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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.

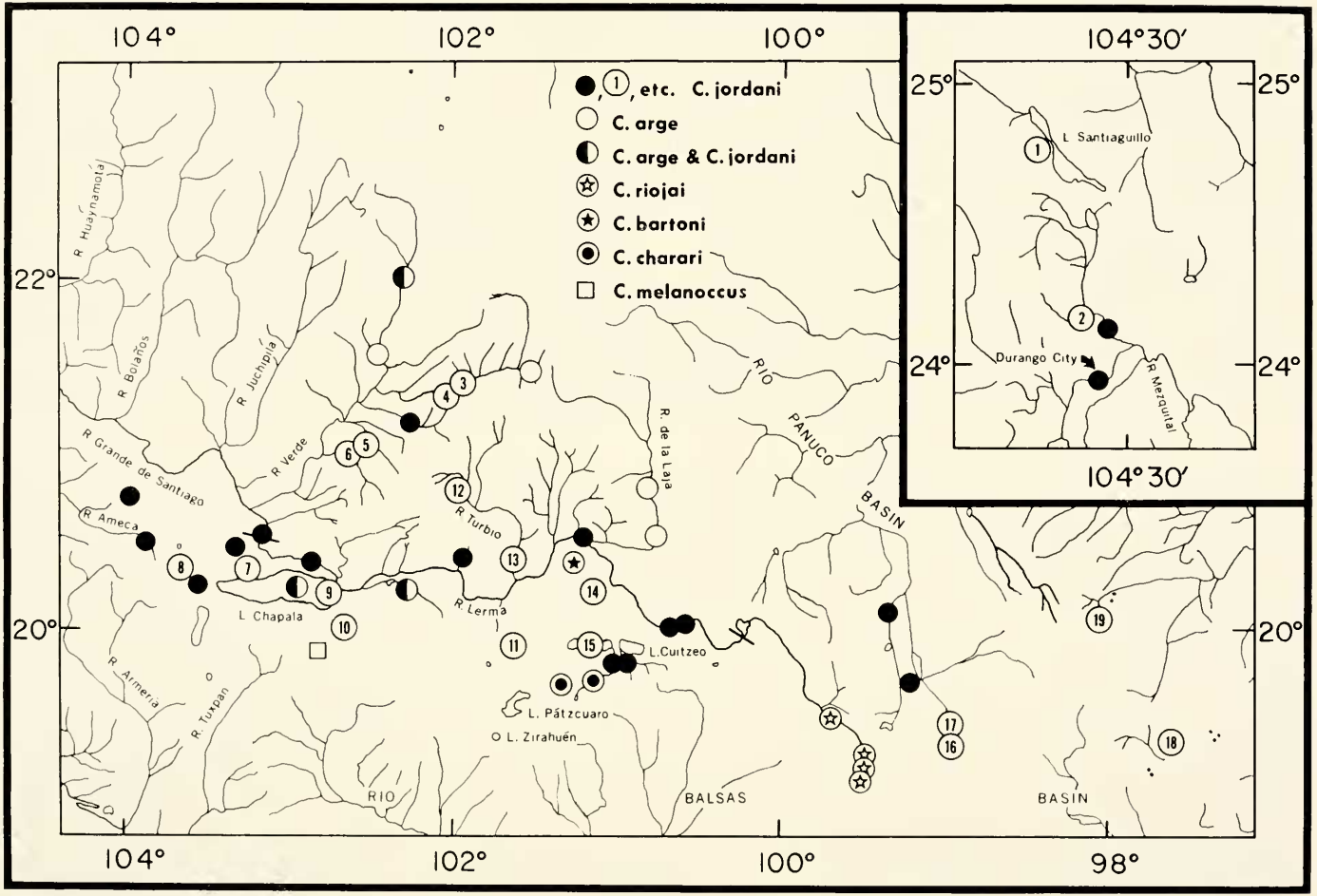
C. jordani was taken from small ponds and streams as well as from the main channel of the Río Santiago and some of the larger lakes. In most cases the species was found associated with vegetation, either drowned terrestrials along the margins of flooded ponds, in and around dense stands of *Scirpus* 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

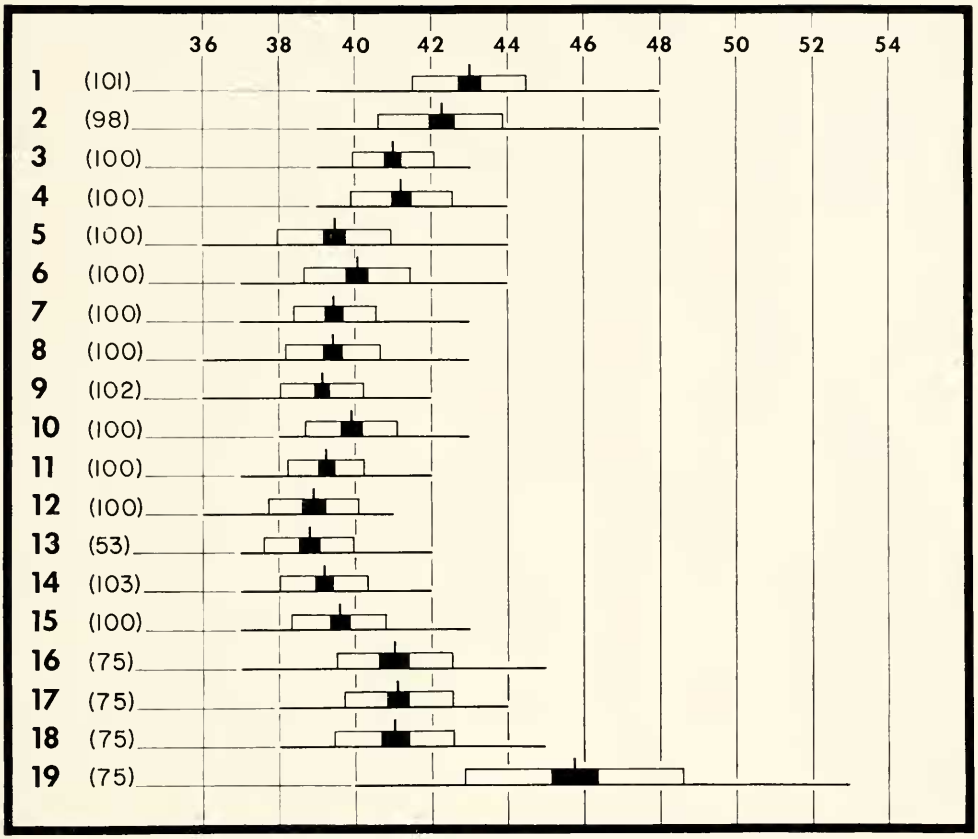


Figure 2. Variation in the number of median lateral scales in *Chirostoma jordani*. For localities and explanation of the diagrams see legends of Figs. 1 and 5.

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.

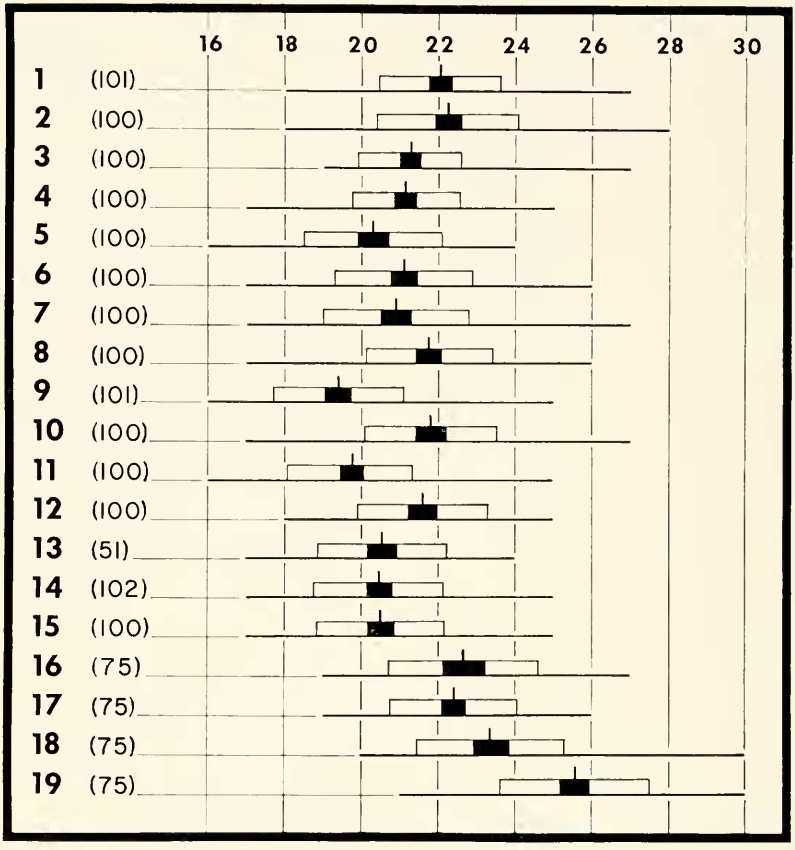


Figure 3. Variation in the number of predorsal scales in *Chirostoma jordani*. For localities and explanation of the diagrams see legends of Figs. 1 and 5.

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

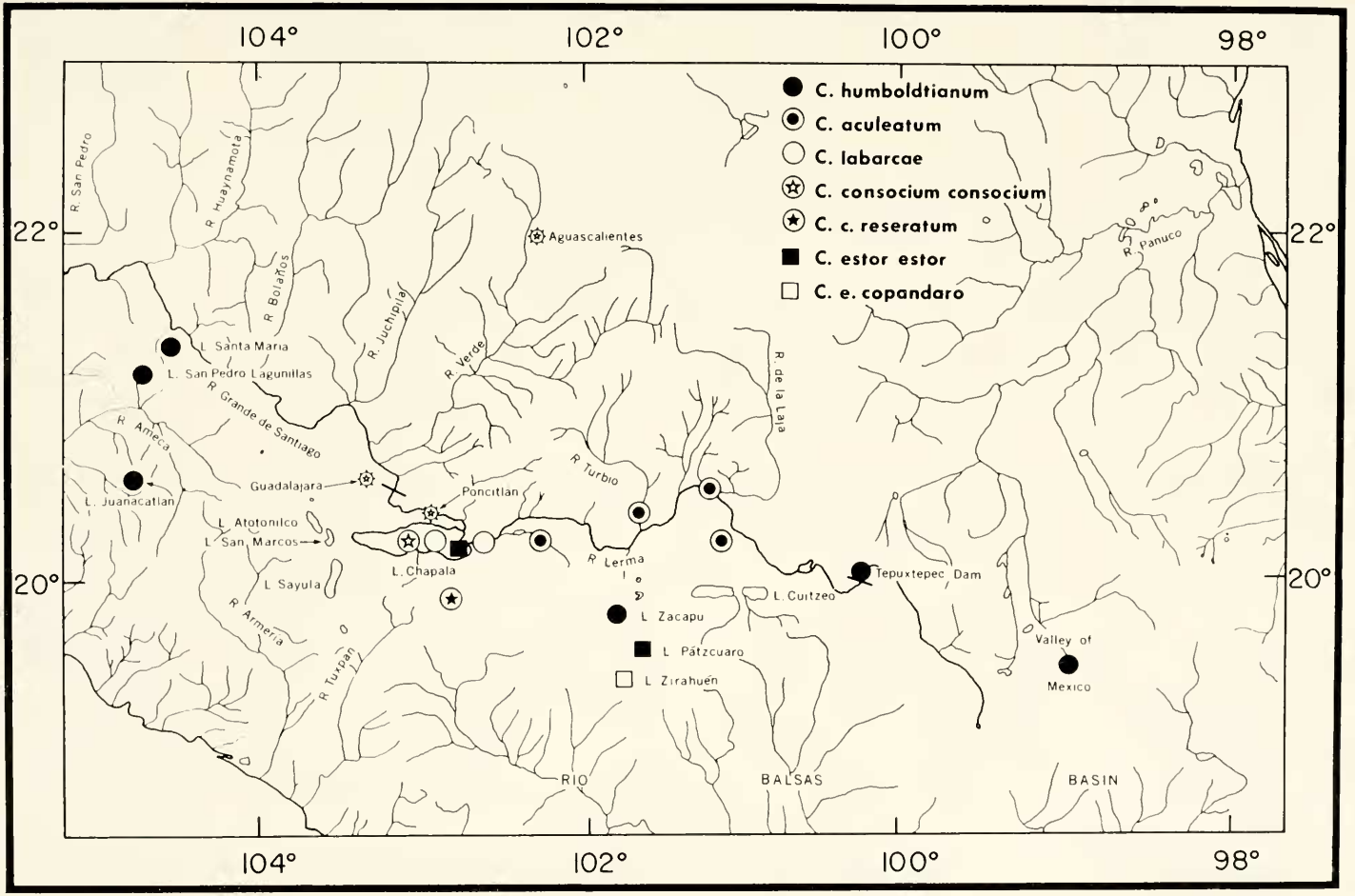
Fig. 18c

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.

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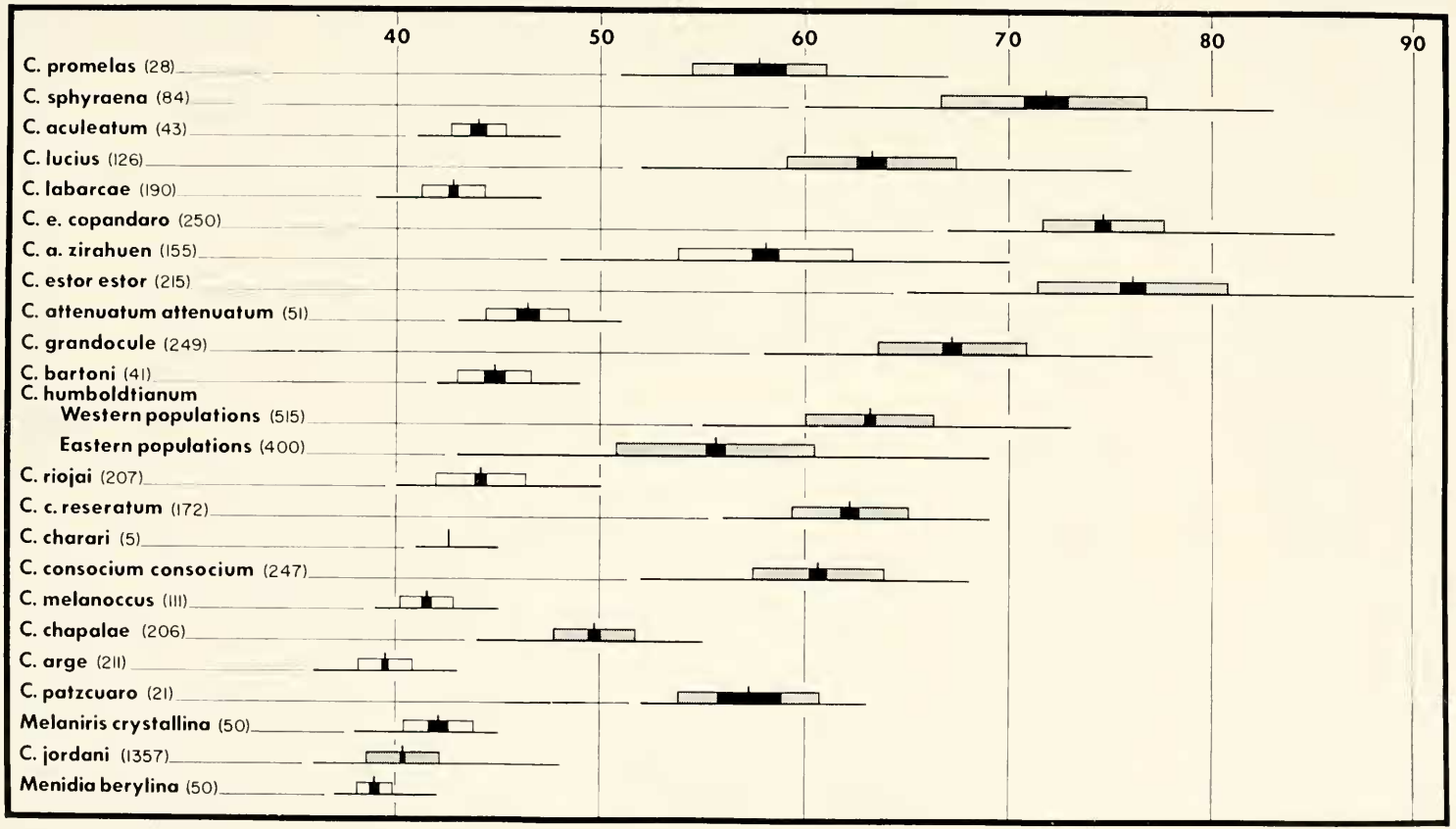
Figure 5. Comparison of the number of median lateral scales in *Menidia berylina, Melaniris crystallina* and *Chirostoma*. The diagrams indicate the mean (center point), 95 percent confidence limits of the mean (black rectangle), one standard deviation on either side of the mean (outer limits of open 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;

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