313 (296)	325-360 (346)	310-339 (327)	333-354 (340)	288-360 (323)

*Predorsal region of 1 specimen abnormal; value not used (see Hubbs and Miller, 1941, table 1). Value for other 2 was 484.

Guatemala⁷ have shown that the gizzard shad does not occur on the Pacific slope in these countries.

Variation.—Counts of fin rays, scales, and ventral scutes were recorded for 19 to 185 specimens (tables 2-4). Unfortunately, most of the scales were missing from a large number of the new series. In addition, 24 proportional measurements were made on each of 27 specimens (table 8). Although more material is needed from Sonora and southern Sinaloa, the anal-ray counts strongly indicate that there is a definite increase in number southward (table 9). There is considerable variation in proportional measurements, as in the predorsal and prepelvic lengths, the width of the interorbital, the length of the snout, the length of the dorsal filament, the size of the dorsal, pectoral, and pelvic fins, the length of the anal fin base, and the length of the lower lobe of the caudal fin. That these measurements are affected to some extent by variation in age is clear (see section on "Changes with Growth"), and it is believed that sexual dimorphism may also be a contributing factor. Evidence that the variations are largely individual is indicated by the lack of positive geographic correlation.

TABLE 9.—North-south variation in number of anal rays in *Dorosoma smithi*

Localities ¹ (Mexico)	Number of anal rays								Total	Average
	22	23	24	25	26	27	28	29		
Sonora:										
Río Muerto.....			2	1					3	24.33
Sinaloa:										
Río del Fuerte.....	1	6	7	10	12	9	6	1	52	25.58
Río Yecorato.....	4	11	24	27	32	9	7	1	115	25.15
Río de Mocorito.....				1	4	3	2		10	26.60
Río Piaxtla.....					2	2		1	5	27.00
Species total.....	5	17	33	39	50	23	15	3	185	25.38

¹ Arranged from northwest to southeast. Río Muerto (a tributary of the Río Yaqui) is approximately 135 miles northward from Río del Fuerte. That stream and the Río Yecorato and Río de Mocorito are nearly equidistant, approximately 40 miles apart. Río Piaxtla is more than 150 miles southward from Río de Mocorito and about 370 miles southward from Río Muerto. This geographic spread is emphasized in the table by separating the five localities into three groups. The data for the Río Yecorato include 2 specimens (U. M. M. Z. No. 143185) from a tributary of the Río Sinaloa, about 1 mile downstream in the same drainage system.

As shown in table 5, the length of the mandible and the upper jaw are somewhat longer in *smithi* than in *anale*, and this might seem to indicate an approach toward the large mouth of *chavesi*. Measurements of these structures in a comparable series of *cepedianum*, how-

⁷ I recently spent over a month collecting fishes along the Pacific coastal plain of Guatemala, working habitats typical of *Dorosoma*, with negative results.

ever, indicate very close agreement between *smithi* and *cepedianum*, as shown by the following data (range, followed by mean in parentheses):

Measurement	<i>cepedianum</i>	<i>anale</i>	<i>chavesi</i>	<i>smithi</i>
Mandible, length	87-116 (99)	82-99 (88)	110-165 (128)	90-104 (96)
Upper jaw, length	71-90 (80)	61-76 (69)	91-130 (106)	72-89 (79)

The data for *cepedianum* are based on 20 specimens from Maryland and the Great Lakes region southward and westward to Texas; these specimens varied in standard length from 83 to 153 mm., with a mean of 118 mm. Measurements for the other species are taken from table 5.

In discussing the variant series of three specimens from Río Muerto, Sonora, Hubbs and Miller (1941, pp. 237-238) pointed out certain characteristics by which these specimens differed from the five then known from Sinaloa. It was thought that the Sonoran individuals might possibly represent a distinct subspecies. In the number of anal rays they still show a lower average value, but the gap between their counts and those of the five types from Río Piaxtla has been completely bridged by the new material (table 9). The total number of ventral scutes, 27 to 29, contrasts with that of 26 to 27⁸ for the types but again is overlapped by counts of 26 to 30 (usually 27 to 28) for specimens from the intervening regions. The measurements by which variants and the types differ are now largely bridged over by those of the new material (table 8). In the few measurements that still distinguish the northern stock from the rest, such as the shorter and narrower head and the smaller snout and eye, the differences may well be the result of emaciation. A good series from the basin of the Río Yaqui, Sonora, should clarify this interpretation.

The caudal rays of 94 specimens were 19 except for two with 18 and one with 17 rays. Counts of 147 pelvic fins gave the following results: 7-6 (1), 7-7 (15), 7-8 (16), 8-7 (15), and 8-8 (100). Thus, although each pelvic fin of *D. smithi* usually has 8 rays, there is considerably more variation in this count than there is in the other species of *Dorosoma*.

Material examined.—A total of 185 specimens, all from Mexico, were examined as follows:

U. M. M. Z. Nos. 133749-50: Holotype and 4 paratypes, 46 to 123 mm. long, from Río Piaxtla near Piaxtla, Sinaloa.

U. M. M. Z. No. 133751: 3 adults, 104 to 126 mm. long, from Río Muerto, a coastal tributary of Río Yaqui, about 46 road miles south of Guaymas, Sonora.

U. S. N. M. No. 129952: 52 young to adults, 52 to 122 mm. long, from Río del Fuerte, 0.5 mile from San Blas, Sinaloa.

⁸ In the original description the holotype was recorded as having 28 ventral scutes. Reexamination shows that only 27 are present.

U. S. N. M. No. 133098 and U. M. M. Z. No. 144575: 113 young to adult, 73 to 134 mm. long, from Río Yecorato about 7 miles northeast of Guasave, Sinaloa.

U. M. M. Z. No. 143185: 2 specimens from a tributary of Río Sinaloa, about 6 miles northeast of Guasave, Sinaloa.

U. S. N. M. No. 129951: 10 half-grown, 74 to 91 mm. long, from Río de Mocorito, about three-fourths of a mile from Guamúchil, Sinaloa.

Range.—Known so far only from southern Sonora (Río Yaqui) to southern Sinaloa (Río Piaxtla), Mexico.

CHANGES WITH GROWTH

A detailed study of changes with growth in *Dorosoma* has not been attempted, principally because many of the stages of development are lacking in the material at hand. The data obtained, however, are sufficient to indicate some of the changes that take place with age in gizzard shads. This phase of the study was limited almost exclusively to the three southern species: *anale*, *chavesi*, and *smithi*.

The following changes with age in the relative position or in the relative size of certain structures are indicated by tables 7, 10, and 11 as the normal growth pattern for the southern species: (1) The pelvic and anal fins move forward; (2) the head becomes shorter and less deep; (3) the eye becomes smaller and the snout shorter (as best expressed in the measurement "snout+eye"); and (4) the mandible and the upper jaw become much shorter as the young fish attains maturity. That this general pattern of development is to be expected also in *D. cepedianum* is indicated by measurements (not recorded here) of a young specimen (27.5 mm., standard length) and of an adult (102 mm.) from Mississippi (U. S. N. M. No. 129325). The differences in their measurements agree with the changes described above. An examination of table 1 in Hubbs and Miller (1941, p. 235) demonstrates further agreement of the growth pattern of *cepedianum* with that of the other species.

The growth of the dorsal filament requires special mention because the pattern of development is not uniform in the four species of *Dorosoma*. In *cepedianum*, *anale*, and *smithi* this structure is very small in young fish but increases in length with age, at least up to a certain size range. What the limits of this range may be is undeterminable from the material examined and is only hinted at by the resultant data. For example, in table 10 the structure is seen to grow relatively longer in *D. anale* from a young fish 28 mm. long to specimens ranging from 116 to 165 mm. long.⁹ Specimens varying between 171 and 190 mm. show little change in the relative length of the filament, and in a single fish approximately 256 mm. long this

⁹ Values of 300 or over in the table fall generally between these standard lengths, 165 mm. being the maximum.

structure definitely has decreased in relative size. Comparing young and adults of *D. smithi* from single localities, we see that the dorsal filament increases proportionately with age at least up to a length of 122 mm. (table 11). Since no larger specimens were available, I do not know whether the structure shows the growth pattern with increasing size that is indicated for *anale*. The limited data given for *D. cepedianum* by Hubbs and Miller (1941, p. 235) also demonstrate that there is a general increase with age in the relative length of the dorsal filament from a value (in thousandths of the standard length) of 168 for a specimen 47 mm. long to values of 239 to 285 in size ranges of 115 to 149 mm. long. The single large specimen 245 mm. long gave a value of 258, indicating again that after a certain size range is reached the relative length of this structure appears to remain nearly constant. When we examine the growth of this structure in *D. chavesi*, however, we find a complete reversal from the pattern for the other three species. In table 7, it is seen that as the fish increases in size from 84 to 142 mm. in standard length the proportionate length of the dorsal filament decreases from a maximum value of 192 to a minimum value of 129, or from an average value of 170 to that of 147. Measurements of three additional specimens (U.S.N.M. No. 22138, labeled "Nicaragua") 145, 149, and 188 mm. long gave the following values, respectively: 120, 126, and 139—values averaging far below that for the largest size group given in table 7. Although these data are not as complete as desirable, they indicate clearly that the dorsal filament does not increase in length with age in *chavesi* as it does in the other species of *Dorosoma*.

TABLE 10.—Proportional measurements of *Dorosoma anale*, at various sizes, showing changes with age

[Expressed in thousandths of the standard length. Compiled in part from table 6]

Measurement	Young					28 adults		
	U. M. M. Z. No. 143377	C. N. H. M. No. 4681	C. N. H. M. No. 3787	C. N. H. M. No. 4681	C. N. H. M. No. 14628	Range	Range	U. S. N. M. No. 61252
Standard length, in mm.....	28.0	52.2	66.7	80.0	82.9	92-149	154-190	256±
Pelvic insertion to tip of snout.....	525	513	447	447	453	409-454	402-423	408
Anal origin to caudal base.....	318	368	421	465	420	399-445	415-457	410
Head:								
Length.....	357	339	289	281	287	253-294	231-261	228
Depth.....	289	278	232	229	252	200-245	189-222	205
Eye, length.....	103	103	85	79	82	61- 76	56- 69	56
Snout+eye.....	168	165	139	132	135	113-130	100-114	99
Dorsal filament, length.....	89	---	214+	206±	233±	252-319	278-314	201?
Mandible, length.....	143	125	99	114	98	82- 99	74- 84	78
Upper jaw, length.....	100	94	79	79	75	61- 76	61- 69	59

TABLE 11.—*Proportional measurements of Dorosoma smithi at various sizes, showing changes with age*

[Expressed in thousandths of the standard length. Compiled from table 8]

Measurement	Río del Fuerte, U.S.N.M. No. 129952				Río Mocorito, U.S.N.M. No. 129951			
	Young (6)		Adults (8)		Young (4)		Adults (6)	
	Range	Average	Range	Average	Range	Average	Range	Average
Standard length, mm.....	52- 79	65	85-122	104	74- 80	77	82- 91	86
Dorsal origin to tip of snout.....	493-531	514	475-506	484	515-527	521	506-525	512
Pelvic insertion to tip of snout.....	484-526	506	461-479	468	503-507	505	482-494	489
Anal origin to caudal base.....	321-364	340	363-382	374	352-362	357	362-378	367
Head:								
Length.....	318-335	323	286-305	295	323-333	329	305-321	312
Depth.....	246-257	251	215-234	224	254-256	255	237-248	243
Width.....	131-146	141	124-138	128	123-139	134	127-134	130
Eye, length.....	76- 86	80	63- 69	66	78- 79	78	74- 77	75
Snout+eye.....	132-143	138	116-125	120	137-141	139	128-136	132
Dorsal filament, length.....	84-158	126	131-174	161	163-177	169	168-197	179
Anal fin, basal length.....	239-254	245	247-275	263	248-268	258	255-273	264
Pectoral fin, length.....	204-218	212	191-209	199	214-223	217	207-215	211
Pelvic fin, length.....	126-138	134	110-123	117	136-138	137	131-137	135
Mandible, length.....	103-117	111	90-101	95	106-110	109	99-104	102
Upper jaw, length.....	88- 92	90	76- 83	80	87- 90	89	83- 89	85

The reliability of the above discussion of the changes with growth in the dorsal filament is subject to considerable refinement, because there is obvious individual variation, probable racial variation, and possible sexual variation in the length of this structure. The general picture, however, seems clear.

Other changes with age appear to take place in some of but not all the species of *Dorosoma*. Thus the relative position of the dorsal fin advances with age in all but *anale*; the head becomes narrower with growth in *chavesi* and *smithi*, broader in *cepedianum*, but shows no significant change in *anale*; the relative length of the anal fin (as expressed by the length of its base) increases in all but *anale*; the pectoral fins appear to become shorter with increasing size in *chavesi* and *smithi* and longer in *cepedianum*, but show no significant change in *anale*; the pelvic fins also seem to decrease in size in *smithi* but not in the other species (tables 7, 10, and 11 and Hubbs and Miller, 1941, p. 235). The changes in the proportionate sizes of the pectoral and pelvic fins may well be correlated with sex¹⁰ rather than with age, or they may represent a direct environmental response, such as that demonstrated by Hubbs and Whitlock (1929) for certain characters of the young of *Dorosoma cepedianum*.

¹⁰ Because much of the material measured represented types or rare specimens, no sex determinations were made. There appear to be no clear-cut external differences between the sexes.

ACKNOWLEDGMENTS

Through the kindness of several individuals, critical type material and other valuable specimens were generously made available for this study. For these loans I am indebted to K. P. Schmidt and Marion Grey, of the Chicago Natural History Museum; Drs. Reeve M. Bailey and W. A. Gosline, of the University of Michigan Museum of Zoology; and Dr. George S. Myers and Margaret Storey, of the Natural History Museum of Stanford University. Dr. Bailey further assisted by donating a much-needed series of topotypes of *Signalosa petenensis* and specimens of *Dorosoma anale* and *D. smithi*. Henry W. Fowler forwarded information on the northward occurrence of *D. cepedianum* on the Atlantic slope, and Dr. E. C. Raney sent on the valid published records of this species in New York. To all these workers I express my sincere thanks.

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DOI: <https://doi.org/10.5479/si.00963801.3267.387>

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