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THE SYSTEMATICS AND EVOLUTION OF THE GENUS *CHIROSTOMA* SWAINSON (PISCES, ATHERINIDAE)

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ABSTRACT

The genus *Chirostoma* is composed of 18 species and six subspecies not including *C. compressum*, thought to be extinct. Except for a few populations of *C. jordani* near Durango City, Durango, it is restricted to the Mesa Central of Mexico where it makes up approximately 20 percent of the fish fauna.

The following names in current usage are herein synonymized: *Otalia* = *Chirostoma*; *C. ocampoi*, *C. regani* = *C. humboldtianum*; *C. diazi* = *C. sphyraena*; *C. ocotlanae* = *C. lucius*. No subspecies of *C. jordani* are recognized. *C. reseratum* is recognized as a subspecies of *C. consocium*. The name *C. attenuatum* Meek is reapplied to the populations in Lakes Pátzcuaro and Zirahuén currently designated as *C. bartoni*. Five individuals from the lake at Balneario Cointzio, Michoacán are referred to *C. charari* De Buen. *C. **aculeatum*** is described as new.

Chirostoma is divided into two species groups. The jordani group generally has high meristic values, the lateral line scales with canals, scales with laciniate margins and includes *C. jordani*, *C. patzcuaro*, *C. chapalae*, *C. consocium*, *C. humboldtianum*, *C. estor*, *C. grandocule*, *C. lucius*, *C. sphyraena* and *C. promelas*. The arge species group generally has low meristic values, the lateral line scales with round pores (except for the last two species named below) and scales with smooth margins and includes *C. arge*, *C. melanoccus*, *C. charari*, *C. riojai*, *C. bartoni*, *C. attenuatum*, *C. labarcae* and *C. aculeatum*.

The similarity between *C. arge* and *Melaniris crystallina* and the primitive nature of *C. jordani* is noted. The evolution of *Chirostoma* is best explained by considering the genus to be diphyletic; a *Menidia*-like ancestor of the jordani group invaded the Mesa Central first, followed at a later time by the *Melaniris*-like ancestor of the arge group. The evolution of the species is summarized in a hypothetical phylogenetic tree.

CONTENTS

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INTRODUCTION

The Republic of Mexico, by reason of its geographic position and geological history, possesses a large and interesting fish fauna. The coastal lowlands have served as avenues of migration for North and Central American fishes and contain mixed faunas reflecting strong affinities for these regions. On the other hand, the uplifted, central portion of the country, from the transverse volcanic axis northward, contains a large number of unique species. The fishes present in the basins of the north show clear but varying degrees of relationship with the Rio Grande fauna. On the southern one-third of the pleateau, however, in the westward flowing Lerma-Santiago river system and contiguous fluvial and lacustrine basins, endemism reaches generic and familial levels.

Chirostoma is one of the unique groups in this evolutionary microcosm. The genus has been reviewed or revised several times, most notably by Jordan and Evermann (1895; 1896–1900), Meek (1904), Regan (1906–1908), Jordan and Hubbs (1919) and De Buen (1945). Through the years the number of species has steadily increased as well as the confusion regarding their relationships. Jordan and Evermann (1895) placed the species into two genera: *Chirostoma*, characterized as having the snout slightly produced, small teeth, an oblong body and a small first dorsal fin placed over the vent and *Eslopsarum*, being close to *Chirostoma*, but with large and entire scales. Jordan and Evermann (1896–1900) erected a third genus, *Lethostole*, for *C. estor* characterized as having thin, translucent, pale flesh and differences in the firmness of its scales and bones. The same authors later decided (Jordan and Evermann, 1896–1900, Vol. 4, p. 3158) that *Lethostole* was not separable from *Chirostoma*. Meek (1904) recognized one genus and allocated the species among three subgenera: *Chirostoma*, *Eslopsarum* and *Lethostole*. Regan (1906–08) and Jordan and Hubbs (1919) could find no consistent method by which the species could be grouped and so recognized no subgenera. Jordan, Evermann and Clark (1930) followed Meek (1904). De Buen (1945) distributed the species among three genera and six subgenera. Alvarez (1950, 1970) recognized two genera in his keys, *Chirostoma* and the monotypic *Otalia*.

The objectives of this paper are to redefine the species which have been included in *Chirostoma* and to discuss their evolutionary relationships. No attempt has been made, however, to diagnose the genus because little comparative data is available for most of the other atherine genera. Patterns of morphological variation within the family (Rosen, 1964) are not yet clear. This somewhat unorthodox presentation is also justified by the biogeographic history of *Chirostoma*, a topic to be discussed in another paper.

METHODS

Counts and measurements were made in accordance with Hubbs and Lagler (1958) in most instances. Where these methods were in appropriate they were modified or new characters used as described below.

The number of median lateral scales was considered to be the number of scales in a series extending from the scapular arch dorsal and anterior to the insertion of the pectoral fin to the end of the hypural plate. The count includes scales which may be reduced in size just posterior to the head. The predorsal scale count was made along an imaginary line between the origin of the first dorsal fin and the head and included, when present, the large scale which usually has its origin on the head, but lies on the nape. Only those scales intersecting the line by at least one-half a scale width were counted. The interdorsal scales, the number of scales in a series lying between the scale upon which the first dorsal fin membrane

inserts and the origin of the second dorsal fin, were counted in the same manner as the predorsals.

The condition of the scale margins and the type of lateral line pore were also found to be useful characters. The former are either smooth (entire) or laciniate (toothed or crenulate). The openings in the scales of the lateral line system are either horizontally elongate (canals) or round (pores).

Nineteen morphometric and nine meristic characters were examined in each of the species of *Chirostoma* over their known ranges and in *Menidia berylina* (Grand Isle, Louisiana) and *Melaniris crystallina* (Río Grande de Santiago at Hwy 15 crossing, Nayarit). Wherever possible body proportions were measured on twenty adult individuals and fifty or more were examined meristically. However, sample sizes were occasionally determined by the availability of specimens. Ranges, means, 95 percent confidence intervals of the means and standard deviations were computed for each character for all samples of more than six specimens and plotted on graph paper according to the method of Hubbs and Hubbs (1953). Each chart was copied, cut apart, and the populations or species arranged in different ways to reveal geographic or phylogenetic trends and patterns. Characters which clearly show trends or patterns important to the understanding of the evolution of *Chirostoma* are presented in Figs. 5–15. Unless otherwise stated, the statistical analyses were performed on pooled data taken from specimens over the known ranges of the species.

Life colors given in the text were observed in the field from living specimens. Pigmentation patterns were more easily examined in the laboratory and were recorded from preserved specimens.

The synonymies are given in abbreviated form with the complete references listed under Literature Cited.

Base maps (semi-diagrammatic) on which distributions are plotted were compiled from appropriate sheets of the Mapa de los Estados Unidos Mexicanos (1:500,000) published by the Comisión Intersecretarial Coordinadora del Levantamiento de la Carta Geographica de la Republica Mexicana (1957), the Map of North America (1:1,000,000) published by the American Geographical Society (1935), the road atlas, *Caminos de México*, published by La Compania Hulera Euzkadi (third edition, 1967) and from my own observations. Where more than one collection was taken from a specific locality, only one is shown on the map. Questionable locality records are not plotted on the maps, but are discussed in the text under *Range*.

The following abbreviations appear in this paper: ca. (circa), about; ft., feet; hwy., highway; jct., junction; km, kilometer; mi., miles; trib., tributary. Geographic directions are indicated by the initial letters of the cardinal points of the compass, North, South, East, West or various combinations thereof.

Acknowledgments

The majority of the specimens forming the basis for this study were taken during the summer of 1963 and during the springs of 1964 and 1969 by collecting parties from Tulane University and the University of Utah and over the past 15 years by Robert R. Miller and his associates and students at the University of Michigan. This material is housed largely at Tulane University (TU) and at the University of Michigan Museum of Zoology (UMMZ) under the care of Royal D. Suttkus and Robert R. Miller and Reeve M. Bailey respectively. I am deeply grateful to these individuals for their prompt assistance in the loan of material and other courtesies too numerous to mention.

It would not have been possible to complete this work without the examination of specimens deposited in other museums and universities. The following persons kindly allowed me to examine collections entrusted to their care and assisted me in numerous ways: José Alvarez, Instituto Politecnico Nacional, México, D. F. (P); James E. Böhlke, Academy of Natural Sciences of Philadelphia (ANSP); Salvador Contreras, Facultad de Ciencias Biológicas, Universidad de Nuevo León, México (FCB); P. Humphry Greenwood, British Museum of Natural History (BM); George S. Myers and Warren C. Freihofer, Division of Systematic Biology, Stanford University (SU), recently moved to the California Academy of Sciences; Wilbur I. Follett and William P. Eschmeyer, California Academy of Sciences (CAS); Leonard P. Schultz and Ernest A. Lachner, National Museum of Natural History, Smithsonian Institution (USNM);

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Thanks go to Salvador Contreras for enduring two field trips to Mexico with me and for translating my summary into Spanish. Aurelio Solórzano extended the hospitality of his laboratory in Mexico City and arranged for the use of the facilities of the Limnological Station at Pátzcuaro, Michoacán. Successful collecting in Lake Pátzcuaro and the surrounding area was due to the enthusiastic cooperation of Juan Pizá, former caretaker of the Limnological Station. José Alvarez generously shared his knowledge of the fishes of central Mexico with me and directed me to several important localities. Finally, I would like to thank the Departamento de Estudios Biólogicos Pesqueros for issuing me permits to collect in Mexico.

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Diagnostic Characters

Single characters or character complexes which are critical for the separation of species are rare in *Chirostoma.* Most of the characters discussed below are diagnostic only in various combinations with themselves. Their utility for differentiating between the species groups is not discussed.

Meristic characters.—The following meristic characters are compared in Figs. 5–10: median lateral, predorsal and interdorsal scales, pectoral and anal fin rays, gill rakers and vertebral numbers. First and second dorsal fin rays were also examined, but did not vary sufficiently to be of use.

Geographic variation was found in certain meristic characters and is discussed following the descriptive data of the appropriate species.

Morphometric characters.—Nineteen morphometric characters were analyzed for this study. The most useful are compared in Figs. 11–14: head length, mandibular length, snout to first dorsal fin origin and anal fin height. In certain instances the following measurements aided in differentiating between species: snout to the origins of the second dorsal, anal and pelvic fins, snout, eye, pectoral fin, postorbital head lengths, lengths of the caudal peduncle and the base of the anal fin, least depth of the caudal peduncle, and the height of the second dorsal fin. Four measurements were found to be of no use for separating the species of *Chirostoma*: lengths of the second dorsal fin base and the pelvic fins, greatest body depth and the fleshy interorbital width.

All morphometric characters showed some degrees of allometric growth. When juvenile to adult specimens of all the species are available for study in adequate numbers, more accurate diagnoses will be able to be

written. Until that time care should be taken in the identification of subadults.

Pigmentation.—The distribution and concentration of melanophores over the body is usually highly variable and dependent on the clarity of the water in which the species or population lives. In a few instances, however, concentrations of pigment cells occur independently of environmental conditions and are useful for distinguishing species.

Dentition.—All species of *Chirostoma* have conical teeth. However, tooth size and placement showed important interspecific differences.

Scales.—The types of scale edge and lateral line opening described under METHODS are most useful for differentiating between the species groups although occasionally they may separate species within a group. The degree of scale edge laciniation shows pronounced intraspecific variation in one case.

Key to Species of the Genera *Chirostoma* and *Melaniris*[1]

1a. Lateral line scales with pores only ... 2
b. Lateral line scales with canals only or pores and canals present on the same specimen ... 9
2a. Length of anal fin base, 28.7–32.6 in percent of standard length; length of pectoral fin, 22.2–28.2; length of caudal peduncle 15.2–19.2 ... *M. crystallina*
b. Length of anal fin base, 14.9–24.4; length of pectoral fin, 12.9–18.8; length of caudal peduncle, 21.4–30.2 ... 3
3a. Teeth large; teeth present on premaxillary outside the mouth and easily seen or felt when mouth is closed ... *C. arge* (See also 26a)
b. Teeth large or small; teeth on premaxillary not outside the mouth ... 4
4a. Premaxillaries project strongly anteriorly, sharply decurved ... *C. charari*
b. Premaxillaries do not project strongly anteriorly, not sharply decurved ... 5
5a. Gill rakers, 12–18 ... 6
b. Gill rakers, 19–26 ... 7
6a. Length of eye, 5.1–6.0 ... *C. riojai*
b. Length of eye greater than 6.0 ... 7
7a. Median lateral scales, 39–45; gill rakers, 17–22; distance from snout to first dorsal fin, 48.1–51.9 ... *C. melanoccus*
b. Median lateral scales, 42–70; gill rakers, 20–26; distance from snout to first dorsal fin, 44.9–50.3 ... 8
8a. Median lateral scales, 42–49; distance from snout to first dorsal fin, 47.4–50.3; length of caudal peduncle, 22.3–24.9; snout angular in profile ... *C. bartoni*
b. Median lateral scales, 43–51; distance from snout to first dorsal fin, 43.1–46.2; length of caudal peduncle, 26.6–30.2; snout blunt to angular, usually the latter ... *C. attenuatum attenuatum*
c. Median lateral scales, 48–70 (rarely 48 or 49); distance from snout to first dorsal fin, 44.4–48.9; length caudal peduncle, 23.9–30.1; snout blunt to subtriangular ... *C. attenuatum zirahuen*
9a. Snout black or partially so; lower jaw equal to or included by upper jaw ... *C. promelas*
b. Snout not black, does not include lower jaw ... 10
10a. Teeth small; lower jaw may project strongly beyond snout ... 11
b. Teeth large; some may be canine-like; lower jaw may project strongly beyond snout or snout may be subtriangular to pointed (barracuda-like) ... 25
11a. Median lateral scales with entire edges, rarely laciniate ... *C. jordani*
b. Median lateral scales laciniate ... 12
12a. Gill rakers, 28–34 ... 13
b. Gill rakers, 19–28 ... 14
13a. Median lateral scales, 58–77; anal rays, 18–22; length caudal peduncle, 21.2–23.5; height of second dorsal fin, 13.3–14.8 ... *C. grandocule*
b. Specimen does not fit description in 13a ... 14
14a. Snout length, 7.2–9.5 ... 15
b. Snout length, 9.6–12.5 ... 21
15a. Median lateral scales, 44–55 ... 16
b. Median lateral scales, 52–69 ... 17
16a. Head length, 23.9–25.5; postorbital head length, 10.7–12.0; snout length, 7.3–8.1; jaw length, 8.6–9.4 ... *C. chapalae*

[1] *Chirostoma compressum*, thought to be extinct, is not included in the key.

b. Head length, 25.6–34.2; postorbital head length, 12.2–16.8; snout length, 8.4–13.4; jaw length, 9.5–15.0 ..... *C. humboldtianum* (See also 20b, 22a)

17a. Predorsal scales, 24–34 18

b. Predorsal scales, 33–79 19

18a. Head length, 24.5–25.9; postorbital head length, 11.2–12.5; snout length, 7.5–8.7; jaw length, 8.8–9.9; length of caudal peduncle, 23.7–25.6; snout slightly pointed ..... *C. patzcuaro*

b. Specimen does not fit description in 18a 16b

19a. Predorsal scales, 33–56 20

b. Predorsal scales, 43–79 ..... *C. consocium consocium*

20a. Gill rakers, 23–30 ($\bar{x}$ = 27); snout to pelvic fin origin, 39.7–43.3 ($\bar{x}$ = 41.0); length of anal fin base, 20.2–23.2 ($\bar{x}$ = 21.4) ..... *C. consocium reseratum*

b. Gill rakers, 19–28 ($\bar{x}$ = 23); snout to pelvic fin origin, 40.9–51.2 ($\bar{x}$ = 44.0); length of anal fin base, 17.1–22.2 ($\bar{x}$ = 19.4) ..... *C. humboldtianum* (See also 16b, 22a)

21a. Predorsal scales, 24–50 22

b. Predorsal scales, 50–117 23

22a. Median lateral scales, 47–73 ($\bar{x}$ = 60) ..... *C. humboldtianum* (See also 16b, 20b)

b. Median lateral scales, 67–86 ($\bar{x}$ = 75) ..... *C. estor copandaro* (See also 23b)

23a. Mandible length, 12.2–17.9 24

b. Mandible length, 10.3–12.2 (based on small specimens) ..... *C. estor copandaro* (See also 22b)

24a. Median lateral scales, 52–76; mandible length, 13.1–17.9; length of anal fin base, 19.2–23.4; lower jaw may protrude beyond snout by as much as one-half the interorbital distance; teeth may be small or large ..... *C. lucius* (See also 28b)

b. Median lateral scales, 65–90; mandible length, 12.2–14.8; length of anal fin base, 16.1–21.0; lower jaw does not protrude beyond snout; teeth always small ..... *C. estor estor*

25a. Gill rakers, 14–20 26

b. Gill rakers, 23–28 28

26a. Snout blunt; teeth on upper lip, easily seen or felt when mouth is closed; fins may be pigmented black ..... *C. arge* (See also 3a)

b. Snout pointed; no teeth on upper lip; anal fin rays, 18–23 27

27a. Snout strongly pointed; premaxillaries sharply decurved leaving gap in bite when mouth is closed; head length, 27.9–29.8; snout length, 10.1–12.1; mandible length, 12.5–14.5 ..... *C. aculeatum*

b. Snout pointed; no gap in bite when mouth is closed; head length, 23.5–27.1; snout length, 8.3–9.9; mandible length, 9.9–11.7 ..... *C. labarcae*

28a. Snout pointed, narrow; lower jaw projects only slightly beyond snout; interdorsal scales, 8–29 ($\bar{x}$ = 18) ..... *C. sphyraena*

b. Snout blunt, wide; lower jaw may project up to one-half the interorbital distance beyond the snout; interdorsal scales, 6–17 ($\bar{x}$ = 10) ..... *C. lucius* (See also 24a)

The Jordani Group

Description.—Lateral line scales usually with canals; scale margins usually laciniate; median lateral scales, 36–90; predorsal scales, 16–136; interdorsal scales, 0–29; gill rakers, 14–34; vertebrae, 35–47; pectoral fin rays, 10–18; anal fin rays, 14–24. The species range in size from small to the largest of all *Chirostoma* and include: *C. jordani*, *C. patzcuaro*, *C. chapalae*, *C. consocium*, *C. humboldtianum*, *C. estor*, *C. grandocule*, *C. lucius*, *C. sphyraena* and *C. promelas*.

CHIROSTOMA JORDANI WOOLMAN

Fig. 16a

Chirostoma jordani Woolman, 1894:62, Pl. 2, lectotype: USNM 125441, type locality: Río Lerma and canals at Salamanca, Guanajuato; Bean, 1898:540; Meek, 1902:112, 1903:783, 1904:169, Fig. 52; Regan, 1906–08:59, Tab. 10, Fig. 3 (in part); Jordan and Hubbs, 1919:70, Pl. 6, Fig. 21; Jordan, Evermann and Clark, 1928:250; Cuesta Terron, 1931:238; Martin del Campo, 1936:272; De Buen, 1940a:306, 1940c:48, 1941c:7, 1943:212; Alvarez, 1950b:92, 1953:98, 1963:129; Alvarez and Navarro, 1957:8, 16, 50; Alvarez and Cortés, 1962:122. *Chirostoma brasiliensis*, Jordan, 1879:299. *Atherinichthys brevis* Steindachner, 1894:49. *Chirostoma breve*, Von Bayern and Steindachner, 1895:526, Pl. 2, Fig. 2; Regan, 1906–08:59, Tab. 10, Fig. 3 (in part). *Eslopsarum jordani*, Jordan and Evermann, 1895:330, 1896–1900:2840, Fig. 335; Jordan and Snyder, 1899:133; Evermann

and Goldsborough, 1900:152. *Chirostoma mezquital* Meek, 1904:170, Fig. 53; Jordan and Hubbs, 1919:70, Fig. 20; Cuesta Terron, 1931:238; Jordan, Evermann and Clark, 1928:250; De Buen, 1940c:48; Martin del Campo, 1940:483. *Eslopsarum jordani mezquital*, De Buen, 1945:503, 1946b:114, 1947: 282. *Chirostoma jordani mezquital*, Schultz, 1948:32; Alvarez, 1950a:101, 1970:124. *Eslopsarum jordani jordani*, De Buen, 1945:501, 1946b:113, 1947:302. *Chirostoma jordani jordani*, Schultz, 1948:31; Alvarez, 1950a:101, 1970:123; Alvarez and Navarro, 1957:43. *Chirostoma hidalgoi*, Alvarez, 1953:25.

Diagnosis.—Median lateral scales, 36–48; gill rakers, 14–22; distance from snout to anal fin origin, 49.0–58.2, $\bar{x} = 53.3$ in percent of standard length; snout length, 4.8–9.8; length of caudal peduncle, 18.6–26.2; height of second dorsal fin, 13.4–22.2, $\bar{x} = 18.3$; length of anal fin base, 18.0–32.4; teeth small to minute, not visible when the mouth is closed, snout usually angular in profile; lateral line scales with either round pores or canals, often on the same specimen with the former predominating; scales on the sides of the body usually with entire edges, laciniate scales present in the predorsal region in large adult specimens (see also below under *Variation*).

Description.—Maximum length for species approximately 70 mm S.L., one specimen from Lake Chapala was 91 mm; body slender to moderately deep; mouth small, oblique, teeth in one or two rows or in a narrow band on premaxillaries and in two rows or a wider band on dentaries, none on vomer or palatines; pectoral fins moderately long and rounded; melanophores faintly concentrated along the posterior margin of the caudal fin in many populations.

Remarks.—Lectotype herein designated, USNM 125441; paralectotypes, USNM 47509 (2), USNM 203104 (1), UMMZ 187660 (1), UMMZ 187661 (1), FMNH 6770 (5), SU 788 (4), CAS 14250 (2), BM 1894 1.27 (7). *C. jordani* was described from a series collected by Woolman and Cox during the summer of 1891. No type was designated, although the description was clearly based on specimens taken from the Río Lerma at Salamanca, Guanajuato. Additional specimens were mentioned as having been collected from canals at Salamanca and from the City of Mexico. The text was accompanied by an illustration of a specimen from Mexico City and presumably was the reason for Jordan and Hubbs' (1919) restriction of the type locality to the Valley of Mexico. As the populations in this basin are slightly different from those found in the Lerma drainage, I here designate the canals and the Río Lerma at Salamanca as the type locality. Unfortunately, the locality on the labels with the type specimens is merely "Salamanca" making it impossible to differentiate between those taken in the canals and in the river.

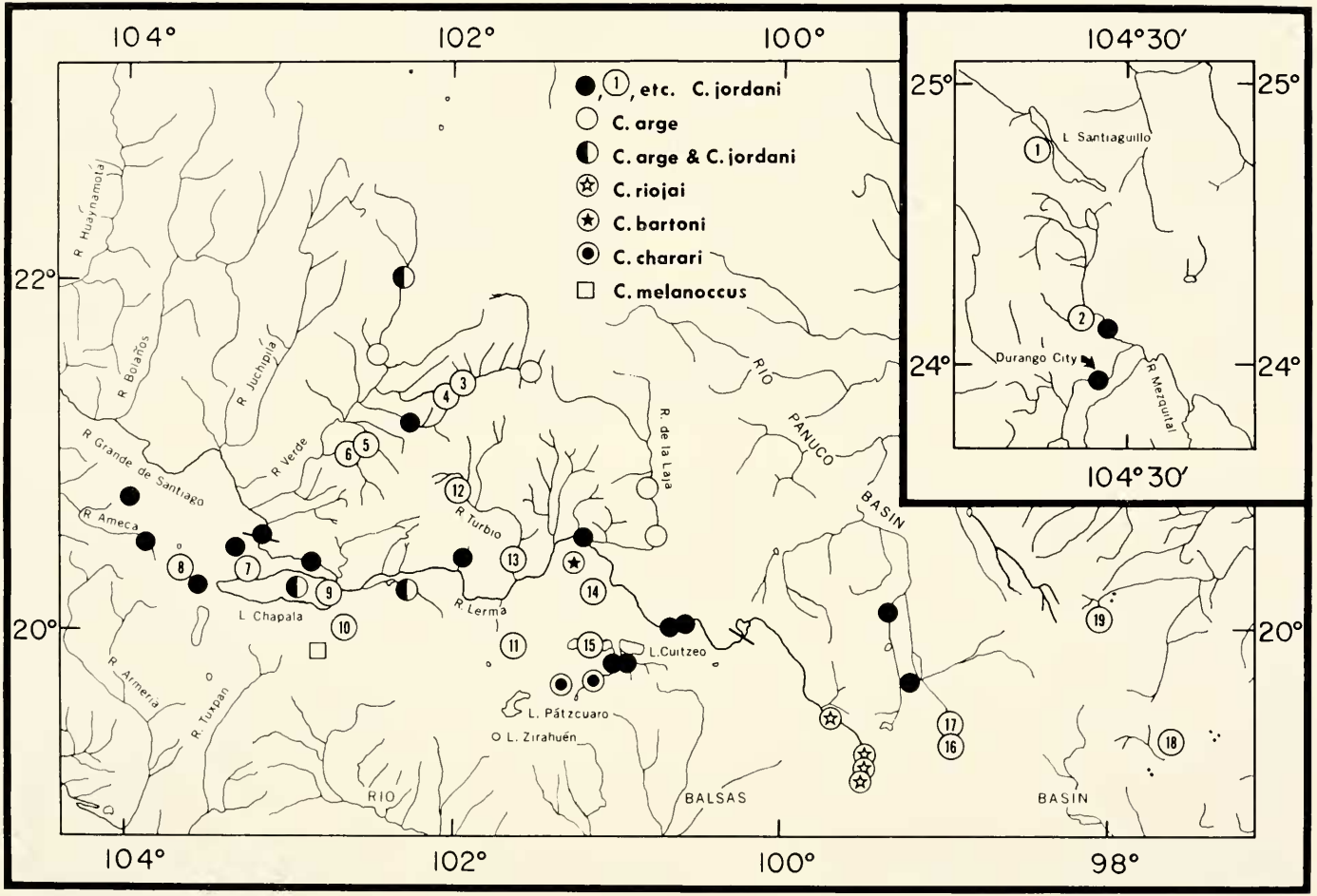
C. jordani was taken from small ponds and streams as well as from the main channel of the Río Santiago and some of the larger lakes. In most cases the species was found associated with vegetation, either drowned terrestrials along the margins of flooded ponds, in and around dense stands of *Scirpus* or under and at the margins of mats of water hyacinth (*Eichornia* sp.). Specimens collected from the Río Santiago at Poncitlán (TU 37759) on July 10, 1963 were spawning and depositing their eggs among the roots of the floating hyacinths.

Variation.—Certain characters are variable over the range of *C. jordani.* Most noticeable are changes in the angularity of the snout and body depth. Most specimens have a very angular snout in lateral view, but large individuals from the Río Grande de Santiago at Poncitlán, Lake Chapala, the Valley of Mexico, El Carmen, Tlaxcala and the Santiaguillo basin north of Durango City, Durango have very blunt snouts. A few individuals from Lake Cuitzeo (UMMZ 172189) share this characteristic. Specimens taken from the above localities, except Lake Cuitzeo, also show a deeper and more robust body.

The number of median lateral and predorsal scales are the only characters demonstrating a pattern of variation (Figs. 2, 3). The recognition of subspecies is not warranted because of the rather uniform differences between the populations. The population in eastern Hidalgo rather than those from the Valley of Mexico or Durango appears to be the most highly differentiated.

The degree of scale laciniation is fairly consistent throughout the range of the species except for the population in eastern Hidalgo. All large individuals collected here had strongly laciniate scales on the sides of the body as well as predorsally.

Range.—Widely distributed on the Mesa Central (Fig. 1). I have not been able to


104°
102°
100°
98°
22°
20°
●, ①, etc. C. jordani
○ C. arge
◐ C. arge & C. jordani
☆ C. riojai
★ C. bartoni
◉ C. charari
□ C. melanoccus
R Huaynamota
R Bolaños
R Juchipila
R Verde
R Grande de Santiago
R Ameca
L Chapala
R Lerma
R Turbio
R de la Laja
RIO PANUCO BASIN
L.Cuitzeo
L. Pátzcuaro
O L. Zirahuén
R Armeria
R Tuxpan
RIO BALSAS BASIN
104°30′
25°
24°
L Santiaguillo
Durango City
R Mezquital

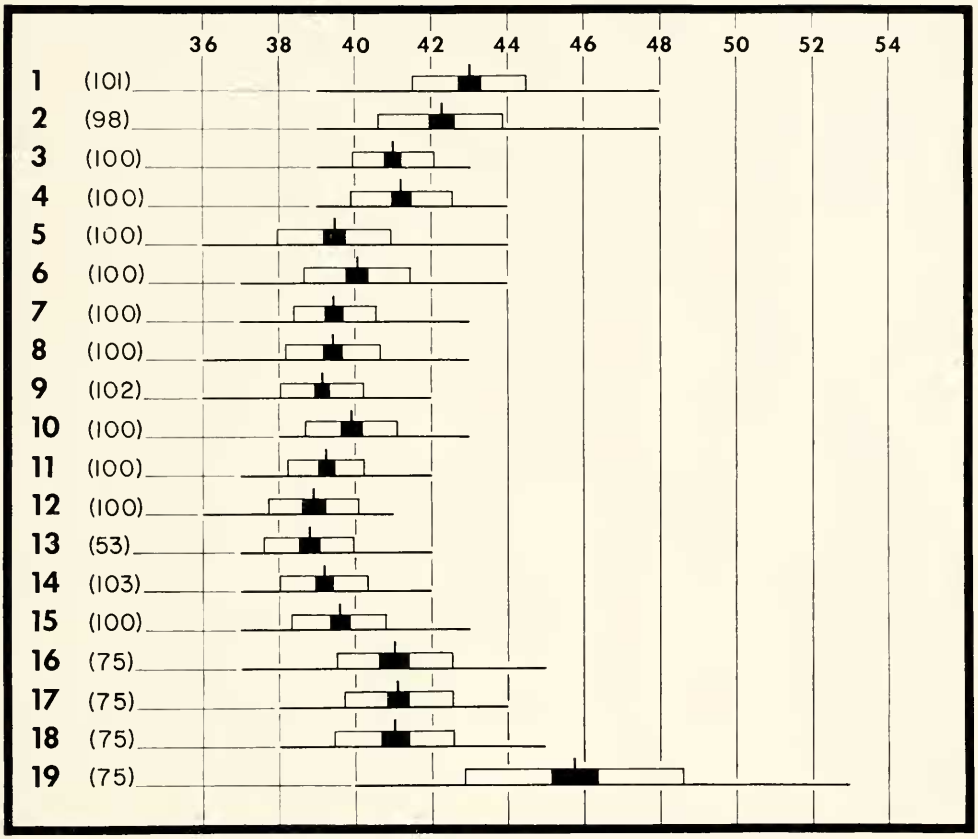


Figure 2. Variation in the number of median lateral scales in *Chirostoma jordani*. For localities and explanation of the diagrams see legends of Figs. 1 and 5.

verify the presence of *C. jordani* in the Balsas system (De Buen, 1945) or recollect this species in the volcanic caldera "La Alberca," Guanajuato. Six specimens were reportedly obtained from the latter locality by A. Dugès, a resident of the city of Guanajuato and cataloged in the U.S. National Museum of Natural History in 1879 (USNM 23135).

Material examined.—The numbers in boldface (1–19) preceding some of the collections correspond to the numbers in Figs. 2, 3. Aguascalientes: FMNH 3581 (7), SU 6178 (2), Río Verde at Aguascalientes. Durango: FMNH 4389, holotype of *Chirostoma mezquital*, Río Mezquital at Durango; ANSP 90855 (1), paratype of *C. mezquital*, Río Mezquital at Durango, out of FMNH 4390; **2**, FCB 484 (1073), TU 40108 (50), TU 37746 (230), at bridge over creek at Guatimapé; TU 40107 (107), **1**, FCB 473 (909), TU 37745 (3289), Presa Peña del Aguila on Río Veintidos ca. 12 mi. N Durango City on hwy. 45 (at Km 1069); CAS 13591 (58), Río Canatlán, trib. of Río Mezquital 22 km N Durango; CAS 13592 (32), Río de Santiago, trib. of Río Mezquital at hwy. crossing 11 mi. E of Durango; USNM 132488 (12), Durango; UMMZ 197644 (12), Río Mezquital and adjacent spring-fed ponds, 9 mi. NE Du-

←

Figure 1. Distribution of six species of *Chirostoma* on the Mesa Central of Mexico. Not all collections at a given locality or within a lake are shown. Lake Chapala species probably occur also in adjacent parts of the Río Lerma and the Río Grande de Santiago. Numbers marking localities of *C. jordani* correspond to the boldface numbers in Figs. 2 and 3 and to those preceding the catalogue numbers in the *Material Examined* section for this species. The solid lines across the Lerma-Santiago river indicate the locations of, west to east, the waterfalls at Juanacatlán and below Tepuxtepec dam. Abbreviations: L., Lake; R., Río.

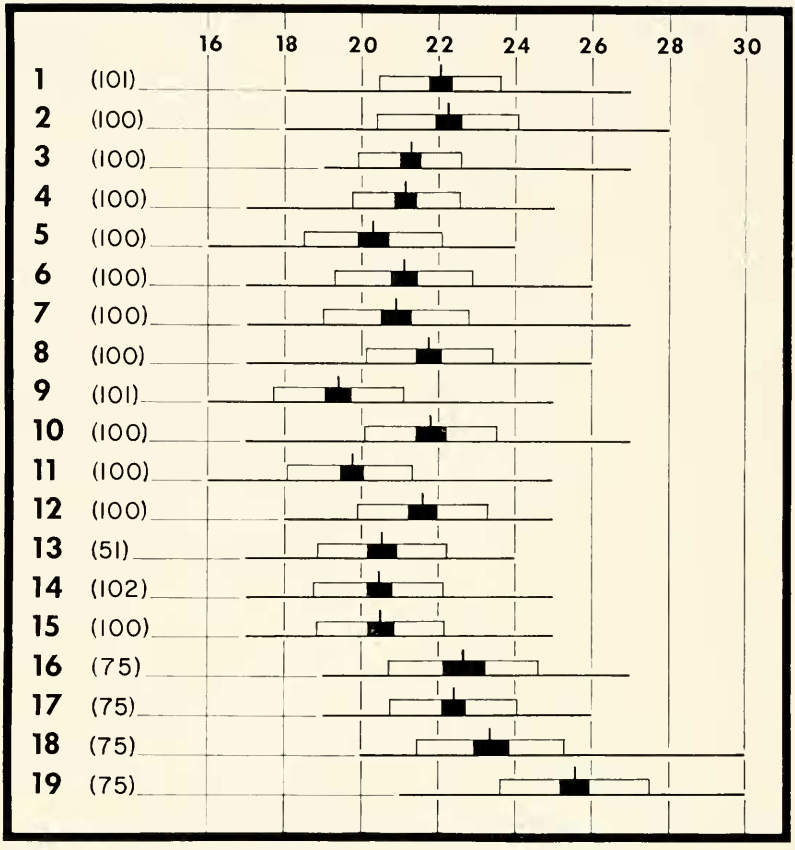


Figure 3. Variation in the number of predorsal scales in *Chirostoma jordani*. For localities and explanation of the diagrams see legends of Figs. 1 and 5.

rango City, hwy. 40; UMMZ 197643 (4), effluent stream below Peñon del Aguila dam, 4.2 mi. N Morcillo, hwy. 45. Guanajuato: USNM 125441, lectotype, USNM 47509 (2), USNM 203104 (1), UMMZ 187660 (1), UMMZ 187661 (1), FMNH 6770 (5), SU 788 (4), CAS 14250 (2), BM 1894 1.27 (7), paralectotypes, Río Lerma and canals at Salamanca; ANSP 90852 (2), USNM 55783 (5), FMNH 3598–3599 (23), Acámbaro; TU 31884 (1), Lake Yuriria, 8.2 mi. around W end of lake from town of Yuriria; UMMZ 197627 (77), **14**, TU 37747 (9126), S shore of Lake Yuriria ca. 1.5 mi. E of Yuriria; USNM 23135 (6), Alberca, Valle de Santiago; UMMZ 197602 (90), **13**, UMMZ 197620 (598), UMMZ 197645 (2), Río Turbio 8 mi. E Pénjamo at hwy. 110 crossing; UMMZ 197603 (23), Solis dam 4 mi. N Acámbaro, UMMZ 197625 (461), ditch draining into W end of Lake Yuriria 2.5 mi. N jct. hwys. 43 and 49; **12**, UMMZ 197621 (386), trib. to Río Turbio 18.5 mi. NW Cuerámaro; UMMZ 197619 (89), trib. to Río Lerma 5 mi. NE Piedad at hwy. 110 crossing. Hidalgo: P 768 (41), Río Tula at Endó dam (Pánuco drainage); **19**, UMMZ 197628 (148), UMMZ 197629 (247), dam 1.1 mi. W jct. hwys. 130 and 119 (to Zacatlán). Jalisco: UMMZ 173567 (ca. 1615), Lake Tilapana (Lake Atotonilco) at town of Tizapanito (Villa Corona); UMMZ 154335 (19), roadside pond 11 mi. SW of Guadalajara; UMMZ 164698 (36), el Canal de la Presa de Logado ca. 12 mi. S of Guadalajara on Jalisco hwy. no. 35—Guadalajara–Chapala; UMMZ 179714 (3), flooded edge of Lake Chapala ca. 1 mi. S of Ocotlán near source of Río Grande de Santiago; UMMZ 108642 (25), Río Grande de Santiago between Ocotlán and Lake Chapala; UMMZ 173561 (41), Lake Colorado sev. mi. E of Etzatlán; UMMZ 173804 (1), Río Ameca, 7 mi. E of Ameca; UMMZ 179744 (1), Lake Chapala at Tuxcueca on S side of lake; UMMZ 179702 (5), lateral irrigation ditch off main E–W canal, 2.5 mi. due N of Etzatlán on road to Magdalena; TU 31956 (25), Río Santiago at Poncitlán; UMMZ 197608 (6), TU 31994 (1), Río Santiago et El Salto de Juanacatlán, below falls; **3**, TU 37761 (633), dam ca. 2 mi. W of Lagos de Moreno on hwy. 80; **4**, TU 37757 (255), dam ca. 7 mi. W Lagos de

Moreno on hwy. 80; TU 37751 (3), Alcala dam on Río San Juan de los Lagos, ca. 2 mi. E San Juan de los Lagos; **5**, TU 37760 (766), trib. to Río Verde ca. 6 mi. NE Valle de Guadalupe on hwy. 80; **6**, TU 37756 (119), trib. to Río Verde 2 mi. NE Valle de Guadalupe on hwy. 80; **9**, TU 37752 (58), Lake Chapala 0.2 mi. E of El Fuerte (E end of lake); **9**, TU 37749 (288), Lake Chapala at source of Río Santiago, 0.5 mi. SW town of Cuitzeo, TU 37759 (26), Río Santiago at Poncitlán; **8**, TU 37758 (819), TU 37750 (242), Lake Atotonilco 0.25 mi. E of Villa Corona; **7**, TU 37748 (1735), Lake Cajititlán at Cajititlán; UMMZ 197609 (1), Río Santiago 3.7 mi. E Atequiza; UMMZ 197607 (36), Lake San Marcos, 8.8 mi. S Acatlán de Juarez, México: UMMZ 197631 (83), small flooded corner of field between San Juan Zitlaltepec and Lake Zumpango. México D.F.: UMMZ 97659 (142), N end of old basin of Lake Texcoco, 2 mi. SE of San Cristobal Exatepec; UMMZ 97660 (53), SW shore of old basin of Lake Texcoco, Valley of Mexico, 9–14 km on Puebla Road; UMMZ 108623 (28), E shore of Lake Texcoco; **17**, UMMZ 173502 (177, additional 71 in exchange coll.), ditch leading into Lake Texcoco, 12 mi. E Mexico City; **16**, TU 37754 (53), canal at W edge of Mixquic; ANSP 90856 (5), FMNH 3685 (13), Xochimilcho. Michoacán: UMMZ 173517 (1306, additional 163 in exchange coll.), Lake Cuitzeo; UMMZ 172189 (31), spring-fed pool on S side of Lake Cuitzeo near causeway; UMMZ 167678 (8), 2 mi. E of La Palma, SE side of Lake Chapala; UMMZ 173627 (16), Lake San Anton (dam at Hauracha) SW of Zamora (not natural lake); UMMZ 173635 (1), canal at Tarecuato (behind dam) SW of Zamora; will form new dam for irrigation; **11**, TU 31923 (288) Wilson dam at La Estancia de Villa Jimenez 14.3 mi. NE Zacapu; **15**, TU 31890 (126), S shore of Lake Cuitzeo at end of causeway, 3.3 mi. S Cuitzeo on hwy. 47; TU 37755 (26), trib. to Río Lerma at NE end of Tanhuato above the bridge; TU 37753 (8), S shore of Lake Cuitzeo along the causeway; USNM 48210 (3), Lake Cuitzeo; UMMZ 197615 (157), trib. to Río Lerma at N end of Tanhuato below earthen dam; **10**, UMMZ 197646 (148), spring-fed pond N Jaripo; UMMZ 197637 (23), irrigation ditch 5.5 mi. NE Alvaro Obregón; UMMZ 197636 (1), irrigation ditch (Río Grande de Morelia?) 3.7 mi. NE Alvaro Obregón; UMMZ 197626 (116), S shore Lake Cuitzeo, E side of causeway around flooded spring. Morelos: USNM 121844 (39), Yautepec, bought in market. Tlaxcala: P 637 (12); Lake Carmen; **18**, UMMZ 197630 (221), effluent from warm spring, S side of hwy. 1 mi. E El Carmen.

CHIROSTOMA PATZCUARO MEEK

Chirostoma patzcuaro Meek, 1902:112, holotype: FMNH 3628, type locality: Lake Pátzcuaro, Michoacán, 1904:174, Fig. 56; Regan, 1906–08:58; Jordan and Hubbs, 1919:73, Fig. 26; Jordan, Evermann and Clark, 1930: 250; Cuesta Terron, 1931:239; Solórzano, 1961:20, Fig. 4; Alvarez and Cortés, 1962: 124; Alvarez, 1970:124. *Chirostoma bartoni* var. *patzcuaro*, De Buen, 1940b:22, 1940c: 49. *Chirostoma regani*, Martin del Campo, 1940:483 (in part). *Chirostoma bartoni*, De Buen, 1941d:73 (in part), 1943:212 (in part). *Chirostoma bartoni bartoni*, De Buen, 1941c:5 (in part), 1942:41 (in part), 1944a: 264 (in part), Schultz, 1948:31 (in part); Alvarez, 1950a:100 (in part). *Eslopsarum bartoni bartoni*, De Buen, 1945:506 (in part), 1946b:114 (in part).

Diagnosis.—Median lateral scales, 52–63; predorsal scales, 24–34; anal rays, 15–18; gill rakers, 23–29; head length, 24.5–25.9 in percent of standard length; eye length, 5.6–6.1; mandible length, 8.8–9.9; length of anal fin base, 16.6–20.6; snout pointed to moderately pointed; scale margins laciniate.

Description.—Maximum length of specimens examined 104 mm S.L.; body slender; head moderate, subtriangular to triangular; snout included by lower jaw; teeth small, in bands, none on vomer or palatines; predorsal scales slightly crowded; lateral line scales with pores and canals; pectoral fins moderately long and pointed.

Range.—Known only from the type locality, Lake Pátzcuaro, Michoacán.

Materials examined.—Michoacán: FMNH 3628, holotype; FMNH 3629 (1), ANSP 90842 (1), paratypes; TU 30882 (6); TU 40852 (16). All from Lake Pátzcuaro.

CHIROSTOMA CHAPALAE JORDAN AND SNYDER

Fig. 17d

Chirostoma chapalae Jordan and Snyder, 1899: 135, holotype: SU 6155, type locality: Ocotlán, Jalisco (Lake Chapala); Jordan and Evermann, 1896–1900:3159; Pellegrin, 1901: 205; Meek, 1902:115, 1904:176, Fig. 58; Regan, 1906–08:61; Jordan and Hubbs, 1919: 76, Fig. 28; Jordan, Evermann and Clark, 1928:251; Cuesta Terron, 1931:239; De Buen, 1940c:49, 1943:212, 1945:515, 1946a:278, 1946b:114; Schultz, 1948:31; Alvarez, 1950: 103, 1970:127; Alvarez and Cortés, 1962:124.

Diagnosis.—Median lateral scales, 44–55; predorsal scales, 29–49; gill rakers, 25–29; head length, 23.8–25.5 in percent of standard length; mandible length 8.6–9.4. Distinguished from *C. consocium consocium* (ranges and means in parentheses) by a smaller maximum size, 87 mm S.L. (125 mm S.L.); having fewer median lateral scales, $\bar{x} = 49.7$ (52–68, $\bar{x} = 60.7$); fewer predorsal scales, $\bar{x} = 37.1$ (43–79, $\bar{x} = 55.6$);

shorter head, $\bar{x}$ = 24.5 (24.4–28.0, $\bar{x}$ = 26.2); shorter mandible, $\bar{x}$ = 8.9 (9.2–11.0, $\bar{x}$ = 10.1); narrower caudal peduncle, 7.6–8.8, $\bar{x}$ = 8.3 (8.2–9.8, $\bar{x}$ = 9.0).

Description.—Body slender; mouth small, oblique, more so than in *C. c. consocium*; jaws weak but project slightly beyond a pointed, angular snout exposing teeth; teeth small, in a narrow band on premaxillaries and in two or three rows or a wider band on the dentaries, none on vomer or palatines; scales deciduous, margins laciniate, but not as strongly so as in the larger species, moderately crowded in predorsal region; lateral line scales with canals; pectorals moderately long and pointed. Melanophores usually found faintly concentrated along the posterior margin of the caudal fin.

Remarks.—Jordan and Hubbs (1919) reported hybrids between *C. chapalae* and *C. consocium*. Their specimens fall within the normal range of overlap between the two species and being small lack adult body proportions. Hybridization between the two forms is not ruled out, but an accurate determination of Jordan and Hubbs' specimens is not possible. A few specimens showing mixed affinities between these two species have been collected from the Río Grande de Santiago at Poncitlán (UMMZ 197612, UMMZ 197613).

Range.—Lake Chapala, Jalisco-Michoacán and the Río Grande de Santiago at Poncitlán. Two collections in the U.S. National Museum of Natural History are labeled "Morelos" and "Puebla." Although records of *C. chapalae* from outside the present Lake Chapala basin would be of great interest, I consider these localities to be in error.

Material examined.—Jalisco: SU 6155, holotype, Lake Chapala at Ocotlán, SU 6209 (6), paratypes, same data as the holotype. UMMZ 108640 (3), Río Grande de Santiago between Ocotlán and Lake Chapala, or outlet end of lake nearby; UMMZ 124463 (127), Lake Chapala; UMMZ 179716 (2), flooded edge of Lake Chapala ca. 1 mi. S of Ocotlán near source of Río Grande de Santiago; UMMZ 173543 (61), Lake Chapala, N shore, 0.5 mi. W town of Chapala at Manglar; TU 40836 (225), Lake Chapala at Ajijic; TU 40813 (1), Lake Chapala 0.2 mi. E El Fuerte, at E end of lake; TU 40873 (1), UMMZ 197612 (22), TU 40822 (1), Río Santiago at Poncitlán; TU 40878 (48), Lake Chapala 4.8 mi. W town of Chapala at Ajijic. Michoacán: UMMZ 187667 (4), La Palma. Morelos: USNM 130898 (1), Morelos? Puebla: USNM 130882 (75), Puebla?

CHIROSTOMA HUMBOLDTIANUM (VALENCIENNES)

Fig. 16b

Atherina humboldtiana Valenciennes, 1835: 479, Pl. 306, holotype: presumably in the Berlin Museum (Maurice Blanc, Paris Museum, pers. comm.), type locality: Valley of Mexico. *Atherina vomerina* Valenciennes, 1835:481. *Atherinichthys humboldtii*, Gunther, 1861:404. *Atherina fontinalis* Cházari, 1884:80. *Chirostoma humboldtianum*, Von Bayern and Steindachner, 1895:522, Pl. 1, Fig. 1; Jordan and Evermann, 1895:330, 1896–1900:793; Evermann, 1893:103; Jordan and Snyder, 1899: 134; Evermann and Goldborough, 1901:152; Meek, 1902:114 (in part), 1904:175 (in part); Regan, 1906–08:60; Jordan and Hubbs, 1919:73, Fig. 27; Jordan, Evermann and Clark, 1928:250; Cuesta Terron, 1931:239; Altini, 1940:104; Martin del Campo, 1940:484; De Buen, 1940b:24, 1940c:49, 1942:42, 1943:212, 1945:512, 1946b:114; Schultz, 1948:31; Alvarez, 1950a: 103, 1970:127; Alvarez and Navarro, 1957: 40; Romero, 1967:69. *Chirostoma humboldtiana*, Seurat, 1898:26. *Chirostoma regani*, Jordan and Hubbs, 1919:74; Jordan, Evermann and Clark, 1928:250; Martin del Campo, 1940:485 (in part); De Buen, 1940c: 49, 1941b:5; Schultz, 1948:31; Alvarez, 1950: 100, 1970:124; Alvarez and Navarro, 1957: 46. *Chirostoma bartoni*, De Buen, 1943:214 (in part); Solórzano, 1961:15 (in part). *Chirostoma bartoni bartoni*, De Buen, 1941c: 7 (in part), 1942:41 (in part), 1944a:269 (in part); Alvarez and Cortés, 1962:123 (in part). *Chirostoma breve*, Regan, 1906–08: 59, Pl. 10, Fig. 3 (in part); Altini, 1940:103 (in part). *Eslopsarum regani*, De Buen, 1945:509, 1946b:114. *Chirostoma ocampoi* Alvarez, 1963a:197, 1970:126.

Diagnosis.—Median lateral scales, 43–73; predorsal scales, 24–50; gill rakers, 19–28; distance from snout to pelvic fin origin, 40.9–51.2 in percent of standard length; head length, 25.6–34.2; postorbital head length, 12.2–16.8; eye length, 4.6–7.8; snout length, 8.4–13.4; length of anal fin base, 17.1–22.2.

Description.—Maximum length for species approximately 200–250 mm S.L.; body slender to moderately deep; snout blunt or subtriangular, equal to or included by a slightly projecting lower jaw; teeth small, in bands, two or three occasionally present on vomer; scale margins laciniate lateral line scales with canals; predorsal scales moderately crowded; pectoral fins short, slightly pointed.

Remarks.—The reported presence of *C. humboldtianum* in Lake Pátzcuaro and of

C. estor in the Valley of Mexico by Meek (1902, 1904) has been a steady source of confusion. Alvarez and Navarro (1957) suggest that he either bought them in a market and was given erroneous locality data or that he mixed his collections accidentally. The latter interpretation seems to be the most reasonable. There can be little doubt, however, about the former presence of the nominal *C. regani* in Lake Pátzcuaro although it has not been taken there since Meek's time. Jordan and Hubbs removed the type series for this species (FMNH 73321) from the type series of *C. patzcuaro*. One specimen, possibly a hybrid between the two species, still remains with the paratypes, FMNH 3629.

The morphological differences separating *C. regani* from *C. humboldtianum* noted by Jordan and Hubbs (1919) disappear when specimens of the same size are compared leaving only differences in length and number of median lateral and predorsal scales as diagnostic characters. Length is easily affected by environmental conditions. The two scale characters have too much overlap to justify taxonomic recognition even at the subspecific level. Perhaps *C. regani* represents a form close to *C. patzcuaro* and *C. humboldtianum* once present in the upper Lerma basin but which has introgressed with both species. The capture of a fish in Lake Zacapu, Michoacán identical to the local population of *C. humboldtianum* except for its slightly smaller size and larger scales (median lateral scales, 43; predorsal scales, 20), is significant in this regard.

Chirostoma ocampoi Alvarez described from Lake Zacapu is herein synonymized with *C. humboldtianum*. Although this nominate form has a slightly higher number of gill rakers, taxonomic recognition at any level is not warranted.

The three western populations of *C. humboldtianum* differ from their eastern counterparts by having higher mean values for median lateral and predorsal scales. Overlap is too great, however, to justify a subspecific name. These forms are in danger of extinction. Largemouth bass were introduced into the lake north of Santa Maria in 1961 and into the lake at San Pedro Lagunillas in 1967. All of the poeciliids and goodeids formerly present in the lakes have disappeared. The atherinids have either disappeared (Santa Maria) or have been reduced to an extremely low population level (San Pedro Lagunillas). Lake Juanacatlán, near Navidad, Jalisco, the most remote, was free from introductions in 1963. *C. humboldtianum* is the only fish species at this locality.

The population formerly inhabiting Lake Santa Maria was unusual in possessing a slightly lower number of vertebrae. This was perhaps due to the higher temperature of the water in which they lived.

Specimens of uncertain status.—SU 48299. Three specimens in very poor condition labeled "*Chirostoma humboldtianum* Pátzcuaro." The number of rakers on the first arch, 25, 28, and 28, preclude their being *C. humboldtianum* and an estimated 61, 61, and 63 median lateral scales is slightly low for *C. estor estor*. Strongly projecting lower jaws suggest that they are *C. lucius* from Lake Chapala.

Range.—Lakes within the Valley of Mexico, Río Lerma at Tepuxtepec, Michoacán, Lake Zacapu at Zacapu, Mich., Lake Santa Maria, Santa Maria, Nayarit, Lake at San Pedro Lagunillas, Nay., Lake Juanacatlán, about 10 miles west of Navidad, Jalisco (Fig. 4). See Alvarez and Navarro (1957) for Valley of Mexico localities.

Material examined.—Jalisco: TU 40825 (756) isolated lake about 5 mi. W of Navidad, E of Mascota; USNM 126979 (2), USNM 48839 (3), La Laguna, Sierra de Juanacatlán. México, D. F.: USNM 30485 (3), ANSP 27061–72, City of Mexico; ANSP 14609–13 (6), Lake Chalco; USNM 55785 (6), USNM 55852 (2), UMMZ 187663 (2), UMMZ 187672 (5), UMMZ 187673 (1), FMNH 73320 (109), Xochimilcho; SU 9413 (3), canals, Chalco; SU 9407 (5), Xochimilcho; SU 31945 (3), Valley of Mexico; SU 6210 (28), Mexico City market (said to be from Lake Chalco); SU 17171 (16), Lake Chalco (market, city of Mexico); UMMZ 97662 (1), SW shore of old basin of Lago de Texcoco; UMMZ 97663 (10), Mexico City fish market, vicinity of Xochimilcho, Valley of Mexico; UMMZ 132732 (1), alkaline lake (perhaps Lake Chimalhuacán) Lake Texcoco? Mexico?; FMNH 3687, holotype of *C. regani*, Xochimilcho; FMNH 59536 (10), paratypes of *C. regani*, Xochimilcho; FMNH 43153 (3), paratypes, *C. regani*, Xochimilcho; P 641 (5), P 461 (5), P 810 (4), Chimalhuacán; USNM 51010 (6), Mexico City market, said to have come from Texcoco; UMMZ 187662 (3), USNM 55786 (3), Chalco. Michoacán: USNM 197516 (2), paratypes of *Chirostoma ocampoi*, Laguna de Zacapu; USNM 45534 (3), Michoacán (Pátzcuaro?); UMMZ 197635 (1027),

behind Tepuxtepec dam at Tepuxtepec; UMMZ 197639 (4), outlet stream from Lake Zacapu at Zacapu; TU 40850 (13), TU 31933 (58), Lake Zacapu at Zacapu, mostly in outlet stream; TU 40867 (22), Lake Zacapu at Zacapu; FMNH 73321 (4), Pátzcuaro. Nayarit: FCB 106 (4), TU 40826 (658), Lake just E of San Pedro Lagunillas, about 13 mi. E of Compostela; UMMZ 178317 (319), TU 40828 (10), Lake Santa Maria, about 27 mi. SE of Tepic.

Specimens of unknown localities.—USNM 37804 (2), USNM 39408 (3), USNM 37791 (1).

CHIROSTOMA CONSOCIUM CONSOCIUM JORDAN AND HUBBS

Fig. 17c

Chirostoma consocium Jordan and Hubbs, 1919: 76, holotype: FMNH 3672, type locality: Lake Chapala at La Palma, Michoacán; Jordan, Evermann and Clark, 1928:251; De Buen, 1940c:50, 1943:212, 1945:517, 1946a: 278, 1946b:114; Schultz, 1948:31; Alvarez, 1950a:103, 1970:127; Alvarez and Cortés, 1962:125. *Chirostoma grandocule*, Meek, 1902:115 (in part), 1904:176 (in part). *Chirostoma grandoculis*, Regan, 1906–08:61 (in part).

Diagnosis.—Median lateral scales, 52–68; predorsal scales, 43–79; gill rakers, 24–29; distance from snout to second dorsal fin origin, 63.4–66.7 in percent of standard length; distance from snout to origin of pelvic fin, 37.7–43.0; head length, 24.4–28.0; snout length, 7.2–9.5; least depth of caudal peduncle, 8.2–9.8; snout included by a slightly projecting lower jaw; teeth small.

Description.—Largest specimen examined 125 mm S.L.; body slender, to relatively deep in adults, snout pointed; teeth in bands, outer mandibular and inner median premaxillary series enlarged, none on vomer or palatines; scale margins laciniate; predorsal scales crowded; lateral line scales with canals; pectoral fins long and pointed.

Remarks.—On April 1, 1964 *C. c. consocium* was apparently spawning in very shallow water on the north shore of Lake Chapala 1.6 miles west of the town of Chapala. The eggs were attached to small pebbles and stones by threads and were washed up along the shore in small windrows. In this area the males were bronze colored dorsally while the females were more silvery. Unfortunately, turbid water and near darkness precluded observations of breeding behavior.

Range.—Lake Chapala, Jalisco–Michoacán and the Río Grande de Santiago at Poncitlán (Fig. 4).

Material examined.—Jalisco: UMMZ 179718 (3), flooded edge of Lake Chapala ca. 1 mi. S of Ocotlán, near source of Río Santiago; UMMZ 108637 (3), Río Grande de Santiago between Ocotlán and Lake Chapala or outlet of lake nearby; UMMZ 179720 (6), Lake Chapala at Jamay near E end of lake; UMMZ 179748 (2), Lake Chapala at Texcueca on S side of lake; UMMZ 197613 (4), TU 40819 (23), TU 31957 (13), Río Santiago at Poncitlán; TU 31969 (233), Lake Chapala 1.6 mi. W town of Chapala; TU 31927 (3), Lake Chapala 15.8 mi. W of town of Chapala at Jocotepec; TU 31989 (400), Lake Chapala at Ajijic; TU 40815 (11), Lake Chapala ca. 0.2 mi. E of El Fuerte at E end of lake; TU 40832 (3), Lake Chapala at Ajijic by cement pier; TU 40833 (2), Lake Chapala, Isla de los Alacranes, S shore in areas especially cleared for throw-net by fisherman; TU 40845 (5,000+), Lake Chapala at Ajijic. Michoacán: FMNH 3672, holotype; SU 17776 (6), paratypes; UMMZ 187668 (6), all from La Palma.

CHIROSTOMA CONSOCIUM RESERATUM ALVAREZ

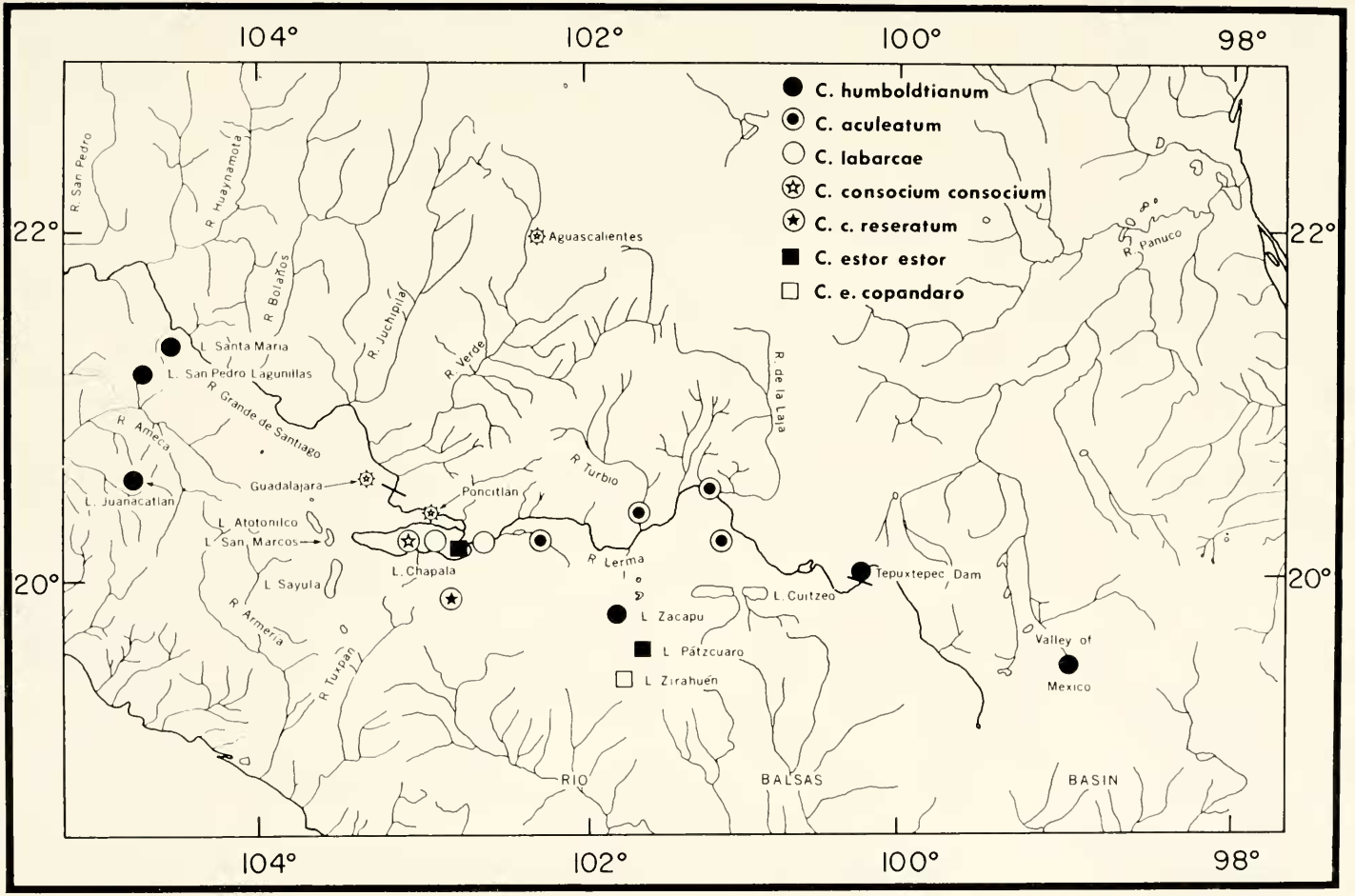
Fig. 18c

Chirostoma reseratum Alvarez, 1963b:130, holotype: P732, type locality: San Juanico dam, near Cotija, Michoacán, 1970:128.

Diagnosis.—Differs from the nominate form (ranges and means in parentheses) by having fewer predorsal scales, 33–56, $\bar{x}$ = 42.4 (43–79, $\bar{x}$ = 55.6); fewer anal fin rays, 16–21, $\bar{x}$ = 18.2 (17–24, $\bar{x}$ = 20.3); shorter anal fin base, 20.2–23.2, $\bar{x}$ = 21.4 (21.7–26.2, $\bar{x}$ = 23.9). Differs from *C. humboldtianum* by having a higher number of gill rakers, 23–30, $\bar{x}$ = 27.2 (19–28, $\bar{x}$ = 23.0); shorter distance from snout to pelvic fin origin, 39.7–43.3, $\bar{x}$ =41.0 (40.9–51.2, $\bar{x}$ = 44.0) in percent of standard length; shorter postorbital head length, 11.5–13.2, $\bar{x}$ = 12.3 (12.2–16.8, $\bar{x}$ = 13.8); longer eye, 6.2–7.4,

→

Figure 4. Distribution of five species and two subspecies of *Chirostoma* on the Mesa Central of Mexico. For explanation of figure see legend of Fig. 1.


104°
102°
100°
98°
22°
20°
C. humboldtianum
C. aculeatum
C. labarcae
C. consocium consocium
C. c. reseratum
C. estor estor
C. e. copandaro
R. San Pedro
R. Huaynamota
R. Bolaños
R. Juchipila
Aguascalientes
R. Verde
R. Panuco
L. Santa Maria
L. San Pedro Lagunillas
R. Grande de Santiago
R. Ameca
R. de la Laja
L. Juanacatlan
Guadalajara
Poncitlan
R. Turbio
L. Atotonilco
L. San Marcos
L. Chapala
R. Lerma
L. Sayula
L. Cuitzeo
Tepuxtepec Dam
R. Armeria
L. Zacapu
L. Pátzcuaro
L. Zirahuén
Valley of
Mexico
R. Turxpan
RIO
BALSAS
BASIN

$\bar{x}$ = 6.9 (4.6–7.8, $\bar{x}$ = 5.9); shorter snout, 7.5–9.5, $\bar{x}$ = 8.6 (8.4–13.6, $\bar{x}$ = 10.0); longer anal fin base, (17.1–22.2, $\bar{x}$ = 19.4). Differs from all other species of *Chirostoma* in the following characters: median lateral scales, 56–69; number of predorsal scales and gill rakers; distance from snout to origin of first dorsal fin, 49.0–51.7; head length, 25.9–28.2; eye length; mandible length, 9.8–11.2; second dorsal fin height, 14.9–18.7; anal fin height, 15.7–18.6.

Description.—Largest specimen examined 114 mm S.L. (218 mm S.L., Alvarez, 1963); body slender; head triangular; snout moderate, included by lower jaw; teeth small, in bands, outer members on dentaries and on median portions of the premaxillaries enlarged, none on vomer or palatines; scale margins laciniate; predorsal scales crowded; lateral line scales with canals; pectoral fins long and pointed.

Remarks.—Morphologically, the nominal *C. reseratum* overlaps both *C. consocium* and *C. humboldtianum* to the extent that recognition at the specific level is not warranted. No differences or apparent patterns emerge when the following characters are compared: distances from snout to first and second dorsal fin origins, length and least depth of caudal peduncle, greatest depth, length of mandible and second dorsal base and interorbital distance. *C. reseratum* falls more or less in between the two species in the number of anal fin rays and in the length of the anal fin base, head, pectoral and pelvic fins. *C. reseratum* and *C. consocium* show varying degrees of concordance when the following characters are examined: number of median lateral scales and gill rakers, height of second dorsal and anal fins, eye width, distances from snout to origin of pelvic and anal fins and snout and postorbital head lengths. Because of the agreement in these characters, *C. reseratum* is treated as a subspecies of *C. consocium*.

Range.—San Juanico dam and effluent stream near Cotija, Michoacán (Fig. 4).

Material examined.—Michoacán: P732 (10), paratypes, TU 40865 (134), TU 31946 (56), San Juanico dam 5 mi. SE Cotija; UMMZ 197642 (3), effluent channel below San Juanico dam 5 mi. SE Cotija.

CHIROSTOMA GRANDOCULE (STEINDACHNER)

Atherinichthys grandoculis Steindachner, 1894: 149, holotype: apparently lost in the collection of the Naturhistorisches Museum, Vienna, type locality: Lake Pátzcuaro, Michoacán. *Chirostoma grandocule*, Von Bayern and Steindachner, 1895:525, Pl. 2, Fig. 1; Jordan and Evermann, 1895:330, 1896–1900:2839; Meek, 1902:115 (in part), 1904:176 (in part); Jordan and Hubbs, 1919:79; Jordan, Evermann and Clark, 1928:251; Cuesta Terron, 1931:239; De Buen, 1940a:307, 1940c: 50, 1941d:74 (in part), 1943:212 (in part), 1945:516, 1946b:114; Martin del Campo, 1940:483; Schultz, 1948:31; Alvarez, 1950a: 102, 1970:126; Alvarez and Cortés, 1962:124.

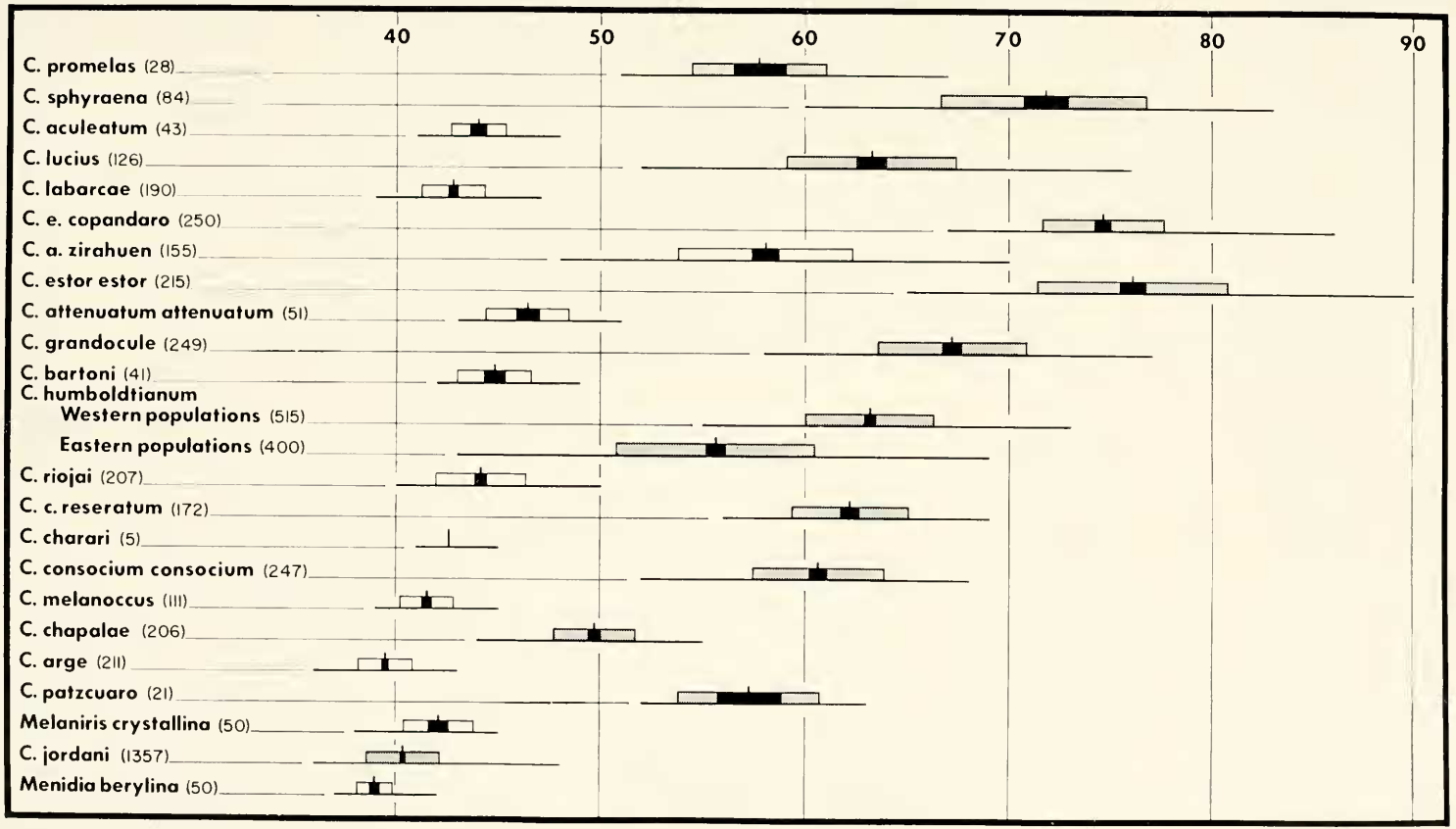
Diagnosis.—Median lateral scales, 58–77; gill rakers, 28–34; anal rays, 18–22; least depth of caudal peduncle, 7.3–8.1 in percent of standard length; height of second dorsal fin, 13.3–14.8; height of anal fin, 13.8–16.2.

Description.—Largest specimen examined 170 mm S.L.; body slender; mouth small; snout short and blunt in adults, included by lower jaw; teeth small, in bands, none on vomer or palatines; predorsal scales moderately crowded; scale margins laciniate; lateral line scales with canals and pores; pectoral fins moderate, slightly pointed.

Remarks.—This species has an exceptionally high number of gill rakers.

→

Figure 5. Comparison of the number of median lateral scales in *Menidia berylina, Melaniris crystallina* and *Chirostoma*. The diagrams indicate the mean (center point), 95 percent confidence limits of the mean (black rectangle), one standard deviation on either side of the mean (outer limits of open rectangle) and sample range (base line). The sample size is given in parentheses following the species name or locality. The sequence of the species is, for the most part, based on presumed phylogenetic relationships with the most primitive at the bottom and the most specialized at the top of the figure. Western populations of *C. humboldtianum* refer to specimens from Lakes Juanacatlán (Navidad), San Pedro Lagunillas and Santa Maria; eastern populations refer to the Tepuxtepec dam, Lake Zacapu and the Valley of Mexico (Fig. 4). Stippling within the standard deviation rectangle denotes members of the jordani species group; clear rectangles denote the arge species group and the possible persistent ancestors of *Chirostoma, Menidia berylina* and *Melaniris crystallina*.


40
50
60
70
80
90
C. promelas (28)
C. sphyraena (84)
C. aculeatum (43)
C. lucius (126)
C. labarcae (190)
C. e. copandaro (250)
C. a. zirahuen (155)
C. estor estor (215)
C. attenuatum attenuatum (51)
C. grandocule (249)
C. bartoni (41)
C. humboldtianum
Western populations (515)
Eastern populations (400)
C. riojai (207)
C. c. reseratum (172)
C. charari (5)
C. consocium consocium (247)
C. melanoccus (111)
C. chapalae (206)
C. arge (211)
C. patzcuaro (21)
Melaniris crystallina (50)
C. jordani (1357)
Menidia berylina (50)

Range.—Known only from the type locality, Lake Pátzcuaro, Michoacán.

Material examined.—Michoacán: TU 40854 (1577), Lake Pátzcuaro, W of Ihuatzio; TU 40861 (4), TU 40880 (14), Lake Pátzcuaro between Napizaro, Jacuaro and Erongaricuaro; TU 40857 (557), Lake Pátzcuaro, S shore of Isla de Yuñen; USNM 55784 (4), UMMZ 187665 (3), Pátzcuaro.

CHIROSTOMA COMPRESSUM DE BUEN

Chirostoma grandocule compressum De Buen, 1940a:306, holotype: lost, originally deposited in the collection of the Pátzcuaro Limnological Station, type locality: Lake Cuitzeo, Michoacán, 1941c:7, 1943:213, 1944a:268. *Chirostoma grandocule*, De Buen, 1941d:74 (in part). *Chirostoma compressum*, De Buen, 1945:518, 1946b:114; Schultz, 1948:31; Alvarez, 1950a:103, 1970:126; Alvarez and Cortés, 1962:125.

Description.—De Buen seems to be the only ichthyologist who has seen this species. His most extensive description (1945), translated, is presented below.

"Body long, compressed; greatest depth and width 72–82 and 42–50 percent of head, respectively; head 19–21 percent of total length; mouth small, weakly oblique, protractile; lower jaw slightly projecting; chin pointed and delicate; orbit 26–30, preorbital distance 33–37.5 and postorbital distance 26–30 percent of head; scales crenulate, 64–67 in the lateral line, 15–16 in the transverse series; teeth small, embedded; 30 long and delicate rakers on the first arch, 23 on the descending portion; first dorsal I, 5–6, origin above insertion of pelvics, midway between tip of snout and base of caudal; second dorsal I, 11–12; anal I, 20–22, inserted in advance of and extending a little behind the second dorsal; color pale, lateral stripe extending along the flanks; dorsal part of head dark; fins pale, second dorsal and caudal slightly darkened; membrane surrounding the ovaries jet black; internal face of the peritoneum is, in part, silver; lengths of two specimens 86 and 101 mm."

Remarks.—*C. compressum* seems to be very close to *C. grandocule*. The species has not been seen since De Buen first collected it and is thought to be extinct. The drying of Lake Cuitzeo during the winter of 1941 (De Buen, 1943) no doubt contributed to its presumed demise. Whereas *C. jordani* was able to survive in small springs and tributaries, a larger species would, perhaps, have difficulty doing so.

Range.—Known only from the type locality, Lake Cuitzeo, Michoacán.

Material examined.—None.

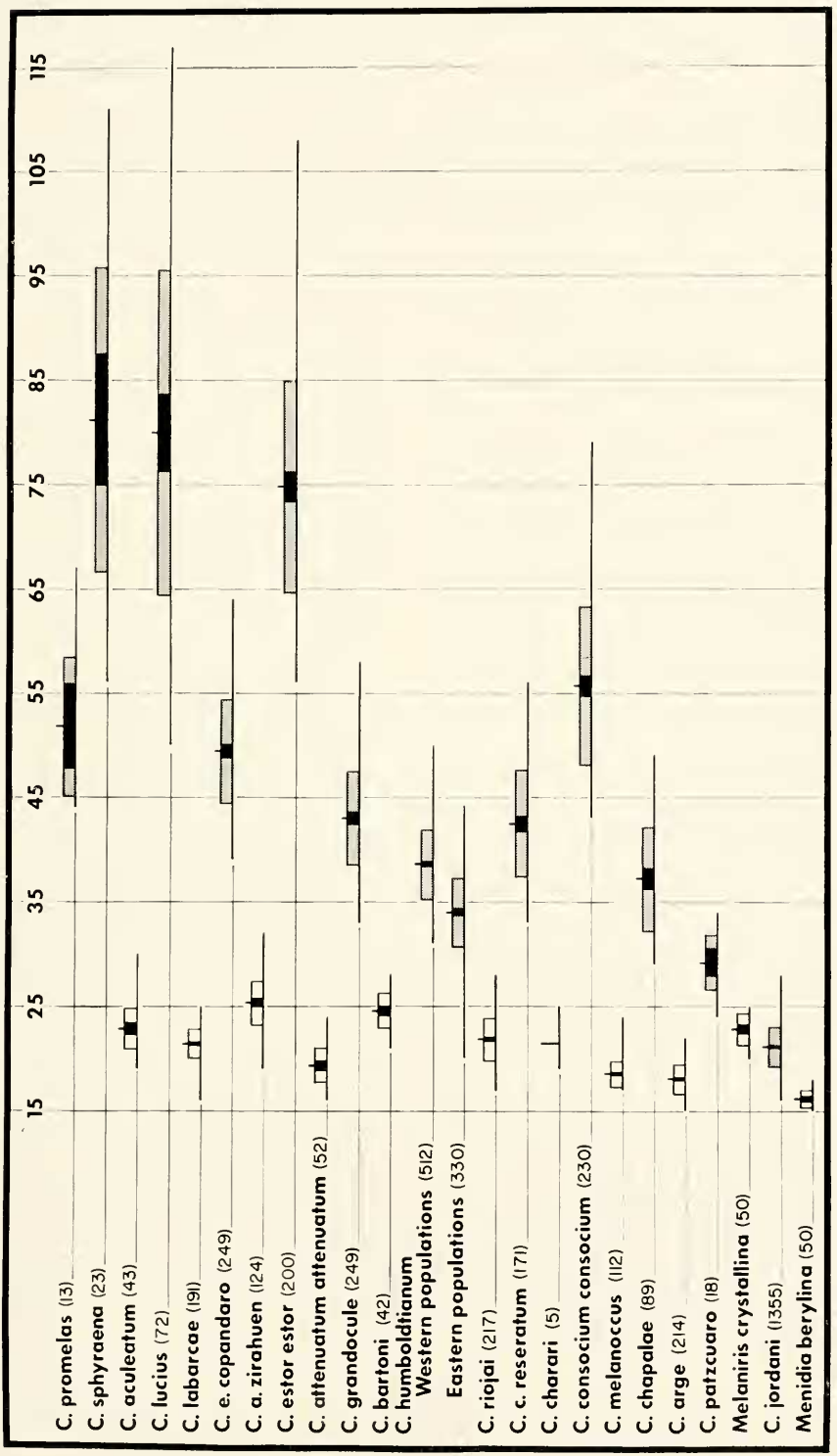
CHIROSTOMA ESTOR ESTOR JORDAN

Chirostoma estor Jordan, 1879:298, holotype: USNM 23124, type locality: Lake Chapala; Von Bayern and Steindachner, 1894:166; 1895:523, Pl. 1, Fig. 3; Jordan and Evermann, 1895:21; Jordan and Snyder, 1899: 141; Jordan and Evermann, 1896–1900:2839, 3165; Jordan, 1900:523; Meek, 1902:116 (in part), 1904:180; Regan, 1906–08:60 in part); Jordan and Hubbs, 1919:81 (in part); Jordan, Evermann and Clark, 1928:251 (in part); Cuesta Terron, 1931:241; Martin del Campo, 1940:485; Altini, 1940:104; De Buen, 1940b:10, Fig. 1, 1940c:51, 1940d:3, 1941d: 75, 1943:212 (in part); Alvarez and Navarro, 1957:48; Solórzano, 1963:1–15. *Chirostoma estor* var. *pacanda* De Buen, 1940a:306, 1940b:12. *Chirostoma estor pacanda*, De Buen, 1941a:30, 1941c:8, 1943:215, 1944a: 265, 1945:523, 1946b:115; Schultz, 1948:31; Alvarez, 1950a:104; Alvarez and Cortés, 1962: 126. *Chirostoma estor* var. *tecuena* De Buen, 1940a:306, 1940b:13, 1940d:5. *Chirostoma estor tecuena*, Martin del Campo, 1940:483. *Chirostoma estor estor*, De Buen, 1941a:30, 1941c:8, 1944a:265, 1945:522, 1946b:115; Schultz, 1948:31; Alvarez, 1950a:104, 1970: 124; Alvarez and Cortés, 1962:126. *Lethostole estor*, Jordan and Evermann, 1896–1900: 792. *Atherinichthys albus* Steindachner, 1894: 148. *Chirostoma* (*Atherinichthys*) *albus*, Von Bayern and Steindachner, 1894:165. *Chirostoma album*, Jordan and Snyder, 1899:146; Jordan and Evermann, 1896–1900:3165. *Chirostoma michoacanae* De Buen, 1940a: 306, 1940b:14, Fig. 20, 1940c:51, 1943:212, 1944a:265; Martin del Campo, 1940:483. *Chirostoma grandocule*, De Buen, 1940b:16, 1945:516.

Diagnosis.—Predorsal scales, 56–108; gill rakers, 23–28; snout to origin of second dorsal fin, 64.1–67.8 in percent of standard length; snout to origin of pelvic fin, 44.1–51.3; postorbital head length, 13.6–16.2;

→

Figure 6. Comparison of the number of predorsal scales in *Menidia berylina*, *Melaniris crystallina* and *Chirostoma*. See legend of Fig. 5 for explanation of the diagrams.


15
25
35
45
55
65
75
85
95
105
115
C. promelas (13)
C. sphyraena (23)
C. aculeatum (43)
C. lucius (72)
C. labarcae (191)
C. e. copandaro (249)
C. a. zirahuen (124)
C. estor estor (200)
C. attenuatum attenuatum (52)
C. grandocule (249)
C. bartoni (42)
C. humboldtianum
Western populations (512)
Eastern populations (330)
C. riojai (217)
C. c. reseratum (171)
C. charari (5)
C. consocium consocium (230)
C. melanoccus (112)
C. chapalae (89)
C. arge (214)
C. patzcuaro (18)
Melaniris crystallina (50)
C. jordani (1355)
Menidia berylina (50)

snout length, 10.5–12.3; least depth of caudal peduncle, 7.3–8.2; length of anal fin base, 16.1–21.0

Description.—Largest specimen examined 273 mm S.L.; head large, triangular; lower jaw projects slightly beyond snout exposing small teeth on anterior portion of mandibles; snout never sharply pointed; gape wide; two or three fang-like teeth occasionally on vomer, none on palatines. Predorsal scales crowded; scale margins laciniate; lateral line scales with canals; pectoral fins small to moderate, rounded or slightly pointed.

Remarks.—Chirostoma estor was described from a specimen received from A. Dugès, a resident of the city of Guanajuato. Dugès presumably bought the fish in the market of that city, obtaining locality information from the vendor. In the catalogue of the U. S. National Museum of Natural History "Guanajuato" is crossed out as the locality and "L. Chapala" written in with the remark: *"Poisson Blanc de Chapala' tel quon l 'apporte a Guanajuato."* As Guanajuato is almost equidistant from Lakes Chapala and Pátzcuaro, it seems reasonable that fishes from both localities were sold there and that the holotype actually came from the latter lake where the species is abundant. However, Meek and Lutz collected seven specimens of *C. estor* from Lake Chapala at La Palma in 1901. As there is a chance that Dugès information was correct, the type locality is retained. To my knowledge, *C. estor* has not been taken from Lake Chapala since 1901.

Meek and Lutz's specimens, FMNH 3672 (1) and SU 17776 (6), labeled "type" and "paratypes" respectively, presumably by Jordan and Hubbs, have no type status.

The food habits and biology of *C. estor estor* have been investigated by De Buen (1944) and Solórzano (1963).

Range.—Known with certainty only from Lake Pátzcuaro, Michoacán and the eastern end of Lake Chapala, Jalisco–Michoacán.

Material examined.—Jalisco: USNM 23124, holotype, Lake Chapala; USNM 44166 (6), Lake Chapala? Michoacán: SU 17776 (6), FMNH 3672 (1), Lake Chapala at La Palma; TU 40855 (21); Lake Pátzcuaro W of Ihuatzio; TU 40863 (90), TU 40886 (135); Lake Pátzcuaro between Napizaro, Jacuaro and Erongaricuaro. UMMZ 187666 (1); Pátzcuaro; USNM 203146 (9); Lake Pátzcuaro.

Specimens of uncertain status.—UMMZ 180082. Two specimens in very poor condition collected by Hobart M. Smith at El Sabeno, near Uruapan, Michoacán during the summer of 1936. In all probability these specimens are close to or conspecific with *C. estor.*

CHIROSTOMA ESTOR COPANDARO DE BUEN

Chirostoma estor copandaro De Buen, 1945:524, holotype: lost, originally deposited in the collection of the Pátzcuaro Limnological Station, type locality: Lake Zirahuén, Michoacán, 1946b:115; Schultz, 1948:31; Alvarez, 1950a:104; Alvarez and Cortés, 1962:127. *Chirostoma estor*, Meek, 1902:116 (in part); Regan, 1906–08:60 (in part); Jordan and Hubbs, 1919:81 (in part); Jordan, Evermann and Clark, 1928:251 (in part); De Buen, 1943:212; *Chirostoma estor pacanda*, Alvarez, 1970:124.

Diagnosis.—Differs from the nominate form (ranges and means in parentheses) by having fewer predorsal scales, 39–64, $\bar{x}$ = 49.3 (56–108, $\bar{x}$ = 74.7); shorter head, 27.3–29.4, $\bar{x}$ = 20.0 (28.0–31.8, $\bar{x}$ = 30.2) in percent of standard length; shorter snout, 9.6–11.4, $\bar{x}$ = 10.2 (10.5–12.3, $\bar{x}$ = 11.4); shorter mandible, 10.3–12.2, $\bar{x}$ = 11.4 (12.2–14.8, $\bar{x}$ = 13.2). Differs from *C. humboldtianum* by having a greater number of median lateral scales, 67–86, $\bar{x}$ = 74.6 (43–73, $\bar{x}$ = 59.7) and a greater number of predorsal scales (24–50, $\bar{x}$ = 36.2). Differs from all other species in the following characters: number of median lateral and predorsal scales; gill rakers, 23–28; snout length; least depth caudal peduncle, 6.6–7.7.

Description.—Similar to *C. estor estor* except that teeth are apparently absent from the vomer of this subspecies.

Range.—Known with certainty only from the type locality, Lake Zirahuén, Michoacán.

Material examined.—Michoacán: USNM 55787 (4), UMMZ 187664 (4), UMMZ 197650 (300), TU 31919 (447), Lake Zirahuén, 19 mi. S of Pátzcuaro.

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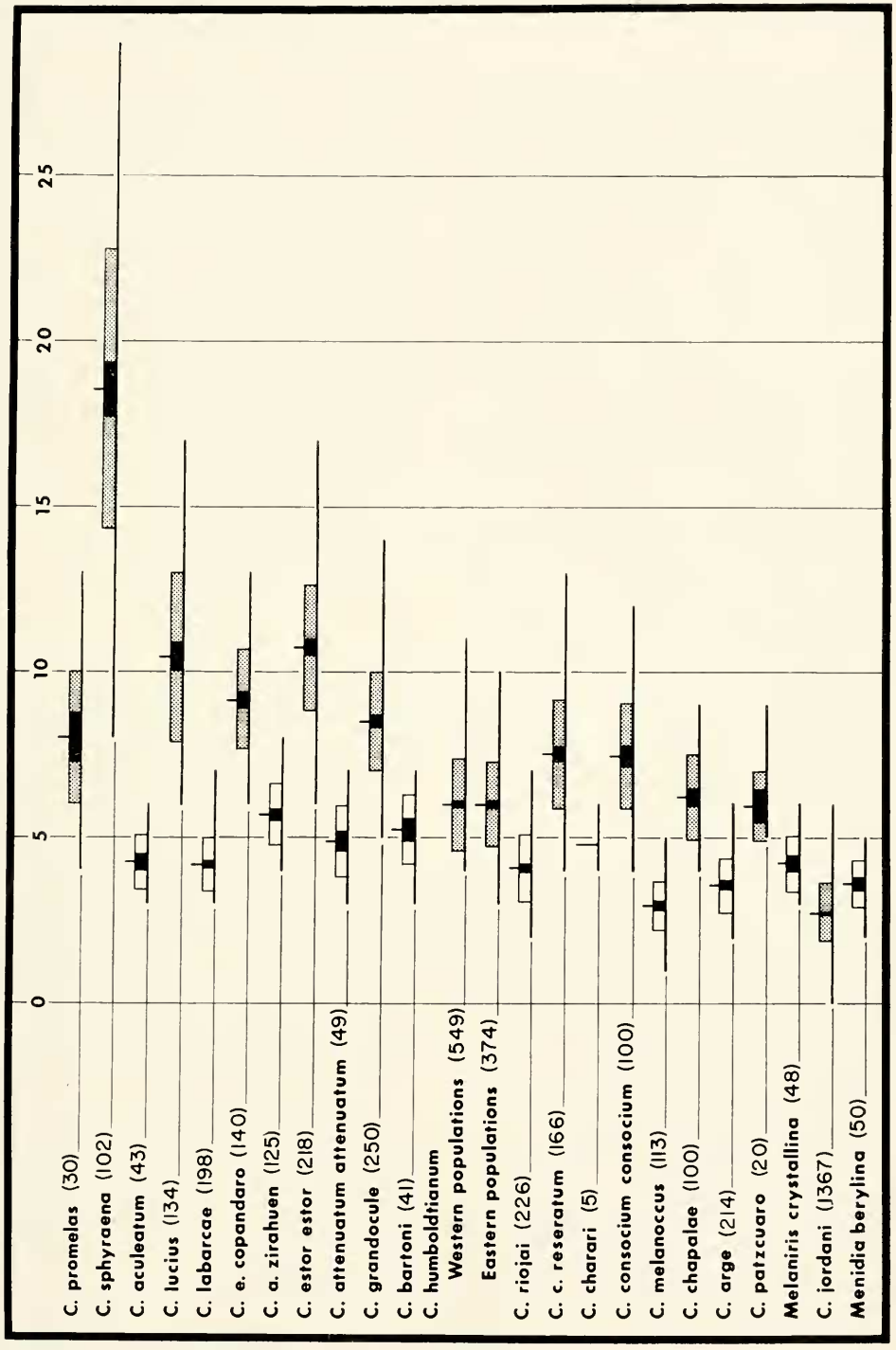
Figure 7. Comparison of the number of interdorsal scales in *Menidia berylina, Melaniris crystallina* and *Chirostoma.* See legend of Fig. 5 for explanation of the diagrams.


0
5
10
15
20
25
C. promelas (30)
C. sphyraena (102)
C. aculeatum (43)
C. lucius (134)
C. labarcae (198)
C. e. copandaro (140)
C. a. zirahuen (125)
C. estor estor (218)
C. attenuatum attenuatum (49)
C. grandocule (250)
C. bartoni (41)
C. humboldtianum
Western populations (549)
Eastern populations (374)
C. riojai (226)
C. c. reseratum (166)
C. charari (5)
C. consocium consocium (100)
C. melanoccus (113)
C. chapalae (100)
C. arge (214)
C. patzcuaro (20)
Melaniris crystallina (48)
C. jordani (1367)
Menidia berylina (50)

CHIROSTOMA LUCIUS BOULENGER
Fig. 17a

Chirostoma lucius Boulenger, 1900:54 (in part, following Regan), holotype: BM 1892.2.8.75, type locality: Lake Chapala; Jordan and Snyder, 1899:137; Evermann and Goldsborough, 1901:152; Meek, 1902:115, 1904: 178, Fig. 60; Regan, 1906–08: 62; Jordan and Hubbs, 1919:79, Fig. 31; Jordan, Evermann and Clark, 1928:251; Cuesta Terron, 1931:240; De Buen, 1940c:50, 1943:212, 1945:519, 1946a:278, 1946b:115; Schultz, 1948:31; Alvarez, 1950a:104, 1970:128; Alvarez and Cortés, 1962:125. *Chirostoma ocotlanae*, Jordan and Snyder, 1899:19; Jordan and Evermann, 1896–1900:3136; Pellegrin, 1901:205; Meek, 1902:116, 1904:180, Fig. 6; Regan, 1906–08:62, Tab. IX, Fig. 1; Jordan and Hubbs, 1919:80, Figs. 33, 34; Jordan, Evermann and Clark, 1928:251; Cuesta Terron, 1931:241; De Buen, 1940c: 51, 1943:212, 1945:520, 1946a:278, 1946b: 115; Schultz, 1948:31; Alvarez, 1950:104, 1970:128; Alvarez and Cortés, 1962:126. *Chirostoma crystallinum* Jordan and Snyder, 1899:139; Jordan and Evermann, 1896–1900: 3162.

Diagnosis.—Predorsal scales, 50–117; interdorsal scales, 6–17; snout length, 10.5–12.5 in percent of standard length; mandible length, 13.1–17.9; least depth caudal peduncle, 8.3–9.2; snout included by lower jaw whose projection beyond the snout may equal approximately one-half the interorbital distance; teeth small to very large, usually the former.

Description.—Maximum length about 300 mm S.L.; body depth moderate, becoming relatively deep in adults; head and gape large, teeth small and in bands, none on vomer or palatines; scale margins laciniate; predorsal scales crowded; lateral line scales with canals; pectoral fins moderate, pointed.

Remarks.—*C. lucius* and *C. ocotlanae* are herein synonymized; there are no known characters which will separate them. The most conspicuous feature of the nominal *C. ocotlanae*, the greatly protruding lower jaw, is extremely variable and thus useless taxonomically.

Range.—Lake Chapala, Jalisco–Michoacán, and the Río Grande de Santiago at Poncitlán, Jalisco. I consider the locality "Colima," USNM 203147, to be an error. If this specimen was bought in a market it probably came from Lake Chapala.

Material examined.—Colima: USNM 203147 (1), Colima. Jalisco: BM 1892.2.8.75, holotype, Lake Chapala; SU 6158, holotype of *C. crystallina*, Lake Chapala; SU 6203 (4), Lake Chapala at Ocotlán; SU 6160, holotype of *C. ocotlanae*, Lake Chapala; TU 40812 (3), Lake Chapala, about 0.2 mi. E of El Fuerte at E end of lake; TU 40872 (1), TU 40820 (1), Río Grande de Santiago at Poncitlán; TU 40838 (144), TU 31986 (13), TU 40829 (3), Lake Chapala at Ajijic; TU 31971 (24), TU 31970 (1), Lake Chapala 15.8 mi. W of town of Chapala at Jocotepec; TU 31980 (3), Lake Chapala 1.6 mi. W town of Chapala; UMMZ 179741 (51), Lake Chapala at Tuxcueca; FMNH 3660 (3), Ocotlán; USNM 130933 (5), USNM 130934 (4), Lake Chapala (?); USNM 126981 (2), Lake Chapala. Michoacán: FMNH 3671 (1), La Palma.

Specimens of unknown localities.—USNM 130924 (1); USNM 130925 (1); USNM 130937 (2).

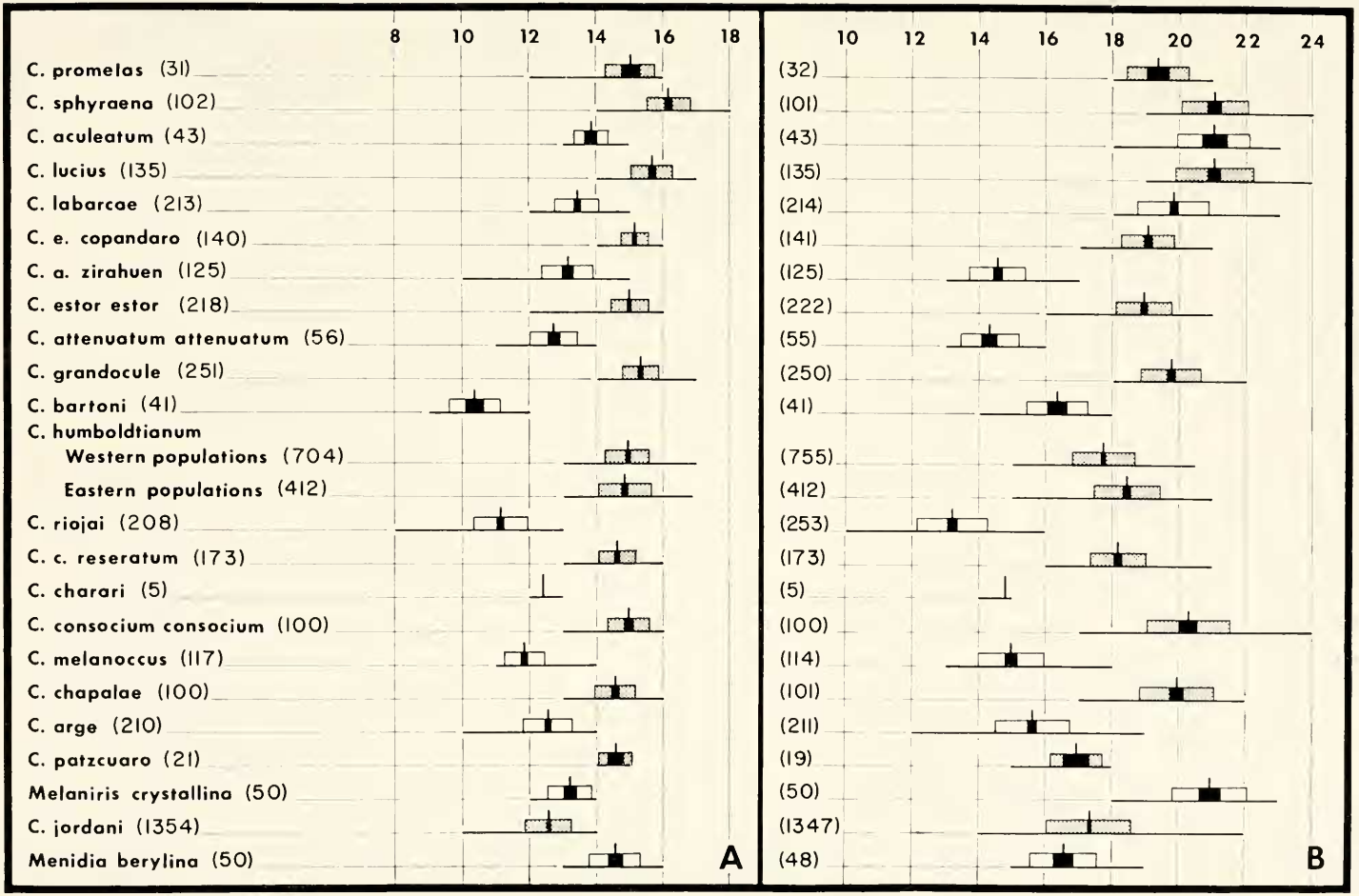
CHIROSTOMA SPHYRAENA BOULENGER
Fig. 17b

Chirostoma sphyraena Boulenger, 1900:54, holotype: BM 1892.2.8.77, type locality: Lake Chapala; Jordan and Snyder, 1899:137; Meek, 1902:116, 1904:177, Fig. 59; Regan, 1906–08:63, Tab. IX, Fig. 2; Jordan and Hubbs, 1919:80, Figs. 35, 36; Jordan, Evermann and Clark, 1928:251; Cuesta Terron, 1931:240; De Buen, 1940c:50, 1943:212, 1945:526, 1946a:279, 1946b:115; Schultz, 1948:31; Alvarez, 1950:102, 1970:126; Alvarez and Cortés, 1962:127; Minckley, 1965:73. *Chirostoma diazi* Jordan and Snyder, 1899:137; Jordan and Evermann, 1896–1900:3161; Regan, 1906–08:62; Jordan and Hubbs, 1919: 80, Fig. 32; Jordan, Evermann and Clark, 1928:251; De Buen, 1940c:50, 1943:212, 1945:527, 1946a:279, 1946b:115; Schultz, 1948:31; Alvarez, 1950a:102, 1970:125; Alvarez and Cortés, 1962:127. *Chirostoma lermae* Jordan and Snyder, 1899:142; Meek, 1902:116, 1904:179, Fig. 61.

Diagnosis.—Predorsal scales, 56–111; interdorsal scales, 8–29; gill rakers, 23–28; snout length, 10.2–12.9 in percent of standard length; mandible length, 12.3–15.2; pointed snout included by slightly projecting lower jar; teeth large, canine-like; body slender, barracuda-like.

→

Figure 8. Comparison of the number of (A) pectoral fin rays and (B) anal fin rays in *Menidia beryllina*, *Melaniris crystallina* and *Chirostoma*. See legend of Fig. 5 for explanation of the diagrams.


8 10 12 14 16 18
C. promelas (31)
C. sphyraena (102)
C. aculeatum (43)
C. lucius (135)
C. labarcae (213)
C. e. copandaro (140)
C. a. zirahuen (125)
C. estor estor (218)
C. attenuatum attenuatum (56)
C. grandocule (251)
C. bartoni (41)
C. humboldtianum
Western populations (704)
Eastern populations (412)
C. riojai (208)
C. c. reseratum (173)
C. charari (5)
C. consocium consocium (100)
C. melanoccus (117)
C. chapalae (100)
C. arge (210)
C. patzcuaro (21)
Melaniris crystallina (50)
C. jordani (1354)
Menidia berylina (50)
A
10 12 14 16 18 20 22 24
(32)
(101)
(43)
(135)
(214)
(141)
(125)
(222)
(55)
(250)
(41)
(755)
(412)
(253)
(173)
(5)
(100)
(114)
(101)
(211)
(19)
(50)
(1347)
(48)
B

Description.—Largest specimen examined 203 mm S.L.; head large, triangular; premaxillaries produced anteriorly; teeth in bands on premaxillaries with those placed anteriorly and medially enlarged, in two or three irregular rows on the dentaries with those in the outer row enlarged, none on the vomer or palatines; scale margins laciniate; predorsal scales crowded; lateral line scales with canals; pectoral fins moderately long and pointed.

Remarks.—There are indications that *C. sphyraena* hybridizes or introgresses with *C. lucius.* Most specimens of *C. lucius* have small teeth carried on a rather wide lower jaw. Some, however, have very large teeth on a jaw tending to be narrow and pointed as in *C. sphyraena.* These individuals were rare during the summer of 1963 but more common during the spring of 1969 when the level of Lake Chapala was much higher and the large silversides more abundant.

Range.—Lake Chapala, Jalisco–Michoacán and the Río Grande de Santiago at Poncitlán, Jalisco. I regard the locality "Colima," USNM 130918, as an error. The specimen probably came from Lake Chapala.

According to Minckley (1965), *C. sphyraena* and another unidentified *Chirostoma* have been introduced into the Río Conchos, Chihuahua.

Material examined.—Jalisco: BM 1892.2.-8.77, holotype, Lake Chapala; SU 6157, type of *C. diazi,* Lake Chapala (Market of Guadalajara); SU 6200 (3), market, Guadalajara; SU 6159, type of *C. lermae,* Lake Chapala (market of Guadalajara); SU 6212 (3), market, Guadalajara; TU 40837 (106), TU 31985 (24); Lake Chapala 4.9 mi. W town of Chapala at Ajijic; TU 40875 (3), Lake Chapala, 15.8 mi. W of Chapala at Jocotepec; UMMZ 179743 (4), Lake Chapala at Tuxcueca; UMMZ 167721 (12) NW side Lake Chapala at 5,000 ft.

CHIROSTOMA PROMELAS JORDAN AND SNYDER

Chirostoma promelas Jordan and Snyder, 1899: 136, Fig. 14, holotype: SU 6156, type locality, Lake Chapala (market of Guadalajara, Jalisco); Jordan and Evermann, 1896–1900: 3160; Pellegrin, 1901:205; Evermann and Goldsborough, 1901:152; Meek, 1902:115, 1904:177; Regan, 1906–08:62; Jordan and Hubbs, 1919:79, Figs. 29, 30; Jordan, Evermann and Clark, 1928:251; Cuesta Terron, 1931:240; De Buen, 1940c:50, 1943:212; Schultz, 1948:31. *Otalia promelas,* De Buen, 1945:529, 1946a:279, 1946b:115; Alvarez, 1950a:99, 1970:128; Alvarez and Cortés, 1962:128.

Diagnosis.—Lower jaw equal to or included by snout; snout pigmented black.

Description.—Largest specimen examined 165 mm S.L.; head triangular, jaw moderately long; snout long and pointed; premaxillaries produced anteriorly; teeth large, in bands, directed sharply posteriorly, none on vomer or palatines. Scale margins laciniate; predorsal scales crowded; lateral line scales with canals; pectoral fins moderately long and pointed.

Remarks.—*C. promelas* is most closely related to *C. sphyraena,* but has a shorter mandible (Fig. 12).

Range.—Lake Chapala, Jalisco–Michoacán, Río Grande de Santiago at Poncitlán, Jalisco.

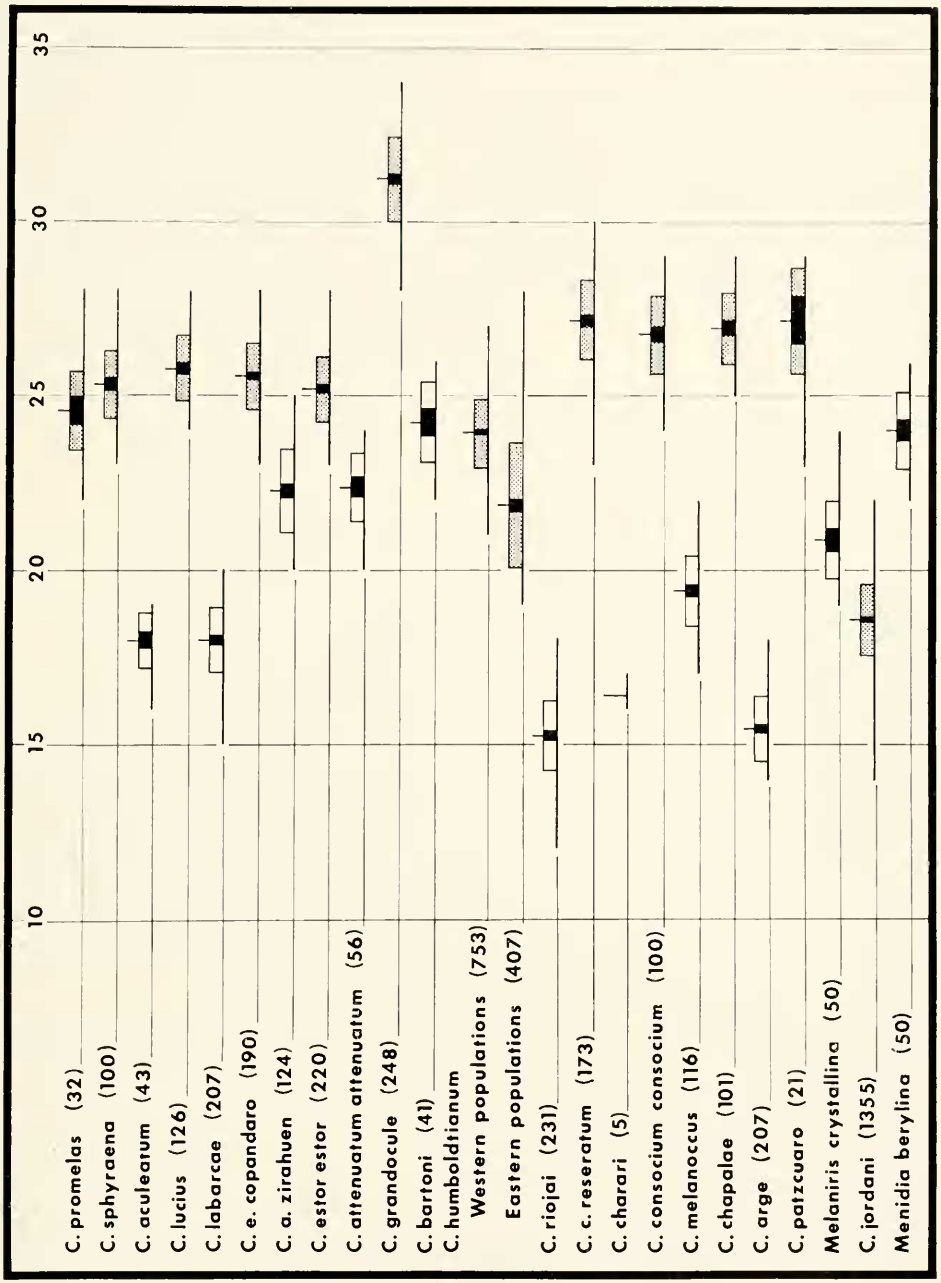
Material examined.—Jalisco: SU 6156, holotype, market of Guadalajara (Lake Chapala); UMMZ 167723 (1), NW side of Lake Chapala at 5,000 ft. el.; UMMZ 173542 (3), Lake Chapala, N shore 0.5 mi. W town of Chapala at village of Manglar; UMMZ 179719 (1), flooded edge of Lake Chapala ca. 1 mi. S Ocotlán near source of Río Grande de Santiago; UMMZ 179740 (1), Lake Chapala at Tuxcueca on S side of lake; LB 4116 (4), UMMZ 124466 (1), Lake Chapala; FMNH 3656 (3), Ocotlán; TU 40843 (11), TU 31987 (1), Lake Chapala 4.8 mi. W town of Chapala at Ajijic; TU 40823 (1), Río Santiago at Poncitlán; TU 40848 (1), Lake Chapala at San Juan Tecomatlán; UMMZ 197649 (1), Lake Chapala 3.8 mi. W Ajijic. Michoacán: FMNH 3664 (9), La Palma.

The Arge Group

Description.—Lateral line scales usually with pores; scale margins usually smooth; median lateral scales, 36–51; predorsal scales, 15–32; interdorsal scales, 1–8; gill rakers, 12–26; vertebrae, 35–43; pectoral fin rays, 8–15; anal fin rays, 10–19 with two species reaching 23. The species range in size from small to moderately large and include: *C. arge, C. melanoccus, C. riojai, C. charari, C. attenuatum, C. bartoni, C. labarcae* and *C. aculeatum.*

→

Figure 9. Comparison of the number of gill rakers in *Menidia berylina, Melaniris crystallina* and *Chirostoma.* See legend of Fig. 5 for explanation of the diagrams.


10
15
20
25
30
35
C. promelas (32)
C. sphyraena (100)
C. aculeatum (43)
C. lucius (126)
C. labarcae (207)
C. e. copandaro (190)
C. a. zirahuen (124)
C. estor estor (220)
C. attenuatum attenuatum (56)
C. grandocule (248)
C. bartoni (41)
C. humboldtianum
Western populations (753)
Eastern populations (407)
C. riojai (231)
C. c. reseratum (173)
C. charari (5)
C. consocium consocium (100)
C. melanoccus (116)
C. chapalae (101)
C. arge (207)
C. patzcuaro (21)
Melaniris crystallina (50)
C. jordani (1355)
Menidia berylina (50)

CHIROSTOMA ARGE (JORDAN AND SNYDER) Fig. 16c

Eslopsarum arge Jordan and Snyder, 1899:133, holotype: SU 6154, type locality: Río Verde near Aguascalientes, Aguascalientes; Jordan and Evermann, 1896–1900:3158; De Buen, 1945:504, 1946b:114. *Chirostoma arge*, Meek, 1902:112, 1904:171, 1907:156; Regan, 1906–08:59; Jordan and Hubbs, 1919:71, Fig. 23; Jordan, Evermann and Clark, 1930:250; Cuesta Terron, 1931:238; De Buen, 1940c: 48; Schultz, 1948:31; Alvarez, 1950a:101, 1970:125.

Diagnosis.—Gill rakers, 14–18; snout length, 6.4–8.5 in percent of standard length; length of caudal peduncle, 21.4–25.9; snout blunt, never angular in profile or pointed; teeth large, present on upper lip, easily visible or felt when mouth is closed; specimens from the Río de la Laja may have black on fins (Fig. 16c) and lateral line scales with canals as well as pores.

Description.—Maximum length around 65 mm S.L.; body relatively deep; head subtriangular; snout equal to or included by lower jaw; teeth in bands, outer members greatly enlarged, none on vomer or palatines; scale margins smooth; predorsal scales not crowded; lateral line usually in the form of pores (see *Diagnosis*); pectoral fins small, rounded or weakly pointed.

Remarks.—The Lake Chapala population of *C. arge* has the following frequency distribution of vertebrae: 38 (4 specimens), 39 (18), 40 (6), 41 (1). These numbers are generally higher than any of the other populations of the species and were not included in the data of Fig. 10. The populations in the Río de la Laja differ most trenchantly from those in the Río de Aguascalientes in the height of the anal fin (Fig. 14).

Range.—Headwaters of the Río Verde (Río de Aguascalientes) and the Río la Laja; Lake Chapala; tributaries to the lower Río Lerma (Fig. 1).

Material examined.—Aguascalientes: SU 6154, holotype, ANSP 26845–911 (17), Río Verde near Aguascalientes. Guanajuato: UMMZ 197622 (186), Río de la Laja 4 mi. S San Miguel de Allende in impoundment; UMMZ 197623 (169), Río de la Laja, below dam just S Empalme Escobedo; FMNH 5565 (50), San Miguel de Allende. Jalisco: FMNH 73319 (40), Lagos; UMMZ 179745 (12), Lake Chapala on S side of lake at Tuxcueca; UMMZ 173541 (28), Lake Chapala 0.5 mi. W town of Chapala at Village of Manglar; UMMZ 172201 (34), trib. to Río Verde at Cuarenta, 15 mi. NE Lagos de Moreno, el. 6,500 ft.; UMMZ 179762 (118), Río de Aguascalientes at E edge of Belén del Refugio; TU 40816 (9), E end of Lake Chapala ca. 4 mi. W town of Cuitzeo at end of road; TU 40830 (33), TU 40842 (4), Lake Chapala at Ajijic; TU 40834 (3), Lake Chapala; S shore of Isla de los Alacranes. Michoacán: UMMZ 197616 (1), trib. to Río Lerma on N side of Tanhuato.

CHIROSTOMA MELANOCCUS ALVAREZ

Chirostoma melanoccus Alvarez, 1963b:127, holotype: P 731, type locality: San Juanico dam, Michoacán, 1970:125.

Diagnosis.—Median lateral scales, 39–45; gill rakers, 17–22; anal fin rays, 13–18; eye length, 6.0–6.8 in percent of standard length; snout to origin of first dorsal fin, 48.1–51.3; snout blunt, never angular in profile; teeth minute; lateral line scales always with pores.

Description.—Maximum length about 65 mm S.L.; body slender; head subtriangular; teeth in two or three rows on the premaxillaries and dentaries, none on vomer or palatines; scale margins smooth; predorsal scales not crowded; pectoral fins moderately long, rounded.

Range.—Known only from the type locality, San Juanico dam near Cotija, Michoacán (Fig. 1).

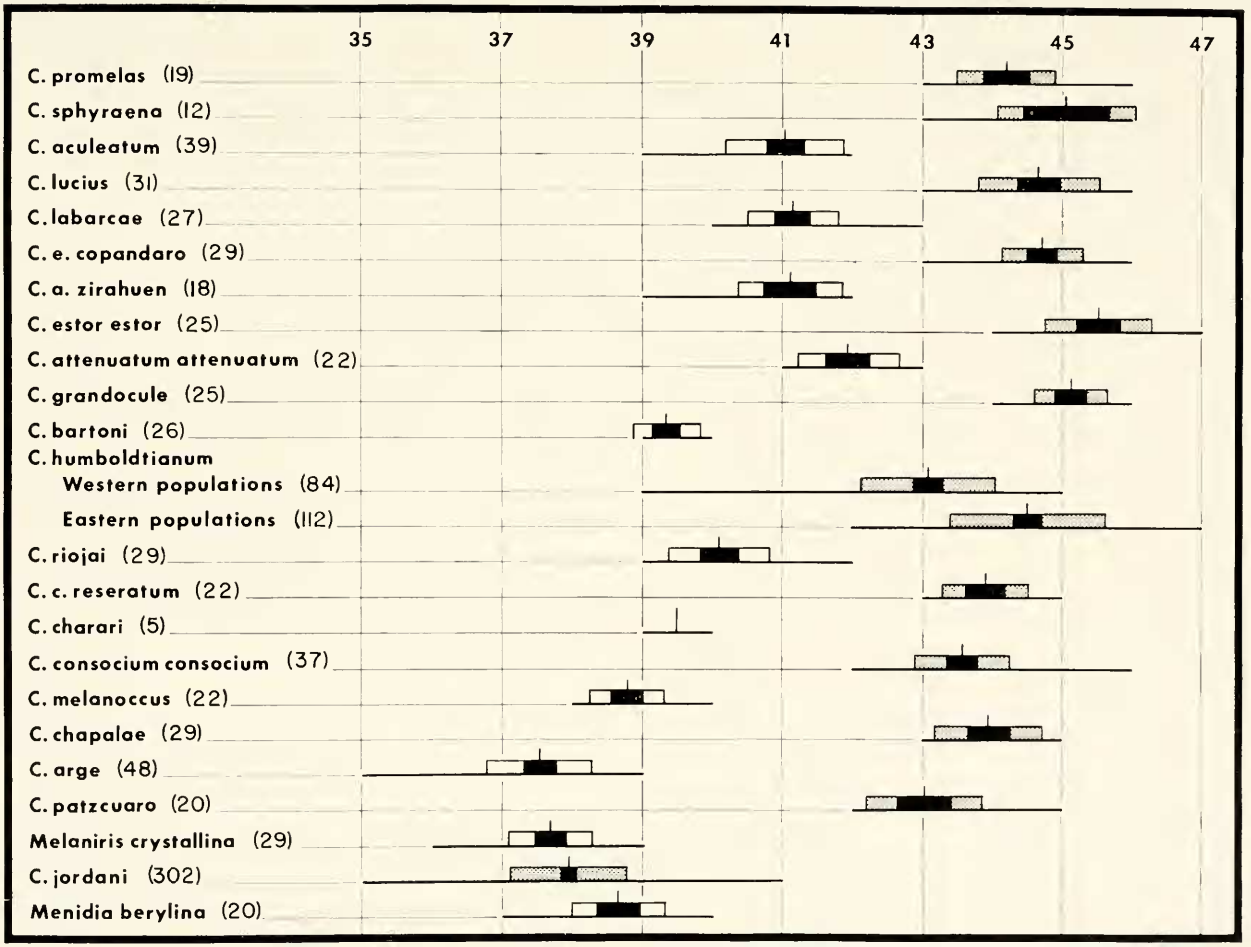
Material examined.—Michoacán: TU 40867 (69), TU 31945 (46), San Juanico dam, 5 mi. SE Cotija.

CHIROSTOMA RIOJAI SOLORZANO AND LOPEZ

Chirostoma riojai Solórzano and López, 1965: 145, holotype: LB 1820, type locality: Lake Santiago Tilapa, Mexico State; Alvarez, 1970: 125. *Chirostoma bartoni*, Evermann and Goldsborough, 1901:152; Meek, 1902:112, 1904:172; Regan, 1906–08:58 (in part); Jordan and Hubbs, 1919:72 (in part); De Buen, 1940c:49 (in part); Romero, 1967:68.

→

Figure 10. Comparison of the total number of vertebrae in *Menidia berylina*, *Melaniris crystallina* and *Chirostoma*. See legend of Fig. 5 for explanation of the diagrams.


35
37
39
41
43
45
47
C. promelas (19)
C. sphyraena (12)
C. aculeatum (39)
C. lucius (31)
C. labarcae (27)
C. e. copandaro (29)
C. a. zirahuen (18)
C. estor estor (25)
C. attenuatum attenuatum (22)
C. grandocule (25)
C. bartoni (26)
C. humboldtianum
Western populations (84)
Eastern populations (112)
C. riojai (29)
C. c. reseratum (22)
C. charari (5)
C. consocium consocium (37)
C. melanoccus (22)
C. chapalae (29)
C. arge (48)
C. patzcuaro (20)
Melaniris crystallina (29)
C. jordani (302)
Menidia berylina (20)

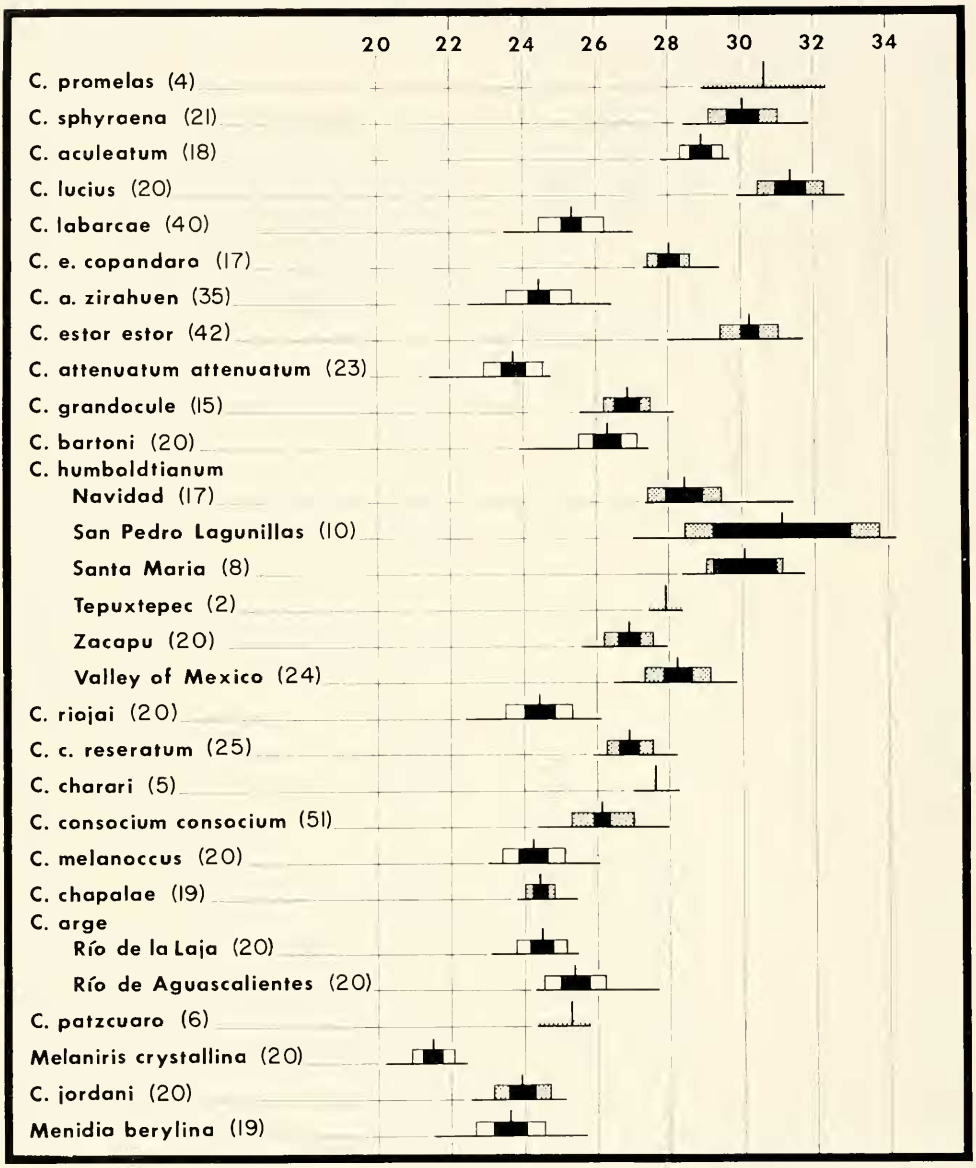


Figure 11. Comparison of head length, expressed as a percent of standard length, in *Menidia berylina*, *Melaniris crystallina* and *Chirostoma*. See legend of Fig. 5 for explanation of the diagrams.

Chirostoma bartoni bartoni, Alvarez, 1950: 100 (in part), 1970:124 (in part); Alvarez and Cortés, 1962:123 (in part). *Eslopsarum bartoni bartoni* De Buen, 1945:506 (in part), 1946b:114 (in part).

Diagnosis.—Gill rakers, 12–18; anal rays, 10–16; snout to origin of first dorsal fin, 45.2–48.4 in percent of standard length; eye length, 5.1–6.0; snout blunt, never angular in profile; premaxillaries not enlarged and produced anteriorly or laterally decurved as in *C. charari*; teeth small, none outside mouth as in *C. arge*; scale margins smooth, no tendency towards laciniation predorsally.

Description.—Maximum length about 74 mm S.L.; body relatively deep; snout equal to or included by lower jaw; teeth in bands,

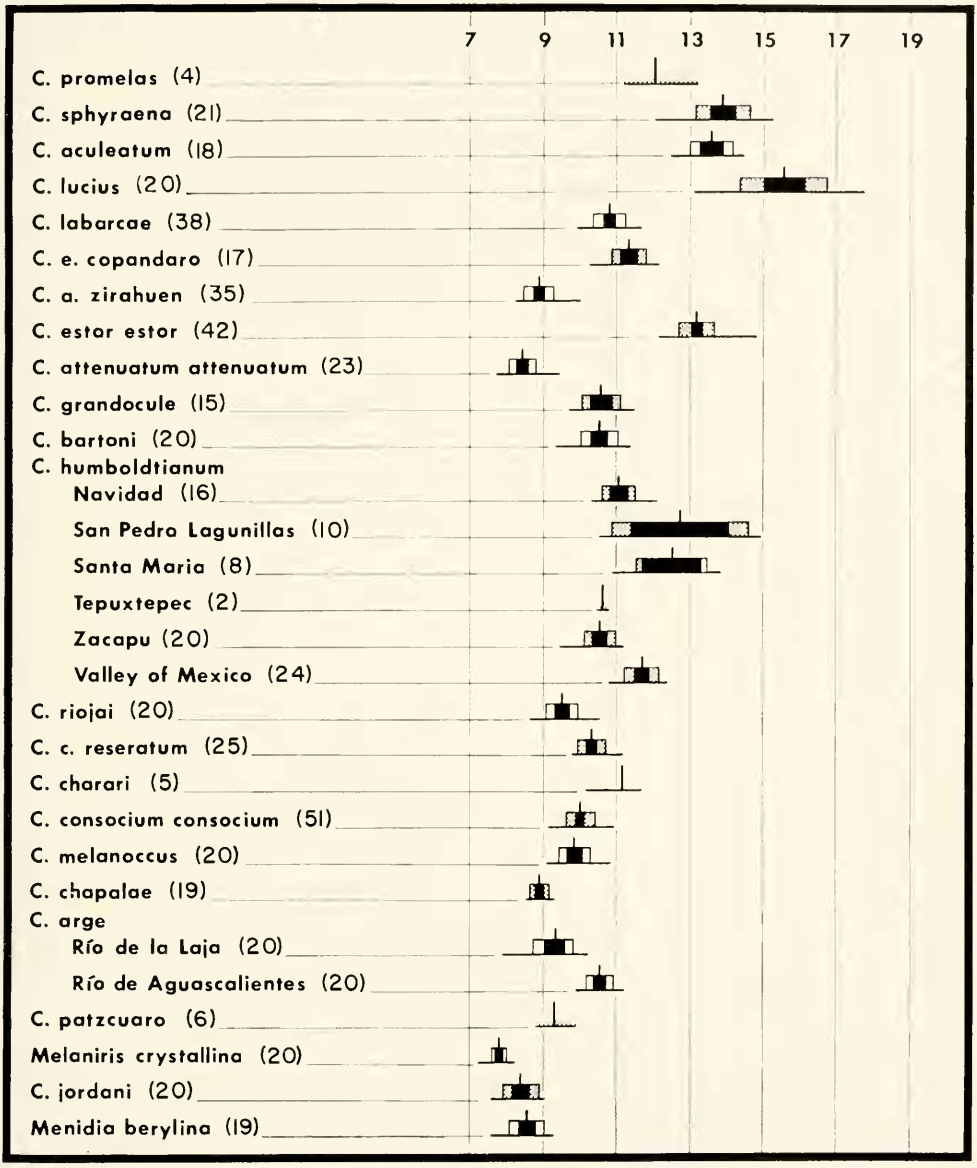


Figure 12. Comparison of mandibular length, expressed as a percent of standard length, in *Menidia berylina*, *Melaniris crystallina* and *Chirostoma*. See legend of Fig. 5 for explanation of the diagrams.

outer members not enlarged, none on vomer or palatines; lateral line scales with pores; predorsal scales not crowded; pectoral fins small, rounded.

Range.—Headwaters of the Río Lerma and Lakes in the Valley of Toluca, Mexico State (Fig. 1).

Material examined.—Mexico: TU 40173 (2), paratypes, Laguna de Santiago Tilapa; UMMZ 172175 (75) Laguna Agua Blanca, 14 mi. by road SW Toluca; TU 31867 (71), Río Lerma, 1.5 mi. W town of Lerma, hwy. 15; UMMZ 197634 (1), TU 31871 (86), Río Lerma, 12.5 mi. NW Toluca, hwy. 55; USNM 126980 (10), USNM 50228 (32), Lake Lerma; UMMZ 197632 (566), Río Lerma just below Alzate Dam, 15.2

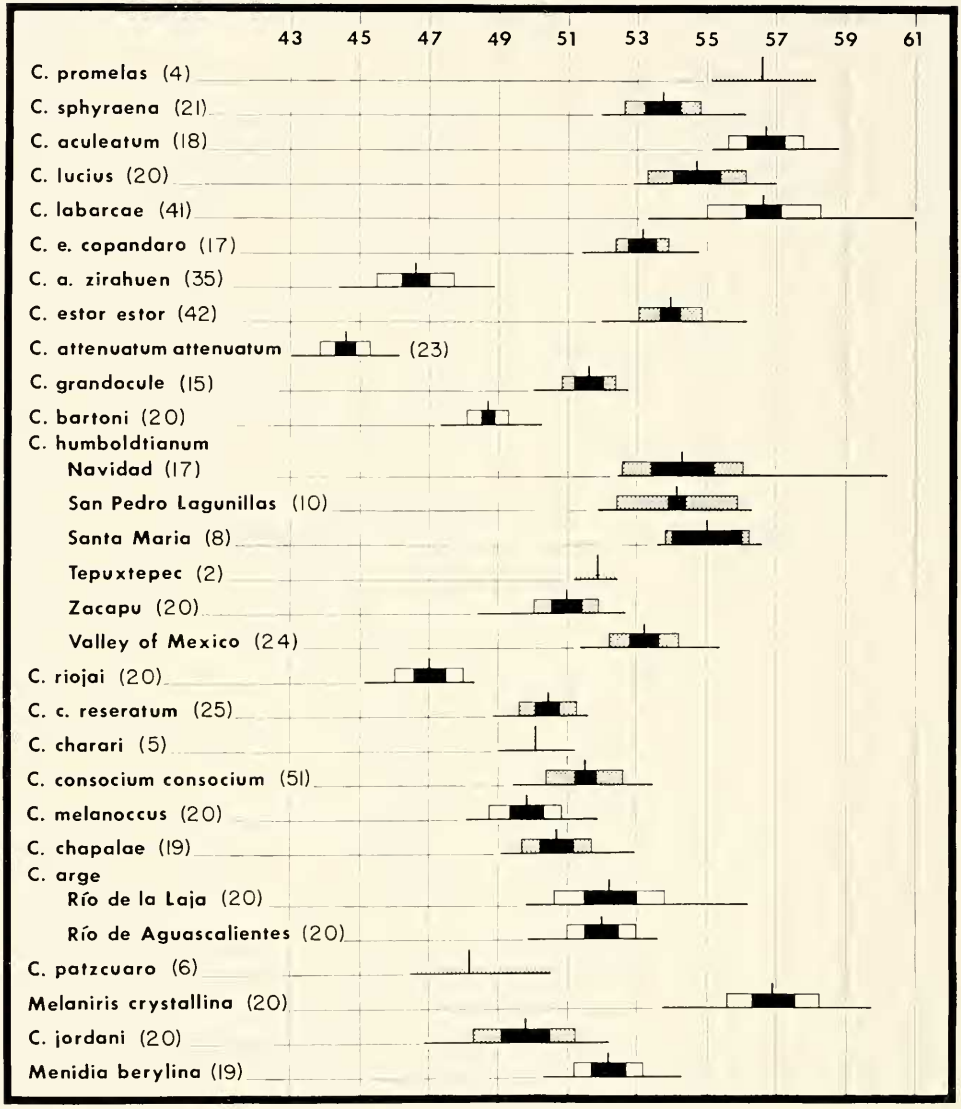


Figure 13. Comparison of the distance from the snout to the origin of the first dorsal fin, expressed as a percent of standard length, in *Menidia berylina*, *Melaniris crystallina* and *Chirostoma*. See legend of Fig. 5 for explanation of the diagrams.

mi. N Toluca, hwy. 55; UMMZ 197633 (78); behind Ignacio Ramirez Dam, W hwy. 55, 20.4 mi. N Toluca.

CHIROSTOMA CHARARI (DE BUEN)

Eslopsarum bartoni charari De Buen, 1945: 509, holotype: lost, originally deposited in the collection of the Pátzcuaro Limnological Station, type locality: Río Grande de Morelia at Morelia, Michoacán, 1946b:114. *Chirostoma bartoni charari*, Schultz, 1948:31; Alvarez, 1950a:100, 1970:124; Alvarez and Cortés, 1962:123. *Chirostoma bartoni*, De Buen, 1943:212, 1944a:264. *Chirostoma bartoni* var. (?) De Buen, 1941a:24.

Diagnosis.—Gill rakers, 16–17; anal rays, 14–15; eye length, 6.6–7.2 in percent of standard length; snout length, 8.6–9.7; snout subtriangular; premaxillaries enlarged, produced anteriorly and decurved laterally.

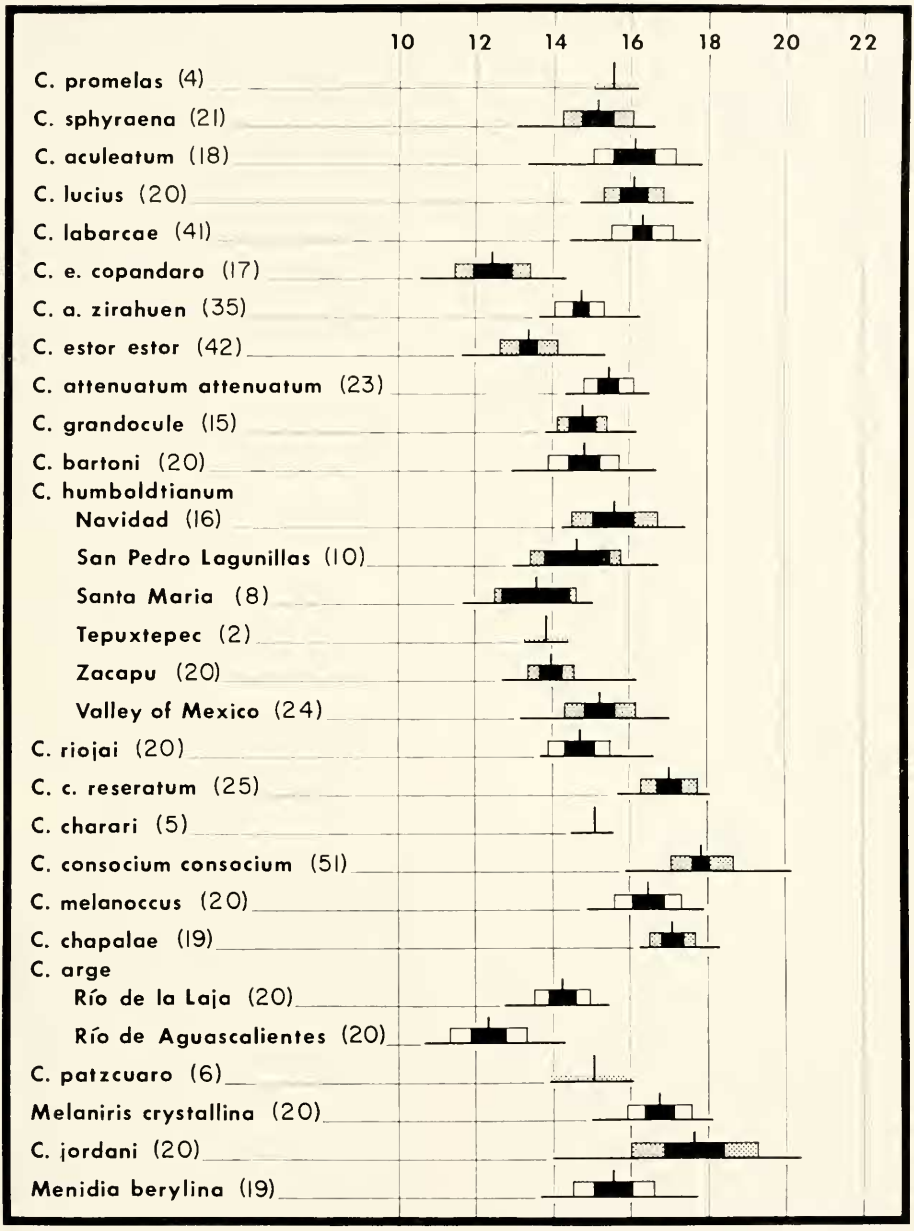


Figure 14. Comparison of anal fin height, expressed as a percent of standard length, in *Menidia berylina*, *Melaniris crystallina* and *Chirostoma*. See legend of Fig. 5 for explanation of the diagrams.

Description.—Largest specimen examined 64.8 mm S.L.; body slender: snout long, weakly pointed; teeth moderately large, relatively few in number, in one or two irregular rows on dentaries and premaxillaries with the outer members slightly enlarged, none on vomer or palatines; scale margins smooth; lateral line scales with pores; predorsal scales not crowded; pectoral fins small, rounded. Proportional measurements of five specimens of *C. charari* (TU 31911, 57.9–64.8 mm S.L.) expressed in thousandths of the

standard length are given below. The range is followed by the mean. Distance from snout to origin of first dorsal fin: 490–513, 501; distance from snout to origin of second dorsal fin: 634–662, 646; distance from snout to origin of pelvic fins: 394–410, 400; distance from snout to origin of anal fin: 555–572, 567; head length: 270–283, 276; postorbital head length: 117–130, 122; eye length: 66–72, 69; snout length: 86–97, 90; mandible length: 102–117, 112; least depth of caudal peduncle: 76–84, 81; length of caudal peduncle: 234–250, 241; height of second dorsal fin: 145–164, 153; length of base of anal fin: 187–207, 196; height of anal fin: 145–158, 151; length of pectoral fin: 151–169, 160.

Remarks.—Although the type is lost, I recognize this species on the basis of five specimens, mentioned above, which seem to agree fairly well with De Buen's descriptions (1941a, 1945). They were collected in a spring-fed lake in the same drainage about five miles from the type locality.

Range.—Río Grande de Morelia basin in the vicinity of Morelia, Michoacán (Fig. 1).

Material examined.—Michoacán: TU 31911 (5), spring-fed lake just N Balneario Cointzio ca. five air miles W Morelia.

CHIROSTOMA ATTENUATUM ATTENUATUM MEEK

Chirostoma attenuatum Meek, 1902:112, holotype: FMNH 3631, type locality: Lake Pátzcuaro, Michoacán, 1904:173, Fig. 55; Cuesta Terron, 1931:241. *Chirostoma samani* Cuesta Terron, 1931:241. *Chirostoma bartoni*, Regan, 1906–08:58, Tab. 10, Fig. 2 (in part); Jordan and Hubbs, 1919:72, Fig. 24 (in part); Jordan, Evermann and Clark, 1928: 250 (in part); De Buen, 1940b:18, Fig. 4 (in part), 1941d:73 (in part), 1943:212 (in part); Martin del Campo, 1940:483 (in part). *Chirostoma bartoni bartoni*, De Buen, 1941a: 24 (in part), 1941c:7 (in part), 1942:41 (in part), 1944a:269 (in part); Schultz, 1948:31 (in part); Alvarez, 1950a:100 (in part), 1970: 124 (in part); Alvarez and Cortés, 1962:123 (in part). *Chirostoma bartoni* var. *attenuatum*, De Buen, 1940b:22, 1949c:49. *Chirostoma bartoni* var. *janitzio*, De Buen, 1940a: 306, 1940b:22, 1940d:7, Figs. 1–14, 1941d: 76; Martin del Campo, 1940:483. *Eslopsarum bartoni bartoni*, De Buen, 1945:506 (in part), 1946b:114 (in part).

Diagnosis.—Median lateral scales, 43–51; gill rakers, 20–24; distance from snout to origin of first dorsal fin, 43.1–46.2 in percent of standard length; length of caudal peduncle, 26.6–30.2.

Description.—Maximum length about 89 mm S.L.; body slender; snout blunt; teeth small, in bands, none on vomer or palatines; scales with smooth edges; predorsal scales not crowded; lateral line scales with pores; pectoral fins short, rounded.

Remarks.—See Remarks under *C. bartoni*. The biology of this species has been discussed by Solórzano (1961).

C. samani Cuesta Terron is synonymized with *C. attenuatum attenuatum* because of its smooth scale margins even though it has a high number of gill rakers (26). The species is known only from the original description.

Range.—Known only from the type locality, Lake Pátzcuaro, Michoacán.

Material examined.—Michoacán: FMNH 3631, holotype; USNM 55782 (2), FMNH 3632 (12), paratypes, all from Lake Pátzcuaro; TU 40851 (32), Lake Pátzcuaro, W of Ihuatzio; TU 40881 (14), Lake Pátzcuaro between Napizaro, Jacuaro and Erongaricuaro; TU 40858 (10), Lake Pátzcuaro, S shore of Isla de Yuñen; USNM 187617 (2), Pátzcuaro; USNM 203145 (7), Lake Pátzcuaro.

CHIROSTOMA ATTENUATUM ZIRAHUEN MEEK

Chirostoma zirahuen Meek, 1902:114, holotype: FMNH 3609, type locality: Lake Zirahuén, Michoacán, 1904:174, Fig. 57; Jordan and Hubbs, 1919:72, Fig. 25; Jordan, Evermann and Clark, 1928:250; Cuesta Terron, 1931: 239; De Buen, 1940c:49. *Chirostoma bartoni*, Regan, 1906–08:58, Tab. X, Fig. 2 (in part). *Chirostoma bartoni zirahuen*, De Buen, 1941a: 23, 1941c:7, 1943:214, 1944b:21; Schultz, 1948:31; Alvarez, 1950a:100, 1970:124; Alvarez and Cortés, 1962:123. *Eslopsarum bartoni zirahuen*, De Buen, 1945:508, 1946b: 114.

Diagnosis.—*C. attentuatum zirahuen* is best distinguished from the nominate form (ranges and means in parentheses) by a greater number of median lateral scales, 48–70, $\bar{x} = 58.1$ (43–51, $\bar{x} = 46.4$); greater number of predorsal scales, 19–32, $\bar{x} = 25.2$ (16–24, $\bar{x} = 19.3$); greater snout to first dorsal fin origin distance, 44.4–48.9, $\bar{x} = 46.6$ (43.1–46.2, $\bar{x} = 44.6$) in percent of standard length. Differs from *C. bartoni* by having a greater number of median lateral scales (42–49, $\bar{x} = 44.8$); greater number of pectoral fin rays, 10–15, $\bar{x} = 13.1$ (9–12,

$\bar{x} = 10.4$); fewer anal fin rays, 13–17, $\bar{x} = 14.5$ (14–18, $\bar{x} = 16.3$). Differs from all other *Chirostoma* by the number of median lateral scales, predorsal scales and anal fin rays; snout to pelvic fin origin distance, 37.3–40.8; least depth caudal peduncle, 6.5–8.1; length caudal peduncle, 24.0–30.1.

Description.—Largest specimen examined 88 mm S.L.; body slender; head subtriangular; snout blunt; premaxillaries not produced anteriorly as in *C. charari*, smoothly decurved laterally, becoming angular in large specimens; teeth small, in two irregular rows or narrow bands, none on vomer or palatines; scale margins smooth; predorsal scales not crowded; lateral line scales with pores, much reduced in some specimens; pectoral fins short, rounded.

Remarks.—Ripe males and females were collected on March 30, 1964. Both sexes were a bronze color. See also Remarks under *C. bartoni.*

Range.—Known only from the type locality, Lake Zirahuén, Michoacán.

Materal examined.—Michoacán: FMNH 3609, holotype; ANSP 90854 (2), paratypes; TU 31918 (266); UMMZ 187669 (8). All from Lake Zirahuén, 19 mi. S Pátzcuaro.

CHIROSTOMA BARTONI JORDAN AND EVERMANN

Chirostoma bartoni Jordan and Evermann, 1896–1900:793, holotype: USNM 23136, type locality: "La Alberca," volcanic caldera W Valle de Santiago, Guanajuato; Regan, 1906–08:58, Tab. X, Fig. 2 (in part); Jordan and Hubbs, 1919:72, Fig. 24 (in part); Jordan, Evermann and Clark, 1928:250 (in part); De Buen, 1940b:18, Fig. 4 (in part), 1940c:49 (in part), 1943:212 (in part); Solórzano, 1961:15 (in part). *Chirostoma bartoni bartoni*, Alvarez, 1950a:100 (in part); Alvarez and Cortés, 1962:123 (in part). *Chirostoma humboldtianum*, Jordan, 1879: 299. *Chirostoma regani*, Martin del Campo, 1940:484 (in part). *Eslopsarum bartoni* Jordan and Evermann, 1895:330, 1896–1900: 2840. *Eslopsarum bartoni bartoni*, De Buen, 1945:506 (in part), 1946b:114 (in part).

Diagnosis.—Median lateral scales, 42–49; pectoral fin rays, 9–12; gill rakers, 22–26; mandible length, 9.4–11.5 in percent of standard length; length of caudal peduncle, 22.3–24.9; snout angular; jaw oblique.

Description.—Largest specimen examined 71 mm S.L.; body moderately slender; head triangular; snout pointed; premaxillaries moderately produced anteriorly; teeth in bands, occasionally present on vomer; scale margins smooth; predorsal scales not crowded; lateral line scales with pores; pectoral fins moderately long, rounded or slightly pointed.

Remarks.—*C. bartoni* is most closely related to *C. attenuatum attenuatum* and *C. a. zirahuen.* The species may be separated from the latter by its fewer number of median lateral scales (overlap of 2) and from the former by its higher number of predorsal scales (overlap of 4). When the following characters are compared, *C. a. attenuatum* and *C. a. zirahuen* always show a greater concordance: number of pectoral and anal fin rays, number of gill rakers on the first arch, snout, mandible, head, eye, postorbital head and caudal peduncle length, distance from snout to anal fin origin and least depth of caudal peduncle. *C. bartoni* also occasionally has teeth on the vomer. For these reasons, *C. bartoni* is retained as a species and *C. a. attenuatum* and *C. a. zirahuen* as subspecies.

Range.—Known only from the type locality, "La Alberca," an extinct volcanic caldera immediately W Valle de Santiago, Guanajuato (Fig. 1).

Material examined.—Guanajuato: USNM 23136, holotype; UMMZ 197624 (30), UMMZ 197638 (15). All from "La Alberca," caldera lake immediately W Valle de Santiago.

CHIROSTOMA LABARCAE MEEK

Fig. 18b

Chirostoma labarcae Meek, 1902:112, holotype: FMNH 3640, type locality: Río Lerma at La Barca, Jalisco, 1904:173; Jordan and Hubbs, 1919:71, Fig. 22; Jordan, Evermann and Clark, 1928:250; Cuesta Terron, 1931: 238; De Buen, 1940c:48, 1943:212; Schultz, 1948:31; Alvarez, 1950a:101, 1970:125; Alvarez and Cortés, 1962:122. *Chirostoma breve*, Regan, 1906–08:59 (in part). *Eslopsarum labarcae*, De Buen, 1945:503, 1946a: 277, 1946b:114.

Diagnosis.—Median lateral scales, 39–47; gill rakers, 15–20; length of caudal peduncle, 16.5–21.1 in percent of standard length; length of pectoral fin, 19.4–22.8; length of anal fin base, 21.7–28.3; head length, 23.5–27.0; snout length, 8.3–9.9; snout pointed; teeth small to large; scale margins weakly laciniate in predorsal region; lateral line scales with fine canals.

Description.—Largest specimen examined 85 mm S.L.; head triangular; premaxillaries produced anteriorly; teeth in irregular rows or band, outer members on dentaries large and canine-like as are those on medial portions of premaxillaries; predorsal scales not crowded; pectoral fins long and pointed.

Range.—Lake Chapala, Jalisco–Michoacán, Río Grande de Santiago at Poncitlán, Río Lerma at La Barca, Jalisco (Fig. 4).

Material examined.—JALISCO: FMNH 3640, holotype, Río Lerma at La Barca; UMMZ 179721 (1), Lake Chapala at Jamay, near E end of lake; UMMZ 179715 (13), flooded edge of Lake Chapala ca. 1 mi. S Ocotlán near source of Río Grande de Santiago; UMMZ 179747 (60), Lake Chapala at Tuxcueca on S side of lake; UMMZ 179709 (1), Lake Chapala at SW end opposite Ajijic; UMMZ 108641 (5), Río Grande de Santiago between Ocotlán and Lake Chapala, or outlet end of lake nearby; UMMZ 124467 (5), Lake Chapala; UMMZ 173539 (2), Lake Chapala, N shore 0.5 mi. W town of Chapala at village of Manglar; UMMZ 167722 (4), NW side, Lake Chapala, 5,000 ft. el.; TU 40831 (33), TU 40839 (35), TU 31988 (6), Lake Chapala 4.8 mi. W of town of Chapala at Ajijic; TU 31966 (22), Lake Chapala 1.6 mi. W town of Chapala; TU 40821 (14), TU 31958 (4), Río Santiago at Poncitlán; TU 40814 (21), Lake Chapala 0.2 mi. E of El Fuerte at E end of lake; TU 40817 (2), Lake Chapala 1–2 mi. W of town of Cuitzeo at end of road, NE end of lake; TU 40835 (44), Lake Chapala, Isla de los Alacranes, S shore in area especially cleared by fisherman for throw net.

CHIROSTOMA ACULEATUM NEW SPECIES

Fig. 18a

Chirostoma jordani Woolman, 1894:62 (in part, misidentification). *Chirostoma arge*, Jordan and Hubbs, 1919:71 (in part, based on USNM 203107).

Holotype.—TU 40889, 85.00 mm standard length, collected along the south shore of Lake Yuriria 1.5 miles east of the town of Yuriria, Guanajuato, 1 August 1963 by commercial fishermen. Paratypes.—GUANAJUATO: TU 40864 (11), same data as holotype; USNM 205784 (3), USNM 205783 (5), Río Turbio 8 miles east of Pénjamo at highway 110 crossing. MICHOACÁN: UMMZ 197682 (2), USNM 205785 (19), tributary to the Río Lerma at the northeast end of the town of Tanhuato on the road to Yurécuaro, below small earthen dam. Two specimens bearing the same data as USNM 205785 have been deposited in the Instituto Nacional de Investigaciones Biológico Pesqueras, Laboratorio Biológico, México, D. F.

Other specimen.—GUANAJUATO: USNM 203107, Salamanca, removed from syntypes of *C. jordani* Woolman.

Diagnosis.—A *Chirostoma*, mostly closely related to *C. labarcae*, distinguished from all other members of the genus by having anal fin rays, 18–23; gill rakers, 15–21; mandible length, 12.5–14.5 in percent of standard length. Distinguished from *C. labarcae* (ranges, means and comments in parentheses) by having a longer head, 27.9–29.8, $\bar{x}$ = 28.9 (23.5–27.1, $\bar{x}$ = 25.4); longer snout, 10.1–12.1, $\bar{x}$ = 11.1 (8.3–9.9, $\bar{x}$ = 9.0); longer mandible, $\bar{x}$ = 13.6 (9.9–11.7, $\bar{x}$ = 10.8); premaxillary strongly decurved (weakly decurved).

Description.—A moderately large species, largest specimen examined 109.4 mm S.L., but according to fishermen reaching a length of 130–140 mm S.L.; body slender; snout long, pointed, included by lower jaw; teeth in two irregular rows on the dentaries, those along the outer edges large, canine-like, those immediately interior small, fine; teeth on the premaxillaries large but, with the exception of one or two canine-like on either side of the median symphysis, somewhat smaller than the large teeth on the dentaries; teeth absent from vomer and palatines; scale margins smooth or very weakly laciniate; predorsal scales not crowded; lateral line scales with canals. Proportional measurements are given in Table 1.

Remarks.—*C. aculeatum* inhabits lakes, rivers and small streams. All of my specimens were found in turbid water not less than two feet deep.

Range.—Lower reaches of the Río Lerma and tributaries (Fig. 4). According to Aurelio Solórzano (pers. comm.), *C. aculeatum* occurs in Lake Chapala at the mouth of the Río Lerma.

Etymology.—The name *aculeatum* is derived from the Latin meaning "sharp, pointed" and alludes to the species' snout.

Specimens of uncertain status.—TU 40844 (1) and TU 40876 (1), Lake Chapala, with the following counts, respectively: median lateral scales, 49, 48; predorsal scales, 32, 32; interdorsal scales, 5, 6; anal fin rays, 22, 19; gill rakers, 23, 22; total number of vertebrae, 43, 43. These specimens appear to be inter-

TABLE 1. Measurements of *Chirostoma aculeatum* expressed in thousands of the standard length; 52.0–109.4 mm S.L.; TU 40889 (1), TU 40864 (10), USNM 205783 (2), USNM 205784 (3), USNM 205785 (2).

		17 paratypes plus holotype			
	Holotype	Mean	Range	95% Conf. lim.	St'd dev.
Snout to first dorsal fin origin	567	567	552–588	5.4	10.8
Snout to second dorsal fin origin	703	700	686–783	4.0	8.0
Snout to pelvic fin origin	442	442	420–456	4.2	8.4
Snout to anal fin origin	593	586	567–607	5.5	10.1
Head length	288	289	279–298	2.9	5.8
Postorbital head length	116	128	116–136	2.3	4.7
Eye length	54	56	42–67	1.4	6.9
Snout length	115	111	101–121	2.6	5.3
Mandible length	145	136	125–145	2.9	5.9
Least depth of caudal peduncle	90	89	79–95	1.9	3.9
Length of caudal peduncle	173	180	160–193	5.1	10.2
Height of second dorsal fin	149	148	132–166	4.6	9.2
Length of anal fin base	241	249	236–269	5.0	10.0
Height of anal fin	158	161	134–179	5.4	10.9
Pectoral fin length	188	189	172–207	4.4	8.8

mediate between *C. labarcae* and/or *C. aculeatum* and one of the larger species in the lake.

PHYLOGENY OF *Chirostoma*

Before it is possible to discuss the evolution of the species of *Chirostoma*, the following topics must be considered: the primitive and derived characters for the genus, the primitive species within the genus and the possible ancestors.

Primitive and Derived Characters

Scale margins.—All juvenile specimens examined (less than 25 mm S.L.) had scales with smooth margins, including those species which as adults are characterized by laciniate scales. Laciniate scales are also associated with the most pronounced morphological specializations (see *C. lucius* and *C. promelas*). For these reasons, smooth-edged scales are considered primitive and laciniate derived.

Lateral line morphology.—All juvenile specimens examined had only pores in their lateral line scales, including those which as adults are characterized by lateral line scales with canals. There is also a correlation between morphological specialization and the presence of canals which cuts across the species groups (*C. lucius*, *C. sphyraena*, *C. promelas*, *C. labarcae* and *C. aculeatum*). Thus pores are considered primitive and canals derived.

Dentition.—Enlarged or canine-like teeth or the presence of teeth on the vomer, palatine, or lips are considered to represent a trophic specialization and thus are derived. One or two rows or a single band of small teeth on the dentaries and premaxillaries is considered the primitive state. It should be noted that there are indications that reversals of this character occur in *Chirostoma* (see arge group); it is not always possible to tell whether a species has a primitive dentition pattern or has undergone a character reversal and may be thus regarded as pseudoprimitive.

Pigmentation.—Distinct pigmentaion patterns other than a general darkening of the body resulting from local environmental conditions are so rare in *Chirostoma* that they are considered derived.

Meristic and morphometric characters.—In interpreting these characters, the assumption is made that *Chirostoma* evolved from a small marine atherinid, perhaps similar to *Menidia berylina* or *Melaniris crystallina*,

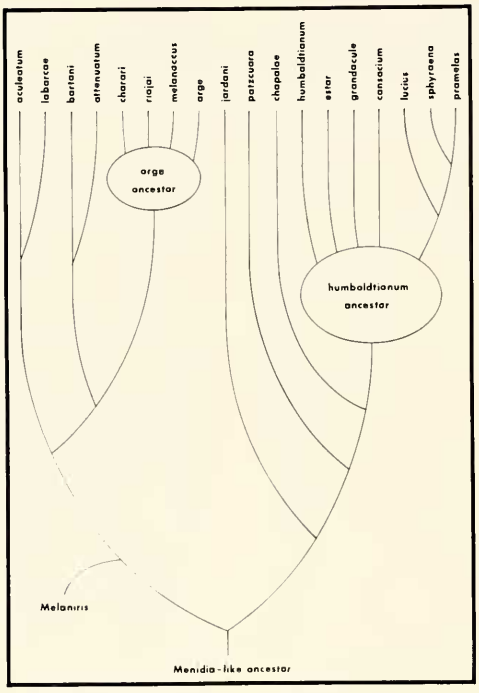


Figure 15. Phylogeny of *Chirostoma.*

which entered the streams and lakes of central Mexico during the Tertiary Period. As it is unlikely that a small ancestor would have very high meristic and morphometric values, species with low values are regarded as primitive for these characters. Care should be taken in interpreting individual cases, however, as extremely low values probably represent character reversals or specializations (e.g., the number of pectoral fin rays in *C. bartoni*, Fig. 8A, the number of anal fin rays in *C. riojai*, *C. aculeatum* and *C. labarcae*, Fig. 8B, the number of gill rakers in *C. riojai* and *C. grandocule*, Fig. 9, and the distance from the snout to the origin of the first dorsal fin in *C. riojai* and *C. attenuatum*, Fig. 13).

Modifications in the head region resulting from trophic specialization are considered derived as are increases in body size.

Primitive Species Within the Species Groups

The most primitive species within the jordani group is *C. jordani.* Its scale margins are usually smooth and canals in the lateral line scales are the exception rather than the rule. The species has no obvious trophic specializations other than a tendency towards an angular rather than a blunt snout. Where interspecific variation exists, *C. jordani* has low values for all morphometric and meristic characters. The species is also small.

Within the arge group, *C. bartoni*, *C. attenuatum*, *C. labarcae*, *C. aculeatum* and *C. charari* may be ruled out as primitive because of one or more high meristic values or obvious trophic specializations. The remaining three species have the following derived characters: *C. arge* has large teeth, some of which are present on the lip of the upper jaw. Specimens from the Río de la Laja have lateral line scales with pores and canals and black on the first and second dorsal, caudal and anal fins. *C. melanoccus* has 17–22 gill rakers on the first arch, an intermediate value for the arge group, and a range in eye length from 6.0 to 6.8 in percent of standard length which is surpassed only by *C. charari.* The species' minute teeth probably represent a character reversal. *C. riojai* has no obviously derived character states except for a low number of anal fin

rays and gill rakers which probably represent character reversals.

Morphological trends, whatever their significance in the jordani group, are not as apparent among the arge species. It is difficult to form a satisfactory hypothesis predicting which is the most primitive of the three species discussed above or to comment on possible relationships between both species groups without first examining the characteristics of related marine genera. This topic is considered next.

Possible Ancestors and the Origin of Chirostoma

A careful revision of the Atherinidae including an osteological analysis has never been made (Rosen, 1964). Any conclusions drawn regarding specific or generic relationships must be regarded as tentative at this time.

Atherinids are predominantly marine and brackish water coastal fishes. A number of species have entered fresh waters but with the exception of *Chirostoma* and perhaps *Basilichthys* and *Odontesthes* have undergone only a limited amount of diversification. This discussion will be limited to those genera occurring in Mexico and Central America.

Archomenidia and *Xenatherina* are probably restricted to the fresh waters of the Papaloapan, Coatzacoalcos and the Grijalva-Usumacinta basins. According to Schultz (1948) both genera have enlarged teeth projecting forward from the premaxillaries. The presence of this character and the species geographic position suggests that they are derived from *Melaniris*. I consider it unlikely that they are related to *Chirostoma* in spite of the fact that they are similar to *C. arge* in dentition.

Membras is too specialized to be a "persistent ancestor" of *Chirostoma* because of its laciniate scales, scale sheaths along the base of the second dorsal and anal fins and sensory grooves on the snout (Robbins, 1969, 1970).

Among the species of *Menidia* (including the nominal *Menidiella* Schultz), *M. berylina* ranges along the Atlantic and Gulf coasts from Massachusetts Bay to northern Vera Cruz. The species occurs in marine, brackish and freshwater habitats frequently in association with vegetation or floating debris. Specimens from Grand Isle, Louisiana are characterized by small teeth placed within the gape, a fairly high number of gill rakers (22–26), smooth scale margins and lateral line scales with canals becoming pores north of Virginia. Proportional measurements and counts tend to fall near the center of the range of variation for the arge group and the less specialized members of the jordani group (Figs. 5–14). A *Menidia berylina*-like stock could have easily given rise to *Chirostoma*.

The genus *Melaniris* is widely distributed along the Atlantic and Pacific coasts and in the fresh waters of Central America. On the east coast of Mexico it extends north to the Río Coatzacoalcos (Miller, 1966). Along the west coast *M. crystallina* (Fig. 16D) ranges from the Río Fuerte, Sonora south to the Río Grande de Santiago, Nayarit. In this drainage it extends inland to a point just above the mouth of the Río Verde (Briggs and Miller, 1960). Compared to the more primitive species of *Chirostoma* discussed above, specimens collected from the Río Grande de Santiago at the highway 15 crossing may be characterized by smooth-edged scales, lateral line scales with pores and canals, a high number of anal fin rays (Fig. 8B) and predorsal scales (Fig. 6) a relatively high number of gill rakers (Fig. 9) and the presence of rostral grooves (absent from all species of *Chirostoma*). Morphometrically, *M. crystallina* differs most in the distance from the snout to the origins of the first (Fig. 13) and second dorsal fins, the lengths of the caudal peduncle, anal fin base, pectoral fins, head (Fig. 11) and mandible (Fig. 12). The species also has black on the first and second dorsals, anal and pelvic fins and large teeth extending onto the lips of the upper and lower jaws.

The dentition and pigmentation patterns shared by *C. arge* and *M. crystallina* (Figs. 16C and D) are unique in *Chirostoma*. Although the former character has varied during the evolution of the genus, the changes have been quantitative rather than qualitative (except for the appearance of vomerine teeth in *C. humboldtianum*, *C. estor estor* and *C. bartoni*). Striking pigmentation patterns have evolved only once in *C. promelas*. I interpret this character concordance as an indication of the close relationship between these species; it is unlikely that they evolved independently. This

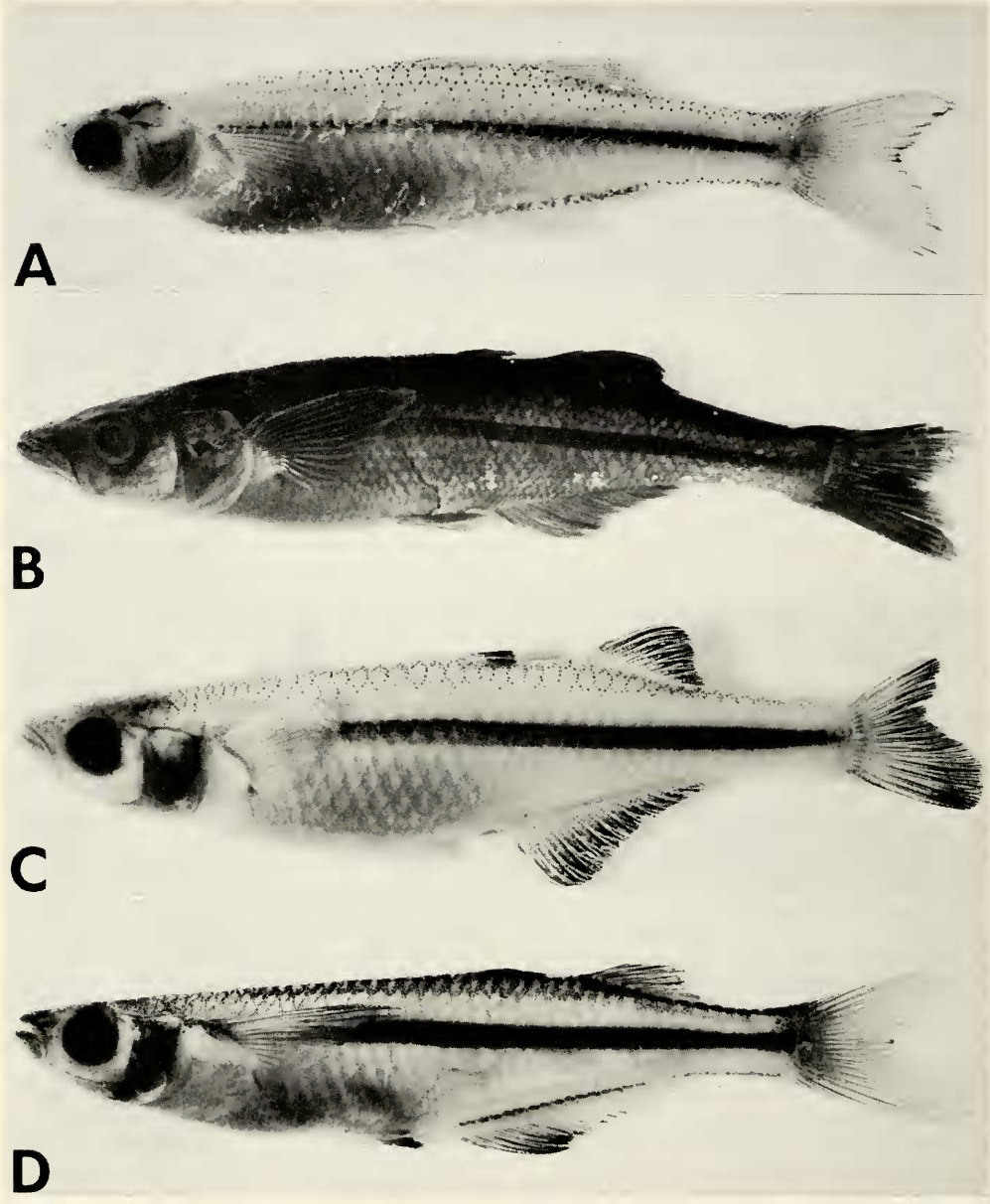


Figure 16. (A) *C. jordani*, UMMZ 197611, 52.8 mm S.L.; (B) *C. humboldtianum*, FMNH 73320, 148.6 mm S.L.; (C) *C. arge*, UMMZ 197622, 59.0 mm S.L.; (D) *Melaniris crystallina*, UMMZ 197605, 68.7 mm S.L.

relationship and the parallel morphological trends in the species groups of increasing body length and meristic and morphometric values suggest that *Chirostoma* is a phyletically unnatural assemblage of species.

There are two or perhaps three independent lines of evolution in *Chirostoma*. The most distinct lineage is the jordani group, which as a whole is the most widely distributed, contains the greatest number of species and is the most consistent in its patterns of variation. This group was prob-

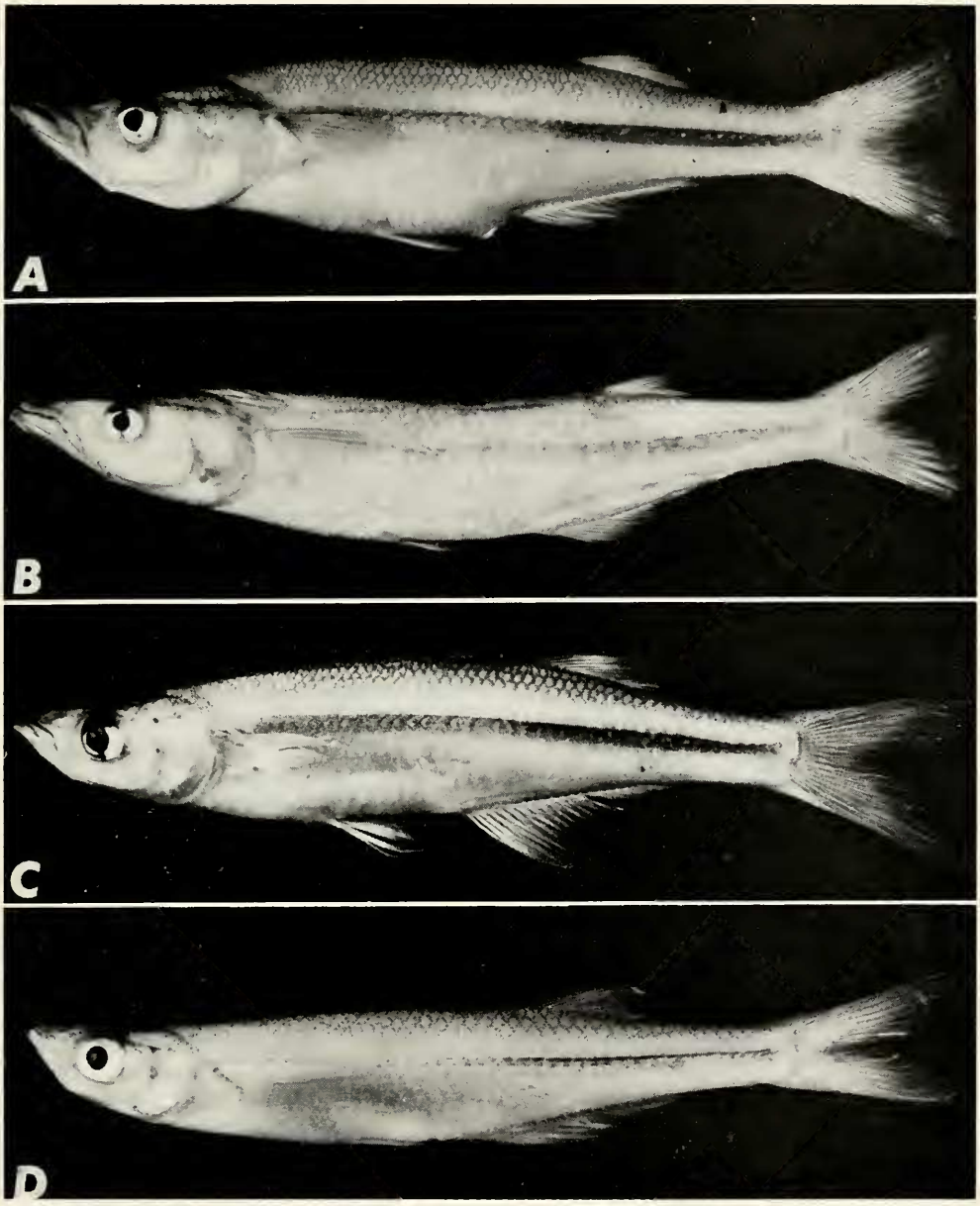


Figure 17. (A) *C. lucius*, UMMZ 197648, 228.3 mm S.L.; (B) *C. sphyraena*, 197647, 204.9 mm S.L.; (C) *C. consocium consocium*, TU 40845, 115.1 mm S.L.; (D) *C. chapalae*, TU 40836, 80.4 mm S.L.

ably the first to begin radiating on the Mesa Central, diverging early from a *Menidia*-like form (perhaps the ancestor of *M. berylina*). While the jordani group was differentiating in fresh water, the lineage leading to *Melaniris* and the arge group diverged from the *Menidia* ancestor evolving its distinctive dentition and pigmentation pattern. A subsequent split in this line led to an invasion of the Lerma-Santiago river system and the arge group on one hand and *Melaniris crystallina* on the other. The morphometric and

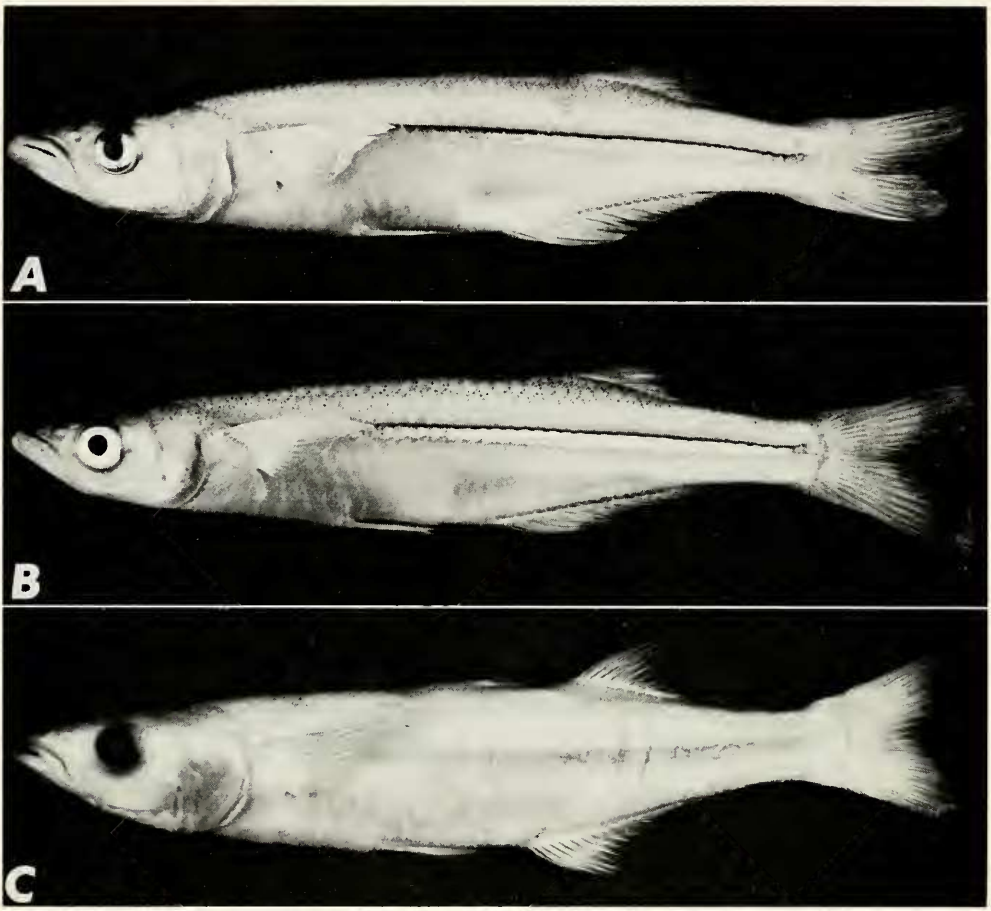


Figure 18. (A) *C. aculeatum*, holotype, TU 40889, 85.0 mm S.L.; (B) *C. labarcae*, TU 31958, 75.9 mm S.L.; *C. consocium reseratum*, UMMZ 197642, 168.1 mm S.L.

meristic specializations characteristic of *M. crystallina* probably appeared after this division.

As described above, pores and canals appear in the scales of the lateral line systems of *Menidia berylina* and *Melaniris crystallina*. The type of opening in the scales of the ancestral species is unknown, but appears to be irrelevant to the course of evolution of this character once the species had invaded the fresh waters of central Mexico. *C. arge* and *C. jordani* have lateral line scales with canals or pores on the same individuals, although in the former species, this condition is restricted to populations in the Río de la Laja. In the other members of the jordani species group, pores have been almost completely replaced by canals; they appear infrequently in only *C. patzcuaro*, *C. humboldtianum* and *C. grandocule*. In the remaining species of the arge group only pores are found, except for *C. labarcae* and *C. aculeatum*. These two species have lateral line scales with canals. The selection pressure responsible for this trend of replacement of pores is not known although it may be related to habitat. Almost all of the species with scale canals have probably evolved or lived for a long time in a lacustrine environment, whereas most of those with pores either live in streams or are recently derived from stream forms.

An alternative hypothesis for the origin of the arge group is the argument that most of the species evolved from a *Melaniris*-like ancestor (similar to *C. riojai*) before the

origin of canals in the lateral line scales and the characteristic pigmentation and dentition patterns and that *C. arge* represents a third, later arrival. Although this scheme eliminates the need for the reversal of these characters, I consider it unnecessary. The variation in *C. jordani* and *C. arge* suggests that the characters may have become unstable and variable when the ancestors first invaded fresh water. In this situation reversals would not be difficult.

The hypothesis that *Chirostoma* is monophyletic and that *M. crystallina* is an offshoot of the arge group is considered to be unlikely.

Chirostoma is most likely diphyletic. A future revision of the Atherinidae will probably result in a breakup of the genus as it is now constituted, hopefully along the lines outlined above.

Evolution Within the Species Groups

The jordani species group.—*C. jordani* is probably a slightly differentiated version of the ancestral stock which originally invaded the Lerma-Santiago system. The first major step in the evolution of the jordani species was the differentiation of the ancestral *C. humboldtianum* from this stock. This transition was accompanied by a great increase in size (from average of about 70–80 mm S.L. to around 200 mm S.L.) and an increase in the number of scales, fin rays, gill rakers and vertebrae. Canals tended to replace pores in the lateral line and the scale margins became laciniate. Morphometrically, the values of the two species overlap considerably, but there seems to have been a relative decrease in eye length, length of the anal fin base and pelvic fins and in the height of the anal and second dorsal fins. A relative increase in the length of the snout, mandible and head and in the distance between the snout and the origins of the pelvic and anal fins can also be detected.

Two species fall between *C. jordani* and *C. humboldtianum*. *C. patzcuaro*, a small species, has an occasional pore in its lateral line and a slightly pointed snout. Its meristic values fall within the range of *C. humboldtianum*, and its predorsal scales are slightly crowded and irregular in some specimens. The apparent close relationship between *C. patzcuaro* and the nominal *C. regani* has been discussed. *C. regani* may represent a level of evolution just ancestral to *C. humboldtianum* and *C. patzcuaro* an offshoot from this stock.

The second species, *C. chapalae*, shares with *C. jordani* a small, oblique mouth, a short head, postorbital distance and snout length and a faint concentration of melanophores along the posterior margin of the caudal fin. Meristically, it is within the range of *C. humboldtianum*, but lacks the higher numbers of predorsal scales. Because of these differences and the pigmentation pattern, I feel that *C. chapalae* also diverged just prior to *C. humboldtianum*.

C. humboldtianum, existing now as relict population, probably ranged more or less continuously from the Valley of Mexico to western Jalisco and Nayarit at various times in the past. The remaining members of the jordani group probably evolved from isolated populations of this species. One lineage leads directly to *C. consocium*. The evolution of this species will be discussed in more detail elsewhere. Suffice it to say here that it is the closest relative to *C. humboldtianum* that exists in the Lake Chapala area.

A second line leads to *C. estor*. This species differs primarily by having a longer body and higher number of median lateral and predorsal scales. It has not evolved any unique trophic structures except for occasional teeth on the vomer.

A third line leads from the *humboldtianum* ancestor to *C. grandocule*. This species still retains an occasional pore in the lateral line scales and has diverged primarily in its exceptionally high number of gill rakers (Fig. 9).

The fourth lineage leads to *C. lucius*, *C. sphyraena* and *C. promelas*. I have assumed this line to be independent of the others, but there is a possibility that these species may have derived their high scale counts from the ancestor to *C. estor*. The increase in the values of these characters in the western populations of *C. humboldtianum* suggests that it can occur independently. The length of the lower jaw has diverged in these three species. In *C. sphyraena* it usually projects little beyond the slender snout whereas in *C. lucius* it may project far beyond a broad snout. In *C. promelas* the lower jaw is shorter and included by the snout. These species are the most derived in the jordani species group.

These relationships are shown in the right hand branch of the phylogeny illustrated in Figure 15.

The arge species group.—The major event in the evolution of the arge group was the isolation and differentiation of populations of the *Melaniris*-like ancestor. There is no generalized species directly comparable to *C. humboldtianum* in the arge group. *C. arge* still partially retains specialized ancestral characters lost in all other species.

The line leading to *C. labarcae* and *C. aculeatum* probably diverged early. Both of these species have pointed snouts, moderately large to large teeth, lateral line scales with canals and an exceptionally high number of anal fin rays.

Three other populations have diverged in a different direction. *C. attenuatum attenuatum* shows an increase in body size and number of gill rakers and *C. a. zirahuen* has developed a very high number of median lateral scales (Fig. 5). *C. bartoni*, on the other hand, has only a slightly higher number of predorsal scales, anal fin rays and gill rakers, but has a more angular snout and occasionally teeth on the vomer.

A third cluster of species seems to have diverged very little from isolated populations of a *C. arge*-like ancestor. *C. melanoccus* differs primarily by having very small teeth and a higher number of gill rakers (Fig. 9). *C. riojai* and *C. charari* differ by having higher anal fins (Fig. 14). The latter species has fewer and smaller teeth and a more anterior placement of the dorsal fins (Fig. 13); the former has larger eyes, a greater postorbital distance and more anteriorly projecting premaxillaries. All have lateral line scales with pores.

The left hand branch of the phylogeny shown in Fig. 15 summarizes the above discussion and considers *Melaniris* to be an offshoot of the line leading to the arge group as a whole. An alternative view of the origin of the four species discussed immediately above is that the *arge* ancestor split into two populations which gave rise to the predecessor of *C. arge* and *C. melanoccus* on one hand and *C. riojai* and *C. charari* on the other. Each of these lineages subsequently divided resulting in the four existing species.

Poorly defined morphological trends, generally low morphometric and meristic values, reversals, and abrupt increases in certain meristic characters (median lateral scales, anal fin rays and gill rakers) suggest that the arge species group is evolving parallel to the jordani group but behind it in time. Similar events must have occurred after the jordani ancestor invaded the Lerma-Santiago river system. A small species, it was preadapted to survive in streams and later successfully entered lacustrine environments. This shift in habitats was accompanied by an increase in body size and most body proportions and an increase in the number of scales, fin rays, gill rakers and vertebrae. Superimposed on these trends are a few specific trophic specializations. It is this view of the evolution of *Chirostoma* which resulted in the arrangement of the species in the figures. This is not an artificial clustering of ecospecies along morphological gradients. It is a reflection of the evolutionary events that can occur when a species enters a relatively open environment and undergoes phyletic differentiation as well as adaptive radiation. There are few critical gaps in the morphological record presented by the existing species. Thus, it is fairly easy to see the direction that evolution has taken and where the morphoclines (Maslin, 1952) have been modified.

Conclusions

1. The genus *Chirostoma* consists of eighteen species and six subspecies not including *C. compressum*, thought to be extinct.

2. Primitive versus derived character states for *Chirostoma* are considered to be, respectively: smooth versus laciniate scale margins, pores versus canals in the lateral line scales, small teeth placed within the gape on the dentaries and premaxillaries versus large teeth so placed or small or large teeth in any other location, low range versus high range of meristic values. Extreme morphometric values in any direction and distinctive patterns of pigmentation are also considered derived.

3. *Chirostoma* is separable into two species groups on the basis of meristic characters and scale morphology. The jordani group tends to have a high range of meristic values, laciniate scales with lateral line canals; the arge group, with few exceptions, has a low

range of meristic values, smooth-edged scales and lateral line pores.

4. *C. jordani* is considered to be the most primitive member of the jordani species group and *C. arge*, *C. melanoccus* and *C. riojai* the most primitive members of the arge species group. However, *C. arge* closely resembles *Melaniris crystallina* in pigmentation pattern and dentition and is considered, in spite of its specializations, closest to the ancestral stock of the arge species group.

5. *Chirostoma* is most likely diphyletic. The jordani species group diverged from a *Menidia*-like species which invaded the Lerma-Santiago river system very early. The arge species group evolved from a *Melaniris*-like stock which invaded the same basin at a later time.

6. Both species groups show trends of replacement of primitive character states by those considered to be derived. The arge species group seems, however, to be at an earlier stage of this process.

7. The most important step in the evolution of the jordani species group was the appearance of a large, generalized species probably very similar to the eastern populations of *C. humboldtianum*. This widespread form seems to have given rise to most of the other members of the species group.

8. The arge species group seems to have evolved from populations of a species similar to *C. arge* and *Melaniris crystallina*. No generalized species comparable to *C. humboldtianum* exists in this group.

Resumen

1. El Género *Chirostoma* consiste de 18 especies y 6 subespecies, sin incluir *C. compressum* De Buen, que se considera está extinguido. Los siguientes nombres en uso corriente se sinonimizan aqui: *Otalia* = *Christoma*; *C. ocampoi* y *C. regani* = *C. humboldtianum*; *C. diazi* = *C. sphyraena*; *C. ocotlanae* = *C. lucius*. No se reconocen subespecies de *C. jordani*. *C. reseratum* se refiere a *C. consocium* a nivel subespecifico. El nombre *C. attenuatum* Meek es revalidado para las poblaciones de los Lagos de Pátzcuaro y Zirahuén, a la fecha designados como *C. bartoni*. Cinco ejemplares del lago que está junto al Balneario de Cointzio, Michoacán, son referidos a *C. charari* De Buen. No se designa neotipo debido al pequeno numero de ejemplares. *C. aculeatum* se describe como nuevo.

2. Estados primitivos versus derivados para caracteristicas de *Chirostoma* se considera son, respectivamente: bordes de las escamas lisos versus laciniados, poros versus canales en la línea lateral, dientes pequeños colocados dentro de la cavidad sobre los dentarios y premaxilares versus dientes grandes colocados igual o dientes pequenos o grandes en cualquier otra posición, números altos de variacion merística versus números bajos. Valores morfométricos extremos en cualquier dirección y patrones distintivos de pigmentación se consideran también derivados.

3. *Chirostoma* es separable en dos grupos de especies sobre la base de características merísticas y morfología de las escamas. El grupo jordani tiende a tener el número alto de valores merísticos, escamas laciniadas con canales en la línea lateral; el grupo arge tiene número baja de los valores merísticos, bordes de las escamas lisos y poros en la línea lateral.

4. *C. jordani* se considera el miembro mas primitivo del grupo de especies jordani y *C. arge*, *C. melanoccus* y *C. riojai* los miembros mas primitivos del grupo de especies arge. Sin embargo, *C. arge* se parece estrechamente a *Melaniris crystallina* en patrón de pigmentacion y dentición, y es considerado, a pesar de sus especializaciones, mas cercano a la forma ancestral del grupo de especies arge.

5. *Chirostoma* es mas probablemente difilético. El grupo de especies jordani divergió de una especie semejante a *Menidia* que invadió el sistema fluvial Lerma-Santiago muy temprano. El grupo de especies arge evolucionó de una entidad semejante a *Melaniris* que invadió la misma cuenca en un tiempo posterior.

6. Ambos grupos de especies muestran tendencias de reemplazo de estados primitivos de características por aquellos que se consideran derivados. El grupo de especies arge parece, sin embargo, estar en una etapa mas temprana de este proceso.

7. El paso mas importante en la evolución del grupo de especies jordani fue la aparición de una especie grande, generalizada, probablemente muy similar a las poblaciones orientales de *C. humboldtianum*. Esta forma ampliamente distribuída parece haber dado lugar a la mayoría de los otros miembros del grupo de especies.

8. El grupo de especies arge parece haber evolucionado de poblaciones de una especies similar a *C. arge*. No existe ninguna especie generalizada comparable a *C. humboldtianum* an este grupo.

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