

NOAA Technical Report NMFS Circular 415

# A Basis for Classifying Western Atlantic Sciaenidae (Teleostei: Perciformes)

Labbish Ning Chao

September 1978



U.S. DEPARTMENT OF COMMERCE  
National Oceanic and Atmospheric Administration  
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**U.S. DEPARTMENT OF COMMERCE**

Juanita M. Kreps, Secretary

**National Oceanic and Atmospheric Administration**

Richard A. Frank, Administrator

**National Marine Fisheries Service**

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# A Basis for Classifying Western Atlantic Sciaenidae (Teleostei: Perciformes)<sup>1</sup>

LABBISH NING CHAO<sup>2</sup>

## ABSTRACT

Sciaenidae of the western Atlantic consist of 21 genera and at least 57 species, and are placed in 11 suprageneric groups: *Cynoscion*, *Larimus*, *Lonchurus*, *Menticirrhus*, *Micropogonias*, *Nebris*, *Pogonias*, *Sciaena*, *Sciaenops*, *Stellifer*, and *Umbrina* groups. The phylogenetic relationships of all western Atlantic genera are assessed on the basis of swim bladder, otoliths (sagitta and lapillus), and external morphology. The *Stellifer* group differs from all other western Atlantic sciaenids in having a two-chambered swim bladder and an enlarged lapillus. Phylogenetic and ontogenetic trends of the swim bladder range from a simple carrot-shape, to a more complicated structure with anterior projections and horns, to a very complicated lateral diverticula system. The sagitta is usually oval or elongate in shape. The thickness and the impression of the sulcus on the inner surface of the sagitta are diagnostic among genera. External morphology is adaptive, especially in relation to feeding habits and habitat, but a trend is evident in that closely related genera often have similar body shapes, mouth positions, and other external features. Species of the genus *Stellifer* are exceptions in having diverse mouth positions and feeding habits.

The synopsis section of the paper includes a diagnosis, a primary synonymy, and lists of types of nominal species for each taxonomic category. Four genera and 22 nominal species of New World freshwater sciaenids are also included. Nomenclatural changes in regard to the genus *Micropogon* (to *Micropogonias*) and for the species *Bairdiella chrysura* (to *B. chrysoura*) is given. A tested key to species and genera of all western Atlantic sciaenids is included. The approximate range of distribution and some counts are listed under each species. This paper is designed to serve as a basis for further revision of western Atlantic sciaenids.

## INTRODUCTION

Sciaenid fishes are characterized by their large otoliths and, with few exceptions, by enlarged lateral-line canals on the head and pores on the snout and lower jaw, and by the extension of the lateral line to the tip of the caudal fin. They are also characterized by a large and often complex swim bladder and by the presence of well-developed drumming muscles. This paper treats all 21 genera and 57 species of Sciaenidae currently recognized in the western Atlantic Ocean. In addition, limited information is also provided for 4 genera and 22 nominal species of sciaenid fishes present in freshwater river systems of the New World.

Current concepts of sciaenid classification are largely based on morphology of the swim bladder, otoliths (sagitta and lapillus), and snout (rostral) and mental (mandibular) pores and/or barbels (Chu et al. 1963; Trewavas 1962, 1964, 1977; Robins and Tabb 1965; Gilbert 1966; Lowe 1966; Lal Mohan 1969; Chao and Miller 1975). Other characters, such as the position of the

mouth, dentition, body form, size of the second anal spine, marginal serration of the preopercle, arrangement of lateral-line scales, color of peritoneal lining, and numbers of gill rakers, fin ray counts, and vertebrae, are important in distinguishing species and have been used by many authors to assign species to genera or to assess the generic relationships of western Atlantic Sciaenidae. However, the generic boundaries have not been well defined and many nomenclatural problems remain.

The purpose of this paper is to clarify generic boundaries, define suprageneric groups, and describe the evolutionary trends of western Atlantic Sciaenidae primarily on the basis of the morphology of the swim bladder, otolith, and snout and mental pore and/or barbel systems.

To classify the taxa above the generic level, the term suprageneric group is used here. Trewavas (1962) grouped eastern Atlantic sciaenids into tribes. Chu et al. (1963) grouped sciaenids of the Chinese coasts into subfamilies. Lal Mohan (1969) placed Indian species into both subfamilies and tribes. The suprageneric groups used here are comparable to the tribes of Trewavas (1962, 1977) and the subfamilies of Chu et al. (1963), but avoid the taxonomic problems inherent in using formal taxonomic categories. Like those studies, the present assessment is also a regional study. Variations in swim bladder, otolith, and external morphology are often found at different taxonomic levels. Therefore, a comparative study of sciaenids from several geographic regions, especially the eastern Pacific area, is necessary

<sup>1</sup>A portion of a dissertation submitted to the School of Marine Science, College of William and Mary, Williamsburg, Va., in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Marine Science, May 1976. Contribution No. 817, Virginia Institute of Marine Science, Gloucester Point, VA 23062, U.S.A.

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before allocating the western Atlantic sciaenid genera to formal taxonomic categories (tribes or subfamilies).

The commendable study of Indo-West-Pacific Sciaenidae by Trewavas (1977), especially in its assessment of diagnostic characters, evolutionary significance and classification of sciaenid fishes, is an important and valuable contribution to this family. Regretably, I was not able to incorporate the information in this publication here because it appeared after the present study was in press.

## MATERIALS

Type-material and other preserved specimens were examined from the following institutions:

- AMNH—American Museum of Natural History, New York, N.Y.  
ANSP—Academy of Natural Sciences, Philadelphia, Pa.  
BMNH—British Museum (Natural History), London, England.  
CAS—California Academy of Sciences, San Francisco, Calif.  
FMNH—Field Museum of Natural History, Chicago, Ill.  
LACM—Los Angeles County Museum of Natural History, Los Angeles, Calif.  
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Mass.  
MNHN—Museum National d'Histoire Naturelle, Paris, France.  
NHMV—Naturhistorisches Museum, Vienna, Austria.  
NMC—National Museum of Natural Sciences, Ottawa, Canada.  
RMNH—Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands.  
SOSC—Smithsonian Oceanographic Sorting Center, Washington, D.C.  
UF—Florida State Museum, University of Florida, Gainesville, Fla.  
UMML—Rosenstiel School of Marine and Atmospheric Sciences, Miami, Fla.  
USNM—United States National Museum, Washington, D.C.  
VIMS—Virginia Institute of Marine Science, Gloucester Point, Va.  
ZMA—Institute voor Taxonomische Zoologie, Universiteit van Amsterdam, Amsterdam, Netherlands.  
ZMK—Zoological Museum, Copenhagen, Denmark.

Freshly frozen and Formalin-preserved specimens were also obtained from various biological surveys along the Atlantic seaboard of the United States. These surveys were conducted by the Virginia Institute of Marine Science on various research vessels; by the National Marine Fisheries Service (U.S.A.) laboratories at Woods Hole, Mass. on RV *Albatross IV* and at Sandy Hook, N.J., on RV *Atlantic Twin*; and by the National Science Foundation's RV *Eastward*, Beaufort, N.C. Specimens examined from Gulf of Mexico and Atlantic

coast of South America were collected mainly by NMFS research vessels, the MV *Oregon I* and *Oregon II*, from 1962 to 1975. Primary type-specimens examined during the study are indicated under the synonymy of each species by their museum catalogue numbers and length of individuals. In other cases, except specifically noted, the type-specimens were not located. Numerous additional specimens have been studied, most of which are deposited at USNM, VIMS, and NMC.

## METHODS

Comparative morphologies of the swim bladder, otolith, and pore systems were studied. Other characters important in the recognition of species and genera are the arrangement and size of lateral-line scales, serrations of the preopercular margin, size of the second anal fin spines, color of the branchial chamber and peritoneal linings, meristics, and morphometrics. The standard methods of Hubbs and Lagler (1964) were used for all counts and measurements except for some modifications described by Chao and Miller (1975). In addition, scales perforated by lateral-line tubes or pores were counted as lateral-line scales from the upper end of the gill slit to the end of the hypural plate. On those species lacking well-defined lateral-line tubules or pores, counts were made on the number of transverse scale rows immediately above the lateral line. Vertebral counts were determined from radiographs and from cleared and stained specimens (Taylor 1967). The first caudal vertebra was identified by the absence of pleural ribs on the haemal process and usually by a short haemal spine just behind the elongate proximal pterygiophore of the anal fin. The urostylar centrum was included in counts.

Otoliths of most species were extracted from freshly caught specimens but some came from preserved specimens. Inner surfaces of the right sagitta and lapillus (in the *Stellifer* group) were illustrated. Ontogenetic changes of otoliths and swim bladder were studied in some species.

All available type-specimens were examined to assure the identities of species and genera of sciaenids studied in this paper. A primary synonymy is listed for each species to clarify nomenclatural problems.

Morphological terminology used here follows Chu et al. (1963), Trewavas (1962, 1964), and Chao and Miller (1975). A modification of the terms used for the snout pores was suggested by E. Trawavas of BMNH, and for otoliths by J. Fitch of the California Department of Fish and Game. Snout pores along the margin of the rostral fold are termed marginal (snout) pores, and pores in front or above them are termed upper (snout) pores (Fig. 1). The surface of the sagitta, with a "tadpole-shaped" sulcus is the inner surface and the obverse side is the outer surface (Fig. 2) which are the in situ position of the sagitta (Fig. 3). Also, the lateral margins of the sagitta are termed dorsal and ventral margins (Frizzell and Dante 1965). The "head section" of the sulcus is called the "ostium" and the "tail section" is called the "cauda" (Stinton 1975; J. Fitch, pers. commun.).

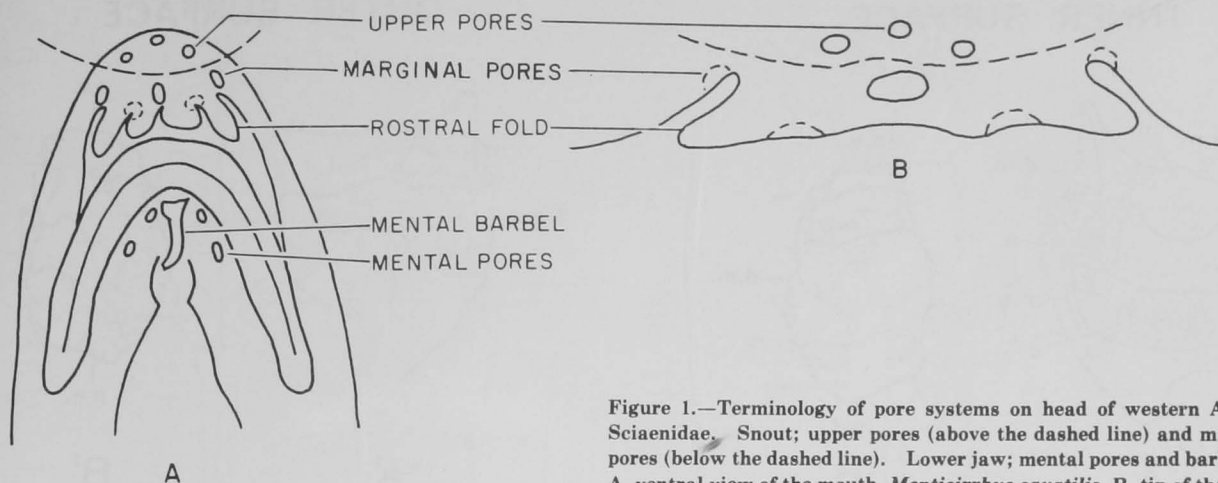


Figure 1.—Terminology of pore systems on head of western Atlantic Sciaenidae. Snout; upper pores (above the dashed line) and marginal pores (below the dashed line). Lower jaw; mental pores and barbels(s). A. ventral view of the mouth, *Menticirrhus saxatilis*. B. tip of the snout, *Stellifer lanceolatus*.

### A BRIEF HISTORY OF THE STUDY OF WESTERN ATLANTIC SCIAENIDAE

Prior to the binominal system of Linnaeus, Catesby in his 1743 edition of "The natural history of Carolina, Florida and the Bahama Islands," illustrated "Perca marina" (= *Micropogonias undulatus*), "THE CROKER" (plate 3), from Chesapeake Bay and "Alburnus Americanus" (= *Menticirrhus americanus*), "THE WHITING" (plate 12), from Charleston, S.C. Edwards (1751) in the appendix of "A natural history of birds" illustrated (plate 210) a "Ribband Fish" (= *Equetus lanceolatus*) from the Caribbean Islands. Linnaeus (1758) in his 10th edition of "Systema Naturae," Pisces Thoracici, recorded the genus *Sciaena* with five species, none of them from the western Atlantic. However, two species of western Atlantic Sciaenidae were named as *Chaetodon lanceolata* (= *Equetus lanceolatus*) based on Edwards' plate and *Cyprinus americanus* (= *Menticirrhus americanus*) from "the whiting" of Catesby. In the 12th edition of "Systema Naturae," 1766, Linnaeus added *Labrus chromis* (= *Pogonias cromis*), *Perca alburnus* (= *Menticirrhus americanus*), *Perca punctata* (= *Bairdiella chrysoura*), *Perca ocellata* (= *Sciaenops ocellata*), and *Perca undulata* (= *Micropogonias undulatus*), although he did not place them with the Sciaenidae from Europe.

Bloch and Schneider (1801) in their "Systema Ichthyologiae" reported six genera and nine species of western Atlantic Sciaenidae: *Johnius regalis* (= *Cynoscion regalis*), *J. saxatilis* (= *Menticirrhus saxatilis*), *Sciaena chromis* (= *Pogonias cromis*), *Lonchurus depressus* (= *Lonchurus lanceolatus*), *Lonchurus ancylodon* (= *Macrodon ancylodon*), *Eques americanus* (= *Equetus lanceolatus*), *Eques punctatus*, *Grammistes acuminatus* (= *Pareques acuminatus*), and *Bodianus stellifer* (= *Stellifer stellifer*). A year later (1802) Lacepède in volume three of "Histoire Naturelle des Poissons" recorded *Dipterodon chrysourus* (= *Bairdiella chrysoura*), *Pogonias fasciatus* (= *P. cromis*), and *Cheilodip-*

*terus acoupa* (= *Cynoscion acoupa*) and in volume four (1803) he added *Lutjanus cayennensis* (= *Cynoscion acoupa*), *Lutjanus triangulum* (= *Sciaenops ocellata*), *Centropomus alburnus* (= *Menticirrhus americanus*), *Sciaena croaker* (= *Micropogonias undulatus*), and *Leiostomus xanthurus* of the western Atlantic and also a freshwater sciaenid *Perca fourcroyi* (= *Pachypops fourcroyi*) from Surinam.

The boundaries of the species, genera, and family Sciaenidae were not well defined, until Cuvier. In the first edition of "Règne Animal" (1817), Cuvier defined limits to the application of some generic names (e.g., *Umbrina* and *Sciaena*). Also four new genera of western Atlantic Sciaenidae were described: the scientific names *Stellifer*, *Umbrina*, *Otolithes*, and *Ancylodon* were derived from Cuvier's vernacular names by Oken (1817). In the second edition, Cuvier (1829) added a new generic name *Corvina*. Cuvier (1830, in Cuvier and Valenciennes) in volume five of "Histoire Naturelle des Poissons," described 7 genera and 21 species of western Atlantic sciaenids. There were four new genera, i.e., *Larimus*, *Nebris*, *Lepipterus*, and *Micropogon*, and five freshwater nominal species, *Corvina oscula* (= *Aplodinothus grunniens*), *C. furcroea* (= *Pachypops fourcroyi*), and *Lepipterus francisci* (= *Panchyurus francisci*), were included. Cuvier also described and illustrated the swim bladders of six western Atlantic sciaenid fishes. Günther (1860) recorded 12 genera and 45 species of Sciaenidae from the western Atlantic including 3 genera and 9 species from freshwater. He used the shape of the swim bladder as one of the diagnostic characters in some of his generic descriptions. Jordan and Eigenmann (1889) listed 22 genera and 60 species, including 4 genera and 11 species of freshwater sciaenids. Jordan and Evermann (1898) included only 21 genera and 50 species of Sciaenidae from the Atlantic in the "Fishes of North and Middle America," including 3 genera and 5 species from freshwater. The studies of Desmarest (1823), Agassiz (1829), Castelnau (1855), Steindachner (1863), Bleeker (1865, 1873), Poey (1881), Berg (1895), and more recently of A. Miranda Ribeiro (1915), Meek and Hildebrand

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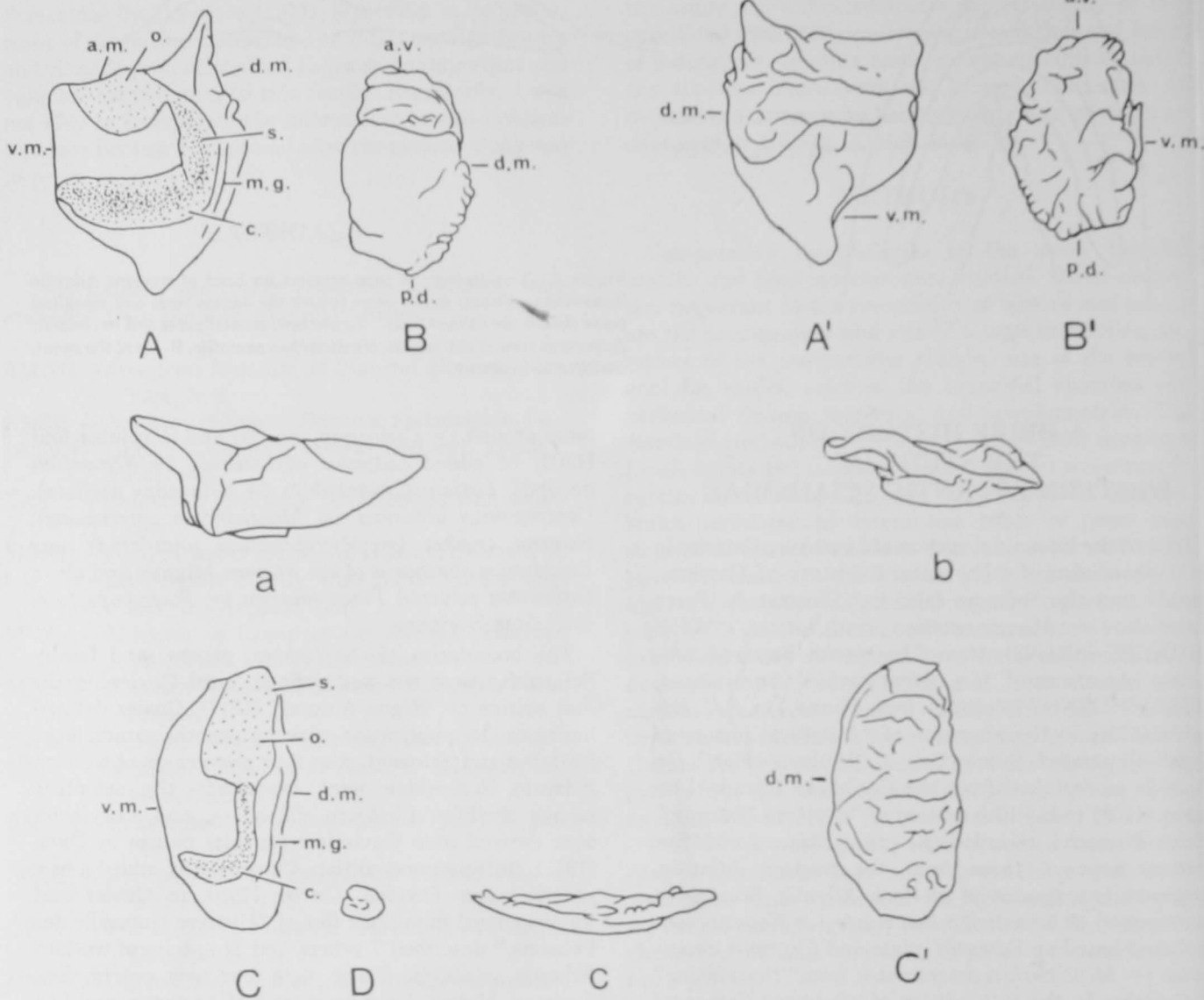


Figure 2.—Terminology of otoliths. A, A', a: sagitta and B, B', b: lapillus of *Bairdiella chrysoura*; C, C', c: sagitta and D: relative size of lapillus in *Leiostomus xanthurus*. A, B, C, D: inner surface; A', B', C': outer surface; a, b, c: lateral view with inner surface down and anterior end to the left. a.m. = anterior margin; a.v. = anterior ventral margin; d.m. = dorsal margin; c. = cauda section of sulcus; m.g. = marginal groove; o. = ostium section of sulcus; p.d. = posterior dorsal margin; s. = "tadpole-shaped" sulcus (dotted area); v.m. = ventral margin. All subsequent figures of otoliths (sagittae and lapilli) are oriented as in this figure.

(1925), Ginsburg (1929), Fowler (1942, 1954), Schultz (1945, 1949), Travassos and Paiva (1957), Lowe (1966), Cervigon (1966a), Cervigon and Holanda Lima (1972), Vazzoler (1969), Travassos and Rego-Barros (1971), Travassos (1973), Roux (1973), Jardim (1973), and Druzhinin (1974) have contributed to the knowledge of taxonomy and distribution of western Atlantic sciaenids in different geographic regions. At present, 21 genera and 57 species of sciaenids are recognized from the western Atlantic. In addition, there is one monotypic genus (*Aplo-dinotus*) recognized from the freshwaters of North America, and three genera (*Pachypops*, *Pachyurus*, and *Plagioscion*) from the freshwaters of South America.

Few studies have been made on the relationships of genera and higher division of western Atlantic Sciaenidae. Gill (1962a, b, c, d) revised the genera and named six subfamilies for North American sciaenids, i.e., Corvininae, Haploidonotinae, Lariminae, Liostominae, Otolithinae, and Sciaeninae. Later, only five subfamilies of Sciaenidae were listed, the Corvininae was not mentioned (Gill 1864a, 1873). Genera and subfamilies were defined by external characters and the boundaries between them were not clear. Bleeker (1874) distinguished *Isopisthus* and *Seriphus* from the rest of the Sciaenidae on the basis of complete separation of the dorsal fins and longer anal fins, and included them

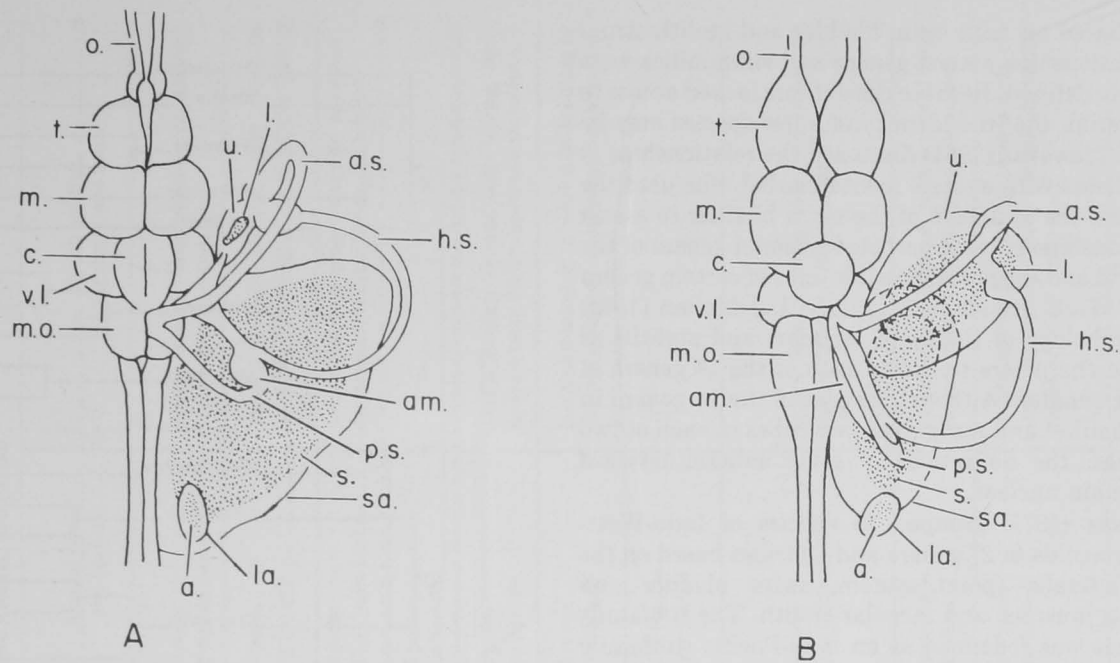


Figure 3.—Inner ears of Sciaenidae. A and A', with only sagitta enlarged, *Pseudosciaena crocea* (Richardson), after Chu et al. (1963:fig. 8A, B). B and B', with both sagitta and lapillus enlarged, *Stellifer lanceolatus* (Holbrook). A, B: dorsal view of right inner ear. A', B': lateral view of left inner ear. a = asteriscus; am. = ampulla; a.s. = anterior semicircular canal; c. = cerebellum; h.s. = horizontal semicircular canal; l. = lapillus; la. = lagena; m. = mesencephalon; m.o. = medulla oblongata; o. = olfactory nerve; p.s. = posterior semicircular canal; s. = sagitta; sa. = sacculus; t. = telencephalon; u. = utriculus; v.l. = vagal lobe.

in a small new family, "Scombrosoidei," which he felt, in some way, was a transition between the sciaenids and the sphyraenids. Later, Bleeker (1876) in part two of "Systema percaram revisum" named two phalanxes (tribes), the Sciaenini and the Hemisciaenini for the "familiar Sciaenoidei." He also described three subphalanxes (subtribes) in the Sciaenini, i.e., Equili, Aplodinoti, and Johnii, and two subphalanxes in the Hemisciaenini, i.e., Pseudosciaeni and Otolithi. Western Atlantic sciaenid genera were described under each subphalanx. The diagnostic characters for each taxon were determined from the external morphology, e.g., mouth position, dentition, scales, and fin rays.

Jordan and Eigenmann (1889) and Jordan and Ever-

mann (1896) divided the Sciaenidae into two subfamilies, the Otolithinae and the Sciaeninae, based on the number of precaudal and caudal vertebrae, lower jaw position, dentition, and size of the second anal spines. In the present study, I did not find these characters useful above the generic level. The first comprehensive studies on the species and generic relationships of sciaenids were published by Trewavas (1962) for tropical west African sciaenids and Chu et al. (1963) for Chinese sciaenids. Trewavas (1962 and pers. commun.) grouped the 16 west African sciaenid species into five tribes, based mainly on swim bladder structure; and the diagnostic characters of each tribe were clearly defined. Chu et al. (1963) grouped 37 species of Chinese sciaenid fishes into seven sub-

families based on both swim bladder and otolith structure. Relationships among genera and subfamilies were also clearly defined. Because the authors lacked access to type-material, the true identity of a few species may be in doubt. Trewavas (1964) discussed the relationships of sciaenid fishes with a single mental barbel. She used the barbels and the structure of the swim bladder to assess the relationships of some barbeled sciaenid genera of the New World and suggested possible links of certain genera with Old World sciaenids. Similarly, Lal Mohan (1969) used morphology of the swim bladders and otoliths as diagnostic characters to define each of the 14 genera of Indian Sciaenidae. Although he placed the 14 genera in five subfamilies and recognized two tribes in each of two subfamilies, the definitions of some subfamilies and tribes remain unclear.

Trewavas (1977) grouped 65 species of Indo-West-Pacific sciaenids in 27 genera and 10 tribes based on the acustico-lateralis (pore) system, swim bladder and drumming muscles, and saccular otolith. The subfamily Otolithinae was redefined as an Indo-Pacific subfamily with one species (*Argyrosomus regium*) in the Mediterranean and eastern Atlantic. She also suggested that the New World genera *Sciaena*, *Umbrina*, and probably *Menticirrhus* are the basis of subfamily Sciaeninae and within this of the tribe Sciaenini. Trewavas recommended that the grouping of sciaenid tribes into subfamilies, I agree, must await further knowledge of the family as a whole.

## DESCRIPTION AND RELATIONSHIPS

The morphology of the swim bladders, otoliths, and snout and mental pores and barbels are diagnostic in the classification of sciaenid fishes. They were described and compared first, then combined to assess the phylogenetic relationships of western Atlantic Sciaenidae. Within each of the characters, there are several structural patterns which may reflect phyletic relationships among groups of genera. The variations within each pattern are important in understanding the boundaries of different taxa. At the species level, the ontogenetic development of certain characters may suggest possible trends in phylogenetic relationships in higher taxa of the family. The presence of drumming muscles in males only or in both males and females of certain taxa is also useful in assessing the relationships of sciaenids. Other characters essential for the identification of genera and species may also be important to the study of their relationships and are described in the key at the end of this paper.

Based on swim bladder, otoliths, and external morphology, phyletic relationships (or kinships) are proposed here for 21 western Atlantic and 2 American freshwater genera of sciaenids (Fig. 4). Relationships among suprageneric groups were determined primarily by swim bladder morphology and secondarily by morphology of the otoliths (Table 1). External morphology was of some use as long as the adaptive and potentially convergent nature of these characters was kept in mind. By following the tactics used by Bolin (1947) for the marine Cot-

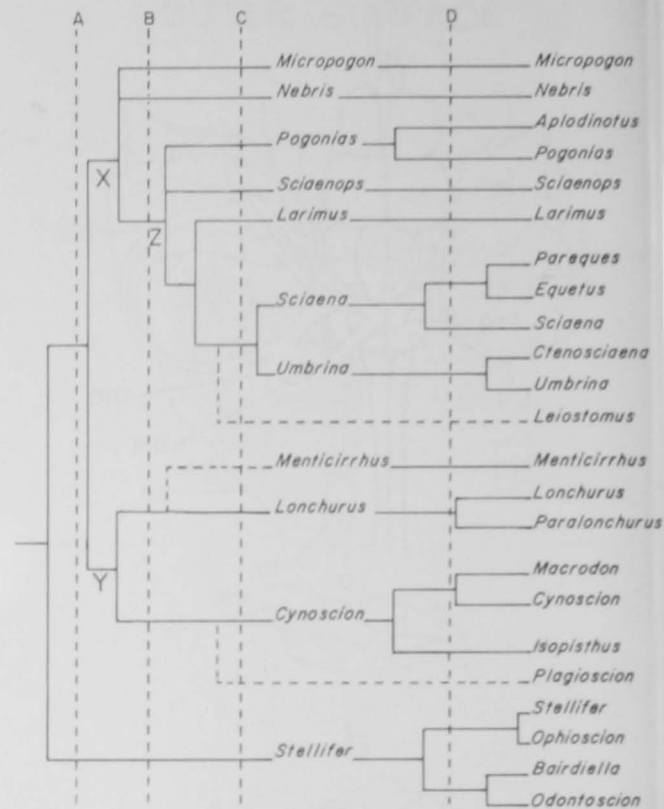


Figure 4.—Proposed phylogenetic relationships of genera and supra-generic groups of western Atlantic Sciaenidae. Subfamily level lies between dashed lines A and B; tribal level lies between dashed lines C and D; X, Y, and Z represent clusters discussed in the text.

tidae of California, the actual or "convenient" classification level for tribes may be drawn as between dashed lines C and D on Figure 4. The subfamily level may be drawn between dashed lines A and B. Between dashed lines B and C, the level could be either subfamily or tribe.

## Groupings Based on Swim Bladder Morphology

Sciaenid fishes have a physoclistous swim bladder with a single or two interconnected chambers. The usually well-developed swim bladder is attached very firmly to the ventral surface of the third to sixth vertebrae, under the postcardinal vein. The associated swim bladder (drumming) muscles usually present in males, are sheathlike or present lateral to the swim bladder (not attached to) on the body wall, except in *Pogonias*, in which they are present on the swim bladder. The drumming muscles are composed of red striated fibers with abundant cytoplasm and conspicuous nuclei (Tower 1908; Jones and Marshall 1953). Tower concluded that contractions of the drumming muscle set up vibrations in the bladder walls, thus producing sounds. Sound production in sciaenid fishes may function as recognition signals associated with spawning, feeding, and/or aggressive behavior (Naval Ordinance Laboratory 1942, 1944;

Table 1.—Summary of morphological characters of the suprageneric groups of western Atlantic Sciaenidae.

Suprageneric Groups	Swim bladder		Otoliths	Snout pores	Mental pores and barbels	Mouth position, body shape, and teeth			
<i>Micropogonias</i>	swim bladder carrot-shaped	with a pair of tubelike diverticula	only sagitta enlarged	Sagitta shield-like, very thick	5 upper 5 marginal	5 pores 3-5 pairs barbels	mouth inferior, body elongate compressed; teeth conical in bands		
<i>Nebris</i>				Sagitta olive shaped, cauda of sulcus very deep	no upper 2 marginal	4 pores no barbels	mouth strongly oblique, body elongate, rounded; teeth minute set in narrow ridge or bands		
<i>Pogonias</i>		with complex diverticula in adults		Sagitta oval or subovoid, moderately thin to very thick	5 upper 5 marginal	5 pores 12-13 pairs barbels	mouth inferior, body oblong to elongated compressed; teeth villiform, set in bands		
<i>Sciaenops</i>						5 pores no barbels			
<i>Larimus</i>		simple without diverticula, sometime with small anterior projections only			no upper 5 marginal	4 pores no barbels		mouth strongly oblique, body oblong, compressed; teeth minute set in one or two rows	
<i>Sciaena</i>					3-7 upper 5-7 marginal	5 pores no barbels			
<i>Umbrina</i>					4 or 5 pores one barbel				
<i>Menticirrhus</i>		atrophied in adults		Sagitta oval elongate thin to moderately thick			4 pores 2 or many barbels	mouth inferior, body elongated, rounded; teeth villiform set in narrow bands	
<i>Lonchurus</i>		with hornlike anterior diverticula and posterior branches, some reduced size in adults							
<i>Cynoscion</i>		with a pair of lateral horns directing anteriorly							no upper 2 or no marginal
<i>Stellifer</i>	two chambers, anterior one yoke-shaped, some with lateral diverticula, separate from carrot-shaped posterior chamber by a constriction	Both sagitta and lapillus enlarged; sagitta thick, oval- to triangular-shaped lappus suboval	3-7 upper 5 marginal						4-6 pores no barbels

Dijkgraaf 1947; Knudsen et al. 1948; Johnson 1948; Jones and Marshall 1953; Tavalga 1964). The sounds produced by different species of sciaenids also have different ranges of frequencies (Knudsen et al. 1948; Tavalga 1964; Fish and Mowbray 1970). This may result from the different morphology of swim bladders in different sciaenids. Comparison of sciaenid swim bladders in the present study is confined to external morphology and in situ position within the fish.

**Morphological patterns of swim bladders.**—All western Atlantic sciaenids have well-developed swim bladders except the genera *Menticirrhus* and *Lonchurus*. The swim bladders in *Menticirrhus* atrophy during the juvenile stage and only a vestige remains in adults. In adult *Lonchurus*, the relative size of the swim bladder is much reduced. Based on the shapes of swim bladders in mature fish, western Atlantic sciaenids can be divided into two groups. One group has a single-chambered swim bladder (Figs. 5 to 14) and the other has a two-chambered

swim bladder (Figs. 15, 16). Several distinct structural patterns of swim bladders are recognized here.

### Single-chambered swim bladder group.

**Sciaena pattern.**—A simple carrot-shaped swim bladder without well-developed anterior horns or diverticula (Fig. 5), its anterior end falling short of, reaching but never passing the septum transversum. Swim bladders of eight genera have this pattern: *Aplodinotus*, *Ctenosciaena*, *Equetus*, *Leiostomus*, *Menticirrhus*, *Pareques*, *Sciaena*, and *Umbrina*. In addition, species with simple swim bladder are also found in other genera. The swim bladder of *Larimus fasciatus* is simple (Fig. 5E) but *L. breviceps* has a pair of anterior projections (Fig. 5F). *Pachyurus schomburgkii* has a simple swim bladder and differs from the diverticulated swim bladder of *P. bonariensis* (Fig. 6). The generic status of *Pachyurus* is discussed in the synopsis section.

The swim bladder of *Menticirrhus* degenerates or

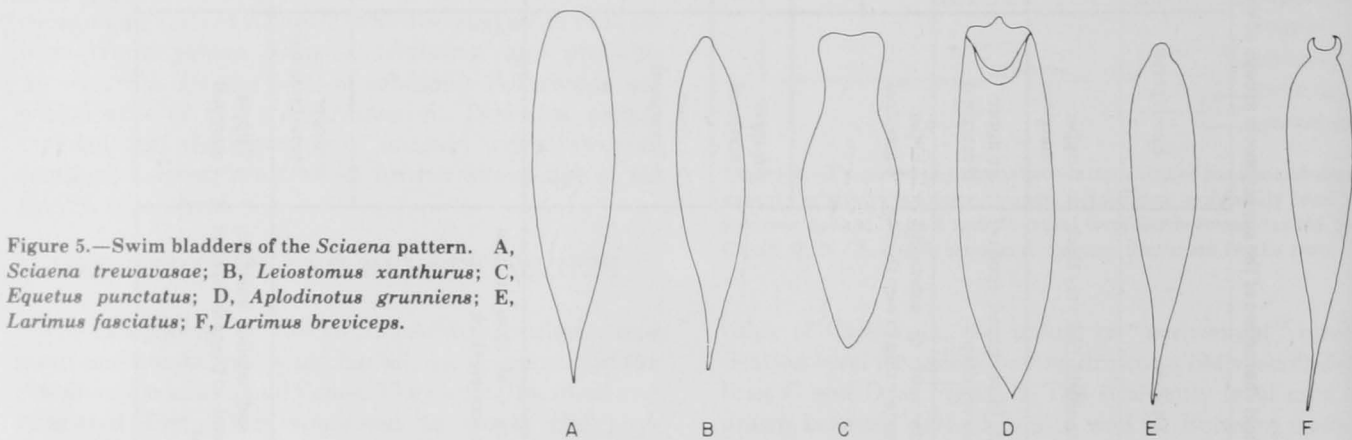


Figure 5.—Swim bladders of the *Sciaena* pattern. A, *Sciaena trewavasae*; B, *Leiostomus xanthurus*; C, *Equetus punctatus*; D, *Aplodinotus grunniens*; E, *Larimus fasciatus*; F, *Larimus breviceps*.

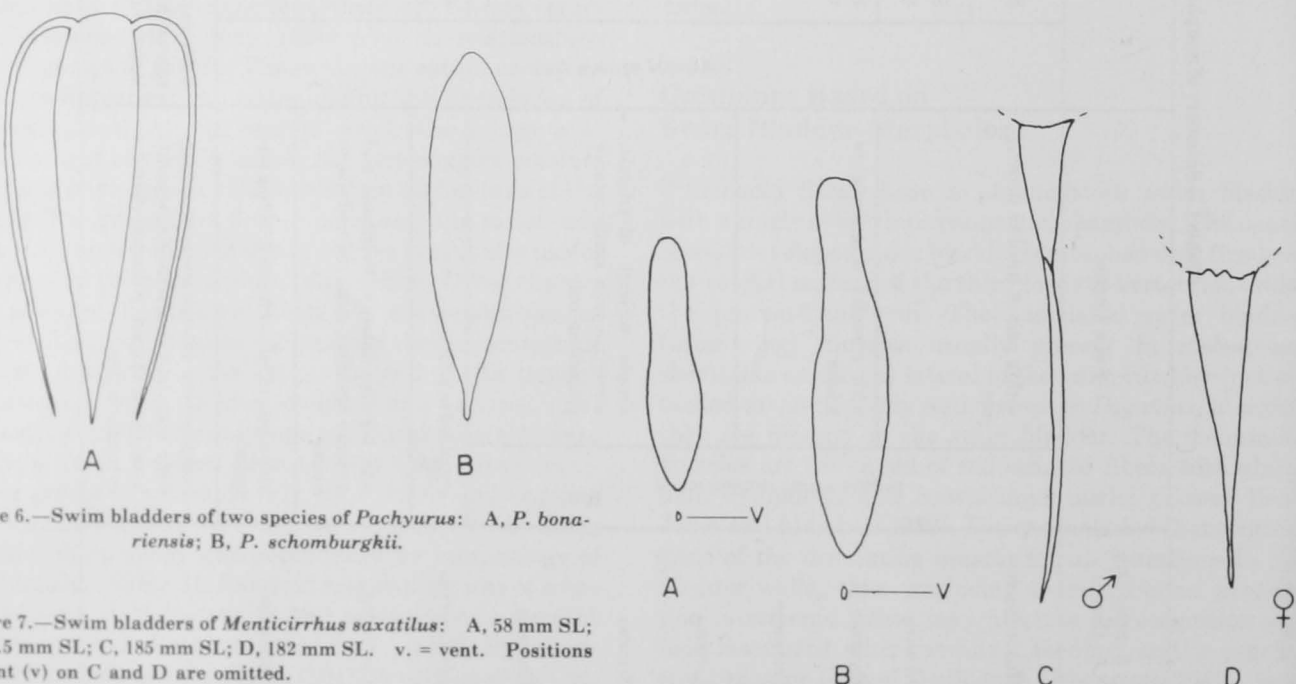


Figure 6.—Swim bladders of two species of *Pachyurus*: A, *P. bonariensis*; B, *P. schomburgkii*.

Figure 7.—Swim bladders of *Menticirrhus saxatilis*: A, 58 mm SL; B, 75.5 mm SL; C, 185 mm SL; D, 182 mm SL. v. = vent. Positions of vent (v) on C and D are omitted.

atrophies in the adult. *Menticirrhus saxatilis* has a well-developed simple bottle-shaped swim bladder in young specimens up to 90-100 mm SL (Fig. 7A, B), but only a trace of the swim bladder remains in the adult (Fig. 7C, D). Bearden (1963) reported the length and condition of the swim bladders of 420 *M. americanus*. His results showed a gradual atrophy of the swim bladder from specimens of 56-60 mm SL (5.6% atrophied) to specimens of 125-130 mm SL (100% atrophied). I examined 28 specimens from 50-108 mm SL. Five specimens 71.1-108 mm SL had completely atrophied swim bladders and the rest had only a trace of the swim bladder less than 7 mm in length. *Menticirrhus americanus* and *M. littoralis* possess an atrophied swim bladder even in juvenile specimens. A much simpler swim bladder pattern may also be present in the juvenile stage of certain species with complicated swim bladder pattern in adults (e.g., *Pogonias* and *Sciaenops* patterns).

***Nebris* pattern.**—The swim bladder has a pair of broad diverticula that originate on the anterolateral mar-

gin of the main chamber, extend posteriorly and loop anteriorly near the posterior end of the main chamber (Fig. 8). The diverticula are tapered and terminate anteriorly at the septum transversum. *Nebris* is the only genus with this pattern. *Pachyurus bonariensis* (Fig. 6A) also has a pair of diverticula which originate anterolaterally, but it is morphologically very different from *Nebris*.

***Micropogonias* pattern.**—The swim bladder of *Micropogonias* has a pair of tubelike diverticula that originate laterally from the posterior half of the main chamber (Fig. 9). The diverticula extend anteriorly as far as the septum transversum, but never reach the skull; they then curve posteriorly to the anterior border of the swim bladder medially. *Micropogonias* is the only genus with this pattern.

***Pogonias* pattern.**—A very complex lateral system of diverticula (Fig. 10) characterizes the swim bladder of *Pogonias*, the only genus possessing this pattern. A serial study of specimens from 24 mm TL to 1,090 mm TL indicates that juvenile fish possess a simple swim bladder (Fig. 10A). As the fish grow, the diverticula first develop anterolaterally (Fig. 10B), then posterolaterally (Fig. 10C-E). These diverticula are connected to each other (anastomose) and to the main chamber, except the portion with the drumming muscles (Fig. 10, shaded area), where they are attached by ligament only. The ontogenetic development of this swim bladder pattern may reveal the developmental pathway of other swim bladder patterns.

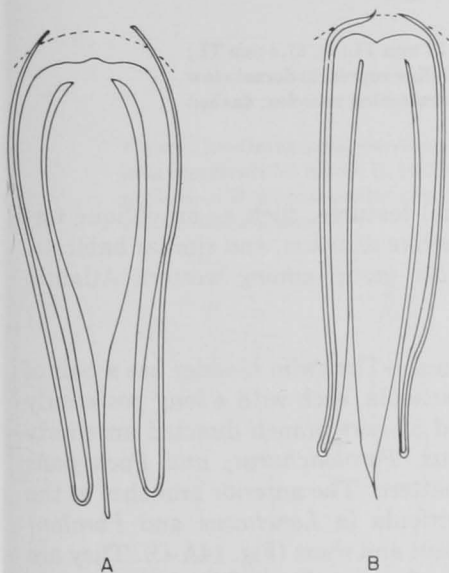


Figure 8.—Development of swim bladder in *Nebris microps*. A, 125 mm SL ( $\times 2$ ); B, 273 mm SL ( $\times 1$ ). Dashed line represents location of septum transversum.

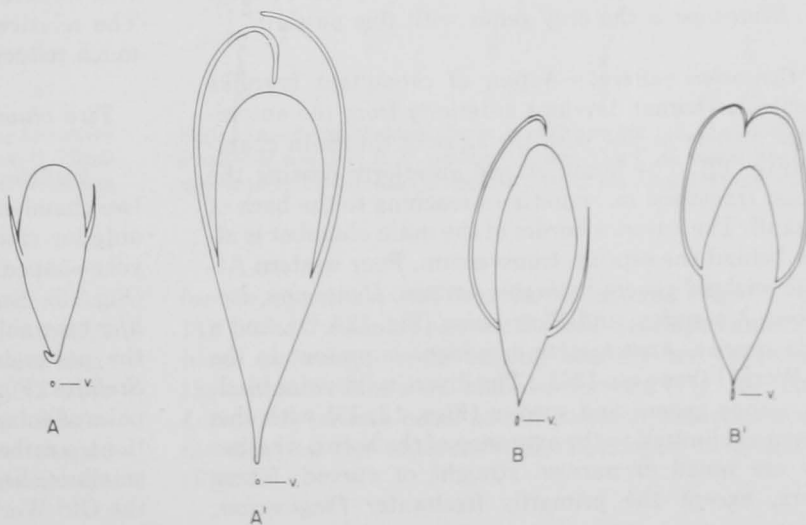


Figure 9.—Variation and development of swim bladders of *Micropogonias*. *Micropogonias undulatus*: A, 67.1 mm SL; A', 180 mm SL; and *M. furnieri*: B, 160 mm SL; B', 162 mm SL. v. = vent.



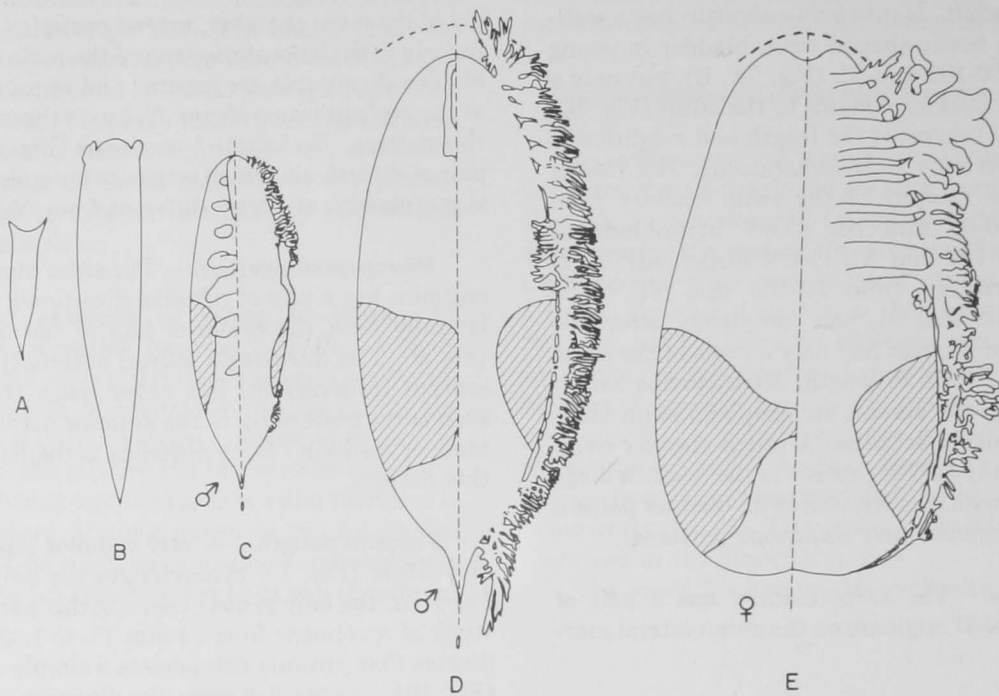


Figure 10.—Ontogenetic development of swim bladders in *Pogonias cromis*. A, 24 mm TL; B, 57.4 mm TL; C, 150 mm TL; D, 236 mm TL; E, 1,090 mm TL. C-E on the left sides of dashed midline represent dorsal view of the swim bladders (diverticula omitted); the shaded areas represent intrinsic drumming muscles; dashed line on top represents location of septum transversum.

**Sciaenops pattern.**—The swim bladder of *Sciaenops* has a pair of tubelike anterior diverticula (Fig. 11A). In large specimens, the complicated lateral diverticula and a pair of saclike projections are found dorsolaterally in the anterior part (Fig. 11B, C). These diverticula are composed of numerous small labyrinthine chambers (Fig. 11D). Sometimes the lateral diverticula are completely covered with fatty tissue (Fig. 11B). A pair of pits (cavities) is also present dorsolaterally in the body wall, between the third and fourth pleural ribs, to receive the "saclike" dorsal projections of the swim bladder. Consequently, these projections extend closer to the body surface behind the base of the pectoral fins. This characteristic may be important in sound reception in large fish. *Sciaenops* is the only genus with this pattern.

**Cynoscion pattern.**—A pair of prominent hornlike diverticula (horns) develops anteriorly from the anterolateral corners in line with the sides of the main chamber (Fig. 12). The horns extend anteriorly passing the septum transversum, sometimes reaching to the back of the skull. The anterior border of the main chamber is always behind the septum transversum. Four western Atlantic sciaenid genera have this pattern. *Cynoscion*, *Isopisthus*, *Macrodon*, and *Plagioscion* (Fig. 12A-D), and a single species, *Atractoscion aequidens* is present in the Old World (Trewavas 1962). The diversity in swim bladders among genera and species (Figs. 12, 13) with this pattern are limited to the extension of the horns, whether they are broad or narrow, straight or curved. These genera, except the primarily freshwater *Plagioscion*,

have similar external features, such as an oblique terminal mouth, caninelike dentition, and similar habitats. They form a distinct group among western Atlantic sciaenids.

**Lonchurus pattern.**—The swim bladder has a pair of forked anterior diverticula, each with a long posteriorly directed branch and a short branch directed anteriorly (Fig. 14). *Lonchurus*, *Paralonchurus*, and *Pachypops fourcroyi* have this pattern. The anterior branches of the swim bladder diverticula in *Lonchurus* and *Paralonchurus* are rather stout and short (Fig. 14A-C). They are thinner in *Pachypops fourcroyi* (Fig. 14D), pierce the septum transversum, and curve under the base of the skull. The relative size of the swim bladder in *Lonchurus* is much reduced (Fig. 14A, A', A").

#### **Two-chambered swim bladder group.**

**Stellifer pattern.**—The swim bladder is divided into two chambers by an anterior constriction. The tip of the anterior chamber reaches into the head region and is yoke-shaped; the posterior chamber is carrot-shaped (Fig. 15). *Bairdiella*, *Odontoscion*, *Ophioscion*, and *Stellifer* have this pattern. A pair of diverticula is present on the posterolateral surface of the anterior chamber in *Stellifer* (Figs. 15B, 16). These genera usually have two pairs of enlarged otoliths (Fig. 2A, B, also see otolith section), a rather strong second anal spine and are relatively smaller fishes. This pattern of swim bladders is absent in the Old World sciaenids.

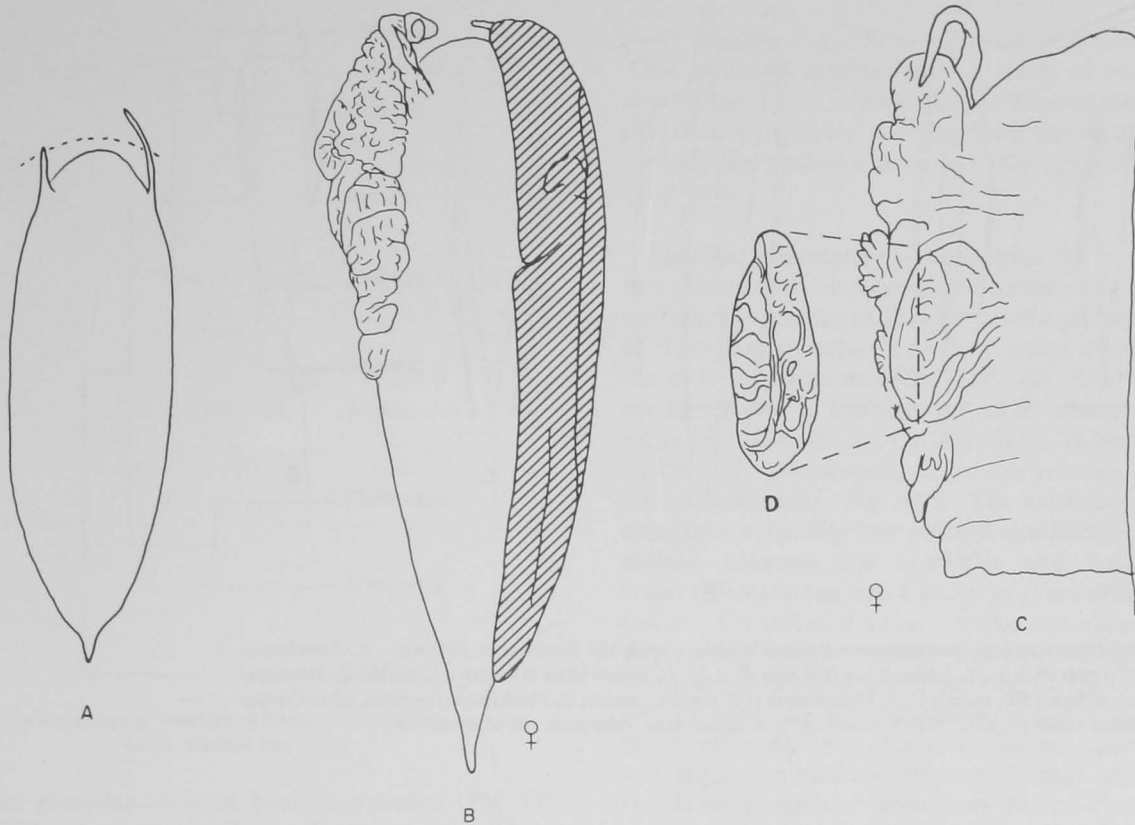


Figure 11.—Ontogenetic development of swim bladder in *Sciaenops ocellata*. A, 197 mm SL; B, 980 mm SL, shaded area represents fat tissue; C, 1082 mm SL, dorsal view of a portion of the swim bladder with the left side of the "saclike" projection; D, a cross section of the dorsal projection to show labyrinthine chambers. Dashed line represents location of septum transversum.

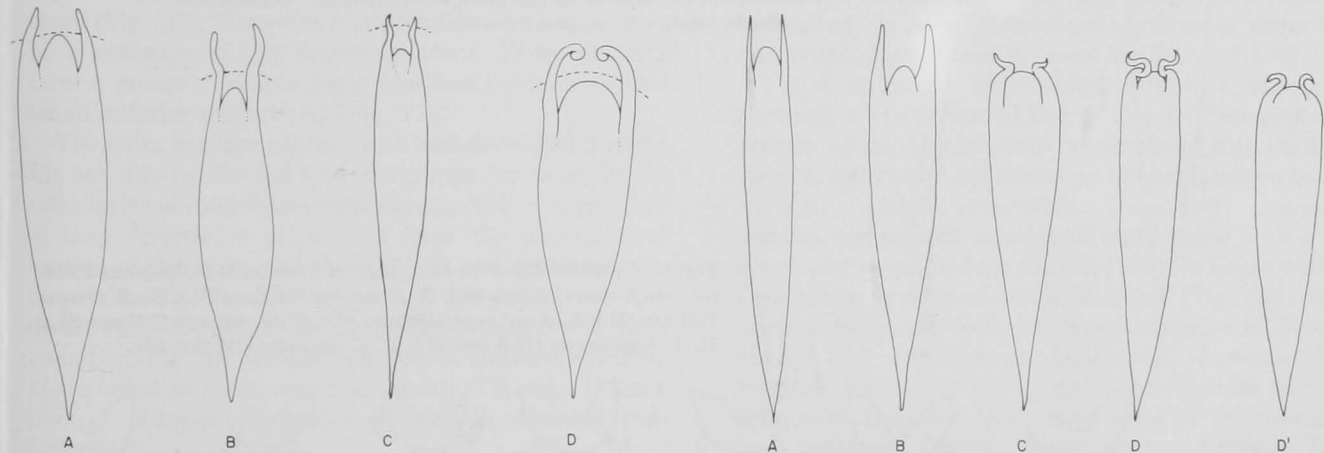


Figure 12.—Swim bladders of the *Cynoscion* pattern. A, *Aynoscion regalis*; B, *Isopisthus parvipinnis*; C, *Macrodon ancylodon*; D, *Plagioscion surinamensis*; Dashed line represents location of septum transversum.

Figure 13.—Swim bladders of species of *Cynoscion*: A, *C. microlepidotus* (393 mm SL); B, *C. nothus* (102 mm SL); C, *C. virescens* (219 mm SL); D, *C. leiarchus* (395 mm SL); D', *C. leiarchus* (191 mm SL).

**Groupings of swim bladder patterns.**—Western Atlantic sciaenids can be separated into two distinctive groups (Fig. 17), based on the number of the swim bladder chambers. The *Stellifer* pattern differs from all other sciaenids by having two chambers (Fig. 15). Single-chambered swim bladders are generally carrot-shaped with or without lateral diverticula (Figs. 5 to 11), except

for the *Cynoscion* and *Lonchurus* patterns (Figs. 12 to 14). In the *Cynoscion* pattern the well-developed anterior horns are unique in developing laterally and following the contours of the main chamber forward (Fig. 12). The *Lonchurus* pattern has a pair of posterior branches from the base of the anterolaterally developed diverticula (Fig. 14).

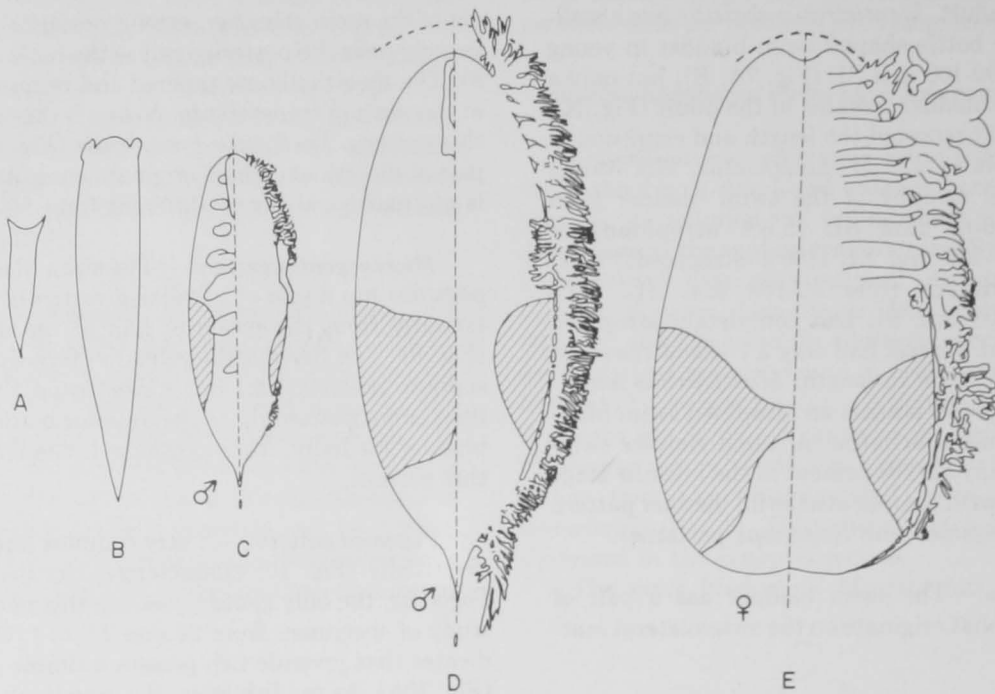


Figure 10.—Ontogenetic development of swim bladders in *Pogonias cromis*. A, 24 mm TL; B, 57.4 mm TL; C, 150 mm TL; D, 236 mm TL; E, 1,090 mm TL. C-E on the left sides of dashed midline represent dorsal view of the swim bladders (diverticula omitted); the shaded areas represent intrinsic drumming muscles; dashed line on top represents location of septum transversum.

**Sciaenops pattern.**—The swim bladder of *Sciaenops* has a pair of tubelike anterior diverticula (Fig. 11A). In large specimens, the complicated lateral diverticula and a pair of saclike projections are found dorsolaterally in the anterior part (Fig. 11B, C). These diverticula are composed of numerous small labyrinthine chambers (Fig. 11D). Sometimes the lateral diverticula are completely covered with fatty tissue (Fig. 11B). A pair of pits (cavities) is also present dorsolaterally in the body wall, between the third and fourth pleural ribs, to receive the "saclike" dorsal projections of the swim bladder. Consequently, these projections extend closer to the body surface behind the base of the pectoral fins. This characteristic may be important in sound reception in large fish. *Sciaenops* is the only genus with this pattern.

**Cynoscion pattern.**—A pair of prominent hornlike diverticula (horns) develops anteriorly from the anterolateral corners in line with the sides of the main chamber (Fig. 12). The horns extend anteriorly passing the septum transversum, sometimes reaching to the back of the skull. The anterior border of the main chamber is always behind the septum transversum. Four western Atlantic sciaenid genera have this pattern. *Cynoscion*, *Isoapisthus*, *Macrodon*, and *Plagioscion* (Fig. 12A-D), and a single species, *Atractoscion aequidens* is present in the Old World (Trewavas 1962). The diversity in swim bladders among genera and species (Figs. 12, 13) with this pattern are limited to the extension of the horns, whether they are broad or narrow, straight or curved. These genera, except the primarily freshwater *Plagioscion*,

have similar external features, such as an oblique terminal mouth, caninelike dentition, and similar habitats. They form a distinct group among western Atlantic sciaenids.

**Lonchurus pattern.**—The swim bladder has a pair of forked anterior diverticula, each with a long posteriorly directed branch and a short branch directed anteriorly (Fig. 14). *Lonchurus*, *Paralonchurus*, and *Pachypops fourcroyi* have this pattern. The anterior branches of the swim bladder diverticula in *Lonchurus* and *Paralonchurus* are rather stout and short (Fig. 14A-C). They are thinner in *Pachypops fourcroyi* (Fig. 14D), pierce the septum transversum, and curve under the base of the skull. The relative size of the swim bladder in *Lonchurus* is much reduced (Fig. 14A, A', A").

#### **Two-chambered swim bladder group.**

**Stellifer pattern.**—The swim bladder is divided into two chambers by an anterior constriction. The tip of the anterior chamber reaches into the head region and is yoke-shaped; the posterior chamber is carrot-shaped (Fig. 15). *Bairdiella*, *Odontoscion*, *Ophioscion*, and *Stellifer* have this pattern. A pair of diverticula is present on the posterolateral surface of the anterior chamber in *Stellifer* (Figs. 15B, 16). These genera usually have two pairs of enlarged otoliths (Fig. 2A, B, also see otolith section), a rather strong second anal spine and are relatively smaller fishes. This pattern of swim bladders is absent in the Old World sciaenids.

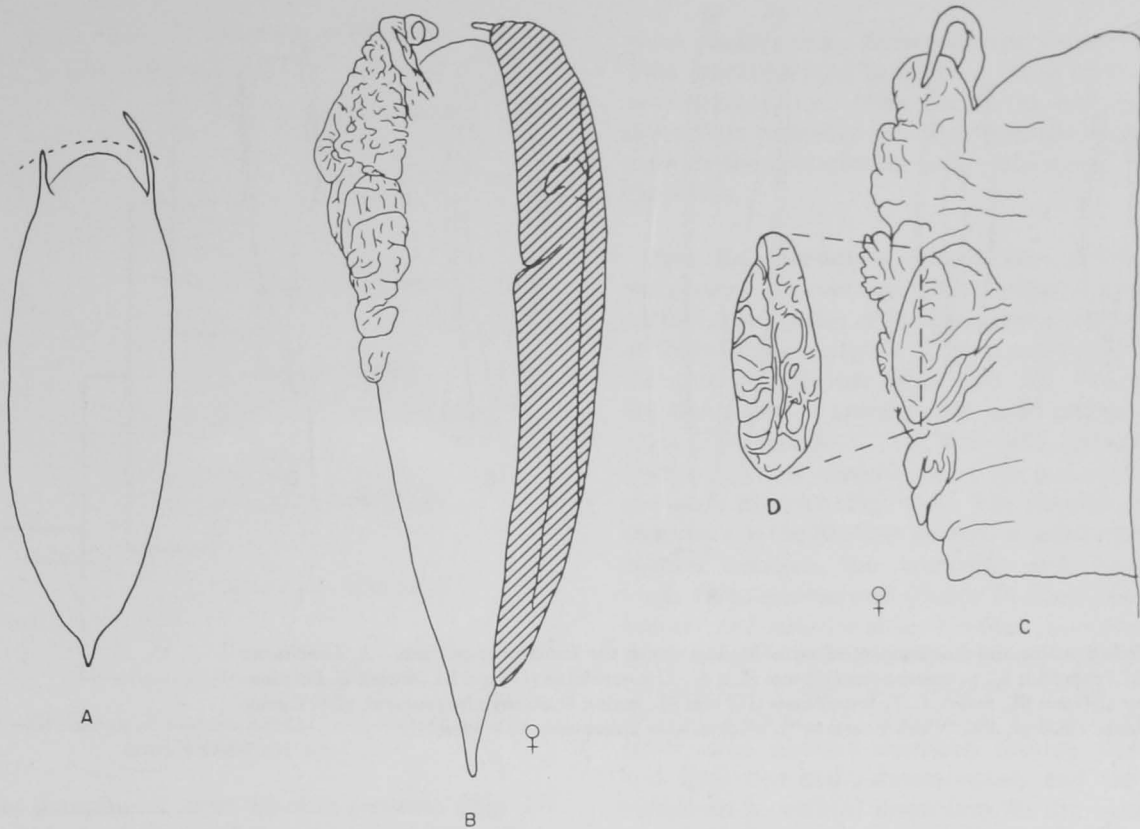


Figure 11.—Ontogenetic development of swim bladder in *Sciaenops ocellata*. A, 197 mm SL; B, 980 mm SL, shaded area represents fat tissue; C, 1082 mm SL, dorsal view of a portion of the swim bladder with the left side of the "saclike" projection; D, a cross section of the dorsal projection to show labyrinthine chambers. Dashed line represents location of septum transversum.

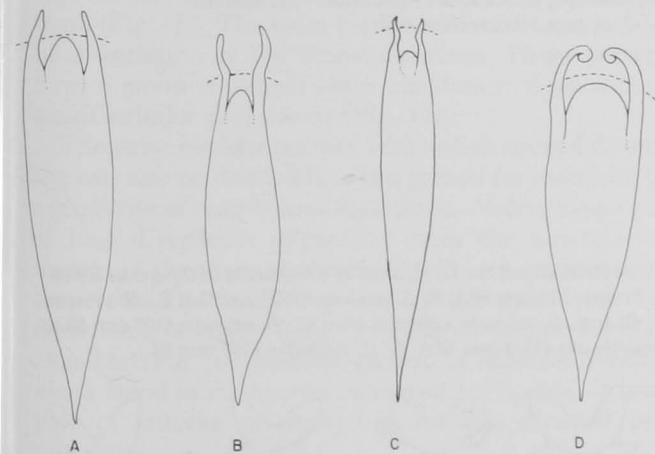


Figure 12.—Swim bladders of the *Cynoscion* pattern. A, *Aynoscion regalis*; B, *Isopisthus parvipinnis*; C, *Macrodon ancylodon*; D, *Plagioscion surinamensis*: Dashed line represents location of septum transversum.

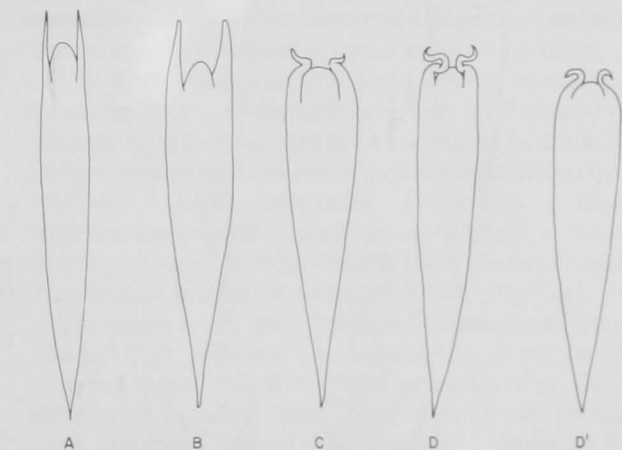


Figure 13.—Swim bladders of species of *Cynoscion*: A, *C. microlepidotus* (393 mm SL); B, *C. nothus* (102 mm SL); C, *C. virescens* (219 mm SL); D, *C. leiarchus* (395 mm SL); D', *C. leiarchus* (191 mm SL).

**Groupings of swim bladder patterns.**—Western Atlantic sciaenids can be separated into two distinctive groups (Fig. 17), based on the number of the swim bladder chambers. The *Stellifer* pattern differs from all other sciaenids by having two chambers (Fig. 15). Single-chambered swim bladders are generally carrot-shaped with or without lateral diverticula (Figs. 5 to 11), except

for the *Cynoscion* and *Lonchurus* patterns (Figs. 12 to 14). In the *Cynoscion* pattern the well-developed anterior horns are unique in developing laterally and following the contours of the main chamber forward (Fig. 12). The *Lonchurus* pattern has a pair of posterior branches from the base of the anterolaterally developed diverticula (Fig. 14).

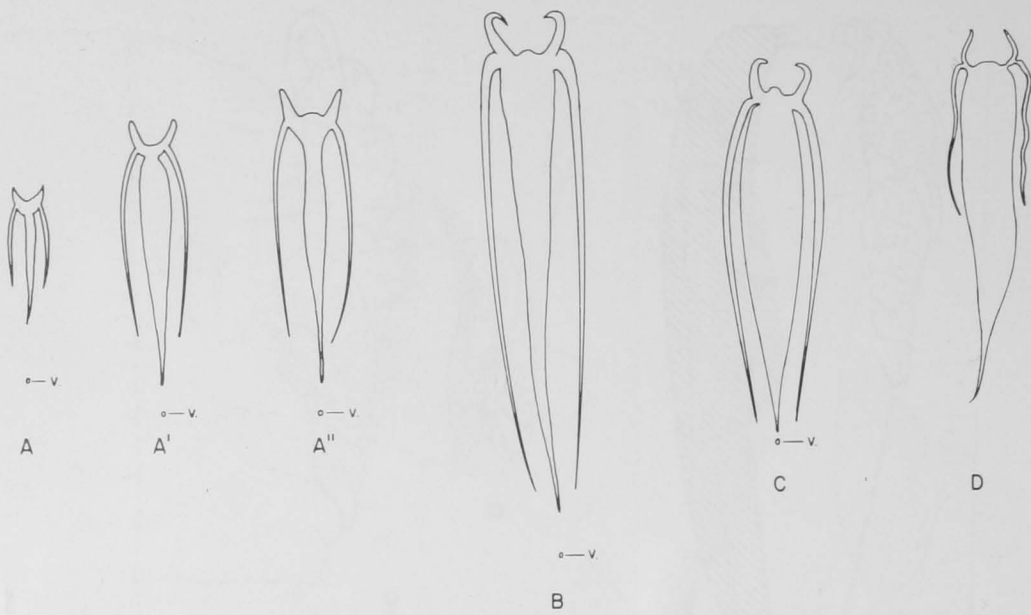


Figure 14.—Relative size and development of swim bladders with the *Lonchurus* pattern. A, *Lonchurus lanceolatus* (87.7 mm SL); A', *L. lanceolatus* (103 mm SL); A'', *L. lanceolatus* (114 mm SL, male); B, *Paralanchurus elegans* (180 mm SL, male); C, *P. brasiliensis* (157 mm SL, male); D, *Pachypops fourcroi*, after Cuvier and Valenciennes (1830:pl. 138, "Corb Fourcroy"), original size unknown. v. = vent.

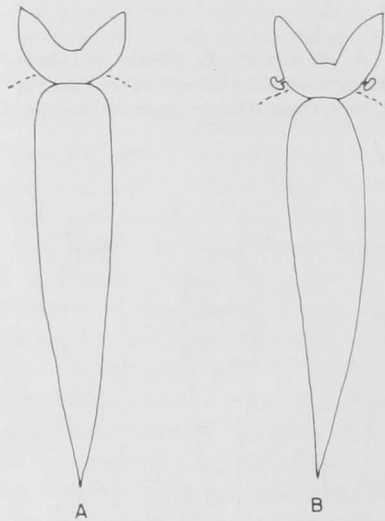
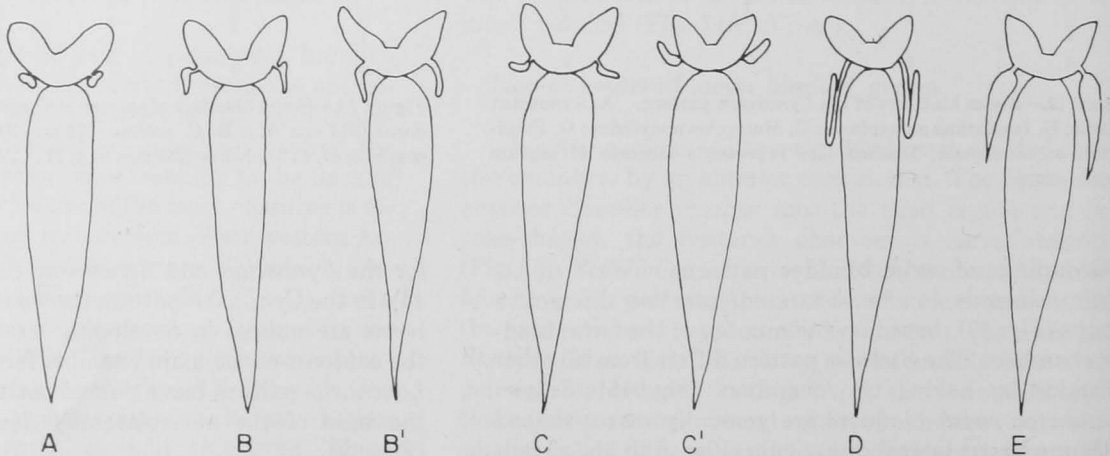


Figure 15.—Swim bladders of the *Stellifer* pattern. A, *Bairdiella*, *Odontoscion*, and *Ophioscion*; B, *Stellifer lanceolatus*. Dashed line represents location of septum transversum.

Figure 16.—Diversity of the swim bladder diverticula in the genus *Stellifer*. A, *S. naso* (75 mm SL); B, *S. griseus* (84.2 mm SL); B', *S. griseus* (108 mm SL); C, *S. microps* (129 mm SL); C', *S. microps* (105 mm SL); D, *S. brasiliensis* (76.6 mm SL); E, *S. rastrifer* (157 mm SL).



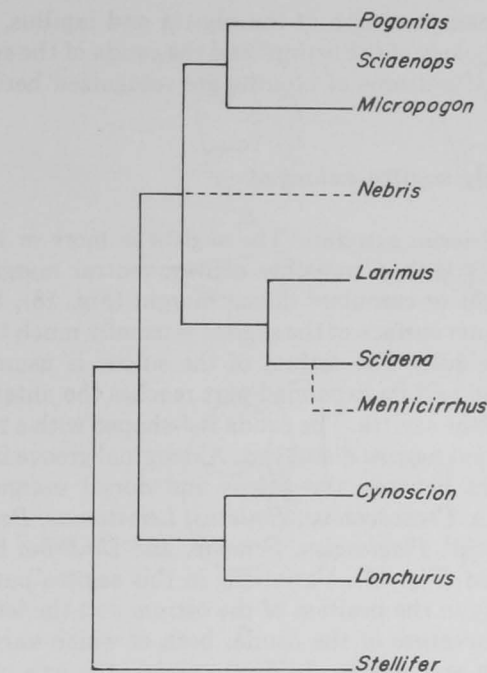


Figure 17.—Groupings of western Atlantic Sciaenidae according to swim bladder patterns.

Further grouping of swim bladder patterns (Fig. 17) relies on the similarity and complexity of swim bladders. The swim bladder of juvenile *Menticirrhus* (Fig. 7) is most similar to the *Sciaena* pattern, although only a vestige remains in adults. Species of *Larimus* usually have a pair of small anterior projections (Fig. 5F), except the northwestern Atlantic *L. fasciatus*, which lacks them (Fig. 5E). The swim bladder of *Larimus* appears to be a variation of the *Sciaena* pattern. These patterns form a group of simple swim bladders with or without small anterior projections (Fig. 17).

The swim bladder pattern with well-developed diverticula can also be divided into two groups (or more) by the complexity of their lateral diverticula. *Nebris* have a pair of long diverticula originating from the anterolateral margin of the main chamber (Fig. 8) and extremely enlarged basally. In *Micropogonias*, the paired tubelike diverticula originate from the posterior half of the main chamber (Fig. 9). Another pattern of tubelike diverticula is found in *Pachyurus bonariensis* (Fig. 6A). It has a pair of anterior originated diverticula directed posteriorly.

*Sciaenops* and *Pogonias* have much more complicated lateral diverticula in adults. *Sciaenops* has a simple short pair of diverticula in young specimens (Fig. 11A) and the "saclike" projections located dorsolaterally develop in larger specimens (Fig. 11C). The complicated diverticula on the swim bladder of *Pogonias* also change ontogenetically (Fig. 10). The ontogenetic development of the swim bladder in *Pogonias* further indicates that the diverticula were developed from the simple swim bladder from anterior to posterior portions of the main chamber.

The grouping of swim bladder patterns from simple to complex coincides with the ontogeny of the complicated

swim bladder (e.g., *Sciaenops* and *Pogonias* patterns). This evidence may indicate a trend of swim bladder development, i.e., from simple to complex with the diverticula probably evolving from the anterior portion towards the posterior portion of the main swim bladder chambers.

**Specific characters.**—Variations in swim bladder morphology are common within patterns. In the *Stellifer* pattern, the species of *Stellifer* have a pair of "bulblike" or "tubelike" diverticula at the posterolateral margins of the anterior chamber (Figs. 15B, 16). Slight variations are also found in species such as *S. griseus* and *S. microps* (Fig. 16B, B', C', C). *Bairdiella*, *Odontoscion*, and *Ophioscion* lack diverticula on the anterior chamber of the swim bladder (Fig. 15A). The yoke-shaped anterior chambers in the *Stellifer* pattern terminate near the articulation between the opercular and hyomandibular bones (Wintersteen and Chao<sup>3</sup>). In *Bairdiella* and *Odontoscion*, the anterior swim bladder chambers curve forward abruptly and their tips end just behind the adductor operculi muscle and medially to the dialator and levator operculi. In *Ophioscion* and *Stellifer*, the anterior swim bladder chambers diverge more laterally, and their tips end subcutaneously and are frequently visible on superficial inspection. In the *Cynoscion* pattern, variations in anterior horn morphology were found among different genera (Fig. 12), species, and also ontogenetically within species (Fig. 13). There is little diversity in morphology among the swim bladders of the *Sciaena* pattern (Fig. 5). The anterior projections are present in *Larimus breviceps* and absent in *L. fasciatus*, indicating the possible extent of variation of swim bladder morphology within a genus and/or a pattern.

The drumming muscle is also useful in assessing relationships within sciaenid fishes. The development of the drumming muscles seems to be correlated with the size of swim bladders and the sound producing function in some western Atlantic sciaenids. Generally, drumming muscles are present in male sciaenid fishes with a well-developed swim bladder (Smith 1905). In fishes with the *Lonchurus* pattern of swim bladders (Fig. 14), drumming muscles are well-developed in males of *Paralonchurus* but reduced in *Lonchurus*. Juvenile *Menticirrhus* have only a vestigial swim bladder and lack drumming muscles. Drumming muscles are present in both male and female *Micropogonias*. *Pogonias* has a unique drumming muscle among western Atlantic sciaenids, located intrinsically on the swim bladder in both sexes (Fig. 10). The drumming muscles of male *Cynoscion regalis* are only well-developed during the spawning season and regress after spawning (J. Merriner, VIMS, pers. commun.).

Possible relationships of western Atlantic sciaenids to sciaenids of other geographic areas may be revealed by the swim bladder shapes. Trewavas (1964) suggested a

<sup>3</sup>Wintersteen, J., and L. N. Chao. A new tribe of sciaenid fishes, with a revision of the genus *Stellifer* Oken, 1817. Manuscr.

possible link of *Pachypops* and *Polyclemus* (= *Paralanchurus*), the *Lonchurus* pattern swim bladder, with the tropical West African tribe Pseudotolithini. The swim bladder of *Atractoscion aequidens* (Cynoscionini of Trewavas) agrees with the *Cynoscion* pattern of the present study. The diverticula on the swim bladder of *Pachyurus bonariensis* (Fig. 6A) is also similar to that of *Bahaba flavolabiata* of the Indo-West Pacific (Chu et al. 1963). The complex swim bladder patterns of the *Pogonias* and *Sciaenops* patterns are common among many Indo-Pacific (Chu et al. 1963; Lal Mohan 1969) and some East Pacific sciaenids (e.g., *Roncador stearnsii*). The branching diverticula of *Pogonias* and *Sciaenops* anastomose with each other, unlike the swim bladders of Indo-Pacific Otolithinae. Their relationships are not known at present.

### Groupings Based on Otolith Morphology

The inner ear of sciaenids consists of three semicircular canals and a large sacculus, containing the sagitta (Fig. 3). The utriculus is an expanded area of the anterior semicircular canal containing the lapillus near the junction with the horizontal semicircular canal. This section is greatly expanded in fishes with a large lapillus (Fig. 3B, B'). Posteriorly, the lagena is a small sac, located posterodorsally to the sacculus, containing the asteriscus (Parker 1908 and Chu et al. 1963). The relative sizes of the three otoliths, particularly the sagitta in all and the lapillus in some sciaenids, are usually larger and thicker than in most Perciformes. The discussion here is based on the general morphology of the sagitta and the lapillus. The sagitta lies obliquely in the sacculus with the smooth surface inside (medially) and is sloping from dorsolateral to ventromedial in situ (Fig. 3). The lapillus is enclosed in the utriculus obliquely, with the smooth surface inside and is oriented laterally. (Fig. 3B, B').

**Morphological patterns of otoliths.**—The sagitta of Sciaenidae is characterized by always having a distinct "tadpole-shaped" sulcus on its inner surface (Fig. 2). A marginal groove is usually present between the dorsal margin and the sulcus of the sagitta. The anterior portion of the sulcus usually is expanded into a pear or oval shape and is termed the "ostium," which always has a short spoutlike groove connecting with the anterior margin of the sagitta (not shown in figures). The elongate narrow posterior portion is usually bent obliquely and is termed the "cauda" of the sulcus (Frizzell and Dante 1965; Stinton 1975). The sagitta distinguishes sciaenids from other perchlike families in that the ostium is merely outlined and never channeled as in other families, whereas the cauda is always channeled (or scooped out) in the Sciaenidae. The outer surface usually has crestlike or bloblike projections or granulations (Fig. 2B', C'). Western Atlantic sciaenids can readily be divided into two groups based on their otoliths: a group with both the lapillus and the sagitta enlarged and a group with only the sagitta enlarged (Fig. 2). Based on the shape,

thickness, and size of the sagitta and lapillus, and the morphology of the ostium and the cauda of the sulcus, 11 distinct patterns of otoliths are recognized here.

### Only sagitta enlarged.

**Sciaena pattern.**—The sagitta is more or less oval, usually with a smoothly convex ventral margin and a straight or crenulate dorsal margin (Fig. 18). Laterally the outer surface of the sagitta is usually much thicker in the middle. The ostium of the sulcus is usually pear-shaped and its expanded part reaches the anterior margin of the sagitta. The cauda is J-shaped with a relatively long and narrow distal end. A marginal groove is usually present between the sulcus and dorsal margin of the sagitta. *Ctenosciaena*, *Equetus*, *Leiostomus*, *Pachyurus*, *Pareques*, *Plagioscion*, *Sciaena*, and *Umbrina* have this pattern (Fig. 18). Variations in this sagitta pattern are mainly in the position of the ostium and the length and the curvature of the cauda, both of which vary among genera and species. In most species, the axis of the ostium is parallel to that of the sagitta or inclined anteroventrally (to the left of Fig. 18). The sagitta of *Leiostomus xanthurus* (Fig. 18D) differs from that of the *Sciaena* pattern in having the ostium inclined towards the dorsal margin and much thinner. *Pachyurus schomburgkii* and *Plagioscion surinamensis* (Fig. 18K, L) also differ in the morphology of their sulci. Their relationship to *Sciaena* pattern is not certain at present.

**Pogonias pattern.**—The sagitta is more or less semicircular in shape with an evenly curved ventral margin and a straight but finely crenulate dorsal margin (Fig. 19). The ostium of the sulcus is broad and its expanded part does not reach the anterior margin of the sagitta. The cauda is J-shaped with a pointed distal end and does not reach to the margin. The marginal groove is present between the sulcus and the dorsal margin of the sagitta. *Pogonias* and *Aplodinotus* have this pattern. The relative size of the "tadpole-shaped" sulcus is larger in *Pogonias* than in *Aplodinotus*. The sagitta is more curved laterally in *Pogonias* than *Aplodinotus*, but the latter has more granulations on the outer surface (Fig. 19B', b).

**Larimus pattern.**—The sagitta is slightly elongate and ovoid with a rather straight and slightly crenulate dorsal margin and a convex ventral margin (Fig. 20). The ostium of the sulcus is large, pear-shaped, and its expanded part does not reach the anterior margin of the sagitta. The J-shaped cauda is bent acutely with a pointed distal end. The marginal groove is not distinct. *Larimus* and *Sciaenops* have this pattern. The sagitta of *Larimus* is broader anteriorly than posteriorly (Fig. 20A, B); both ends are about equal in *Sciaenops* (Fig. 20C, D). The posterior portion of the sagitta is laterally very thick in *Larimus* (Fig. 20a, b). *Sciaenops* has a relatively thinner sagitta (Fig. 20c) and the shape of the sulcus is different from *Larimus*; therefore, a distinct otolith pattern could be recognized.

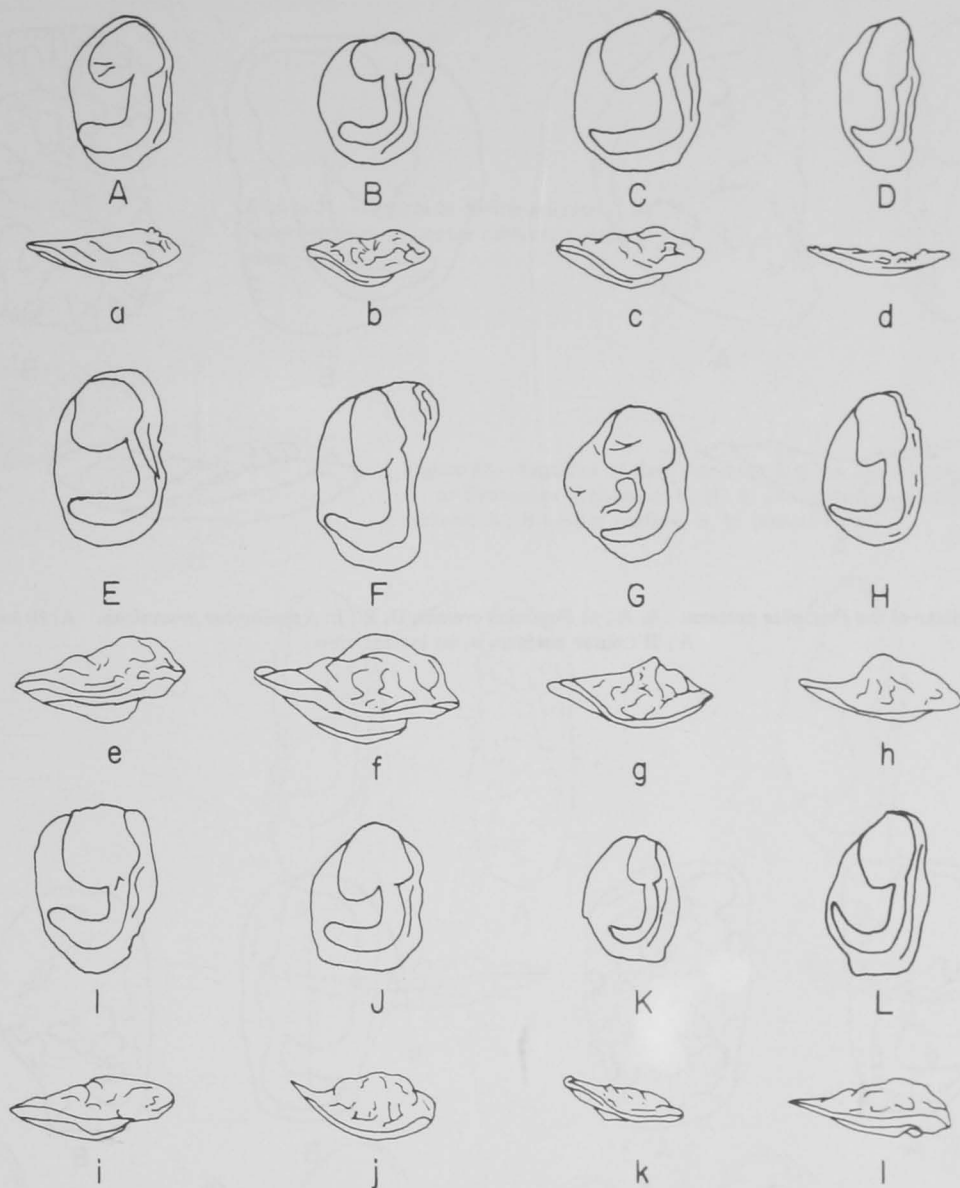


Figure 18.—Inner surface (capital letters) and lateral view (lower case letters) of sagittae of the *Sciaena* pattern. A, a: *Ctenosciaena gracilicirrhus*; B, b: *Equetus lanceolatus*; C, c: *Equetus punctatus*; D, d: *Leiostomus xanthurus*; E, e: *Pareques acuminatus*; F, f: *Paraques umbrosus*; G, g: *Sciaena trewavasae*; H, h: *Sciaena bathytatos*; I, i: *Umbrina coroides*; J, j: *Umbrina milliae*; K, k: *Pachyurus schomburgkii*; L, l: *Plagioscion surinamensis*.

**Nebris pattern.**—The sagitta in *Nebris* is very thick and oval with a notch at the posterior margin (Fig. 21). The ostium of the sulcus is large and ovoid, its expanded part does not reach the anterior margin of the sagitta. The cauda is sharply bent with a very deeply grooved and enlarged distal portion. The marginal groove is absent. The outer surface of the sagitta is extremely elevated and very thick laterally (Fig. 21a).

**Cynoscion pattern.**—The sagitta is elliptical and thin (Figs. 22A, 23), the dorsal margin is usually smoothly convex, and the ventral margin is slightly concave and finely crenulate. Laterally, the posterior portion of the sagitta is thicker than the anterior portion. The sulcus is

usually elongate, the ostium ovoid or pear-shaped (Figs. 22A, 23). The expanded anterior part of the ostium may or may not reach the anterior margin of the sagitta. This varies among species and also within species, ontogenetically (Fig. 23). The cauda is long and bent with a short distal end (Figs. 22A, 23). The marginal groove is usually distinct. The outer surface usually has a granular appearance, especially in large adult specimens (Fig. 23a-c). *Cynoscion* species have this pattern. In some species of *Cynoscion*, a notch is present in the middle of the dorsal margin (Fig. 23C, C').

**Menticirrhus pattern.**—The sagitta is elliptical and thin (Fig. 22B, B', b), the dorsal margin is usually



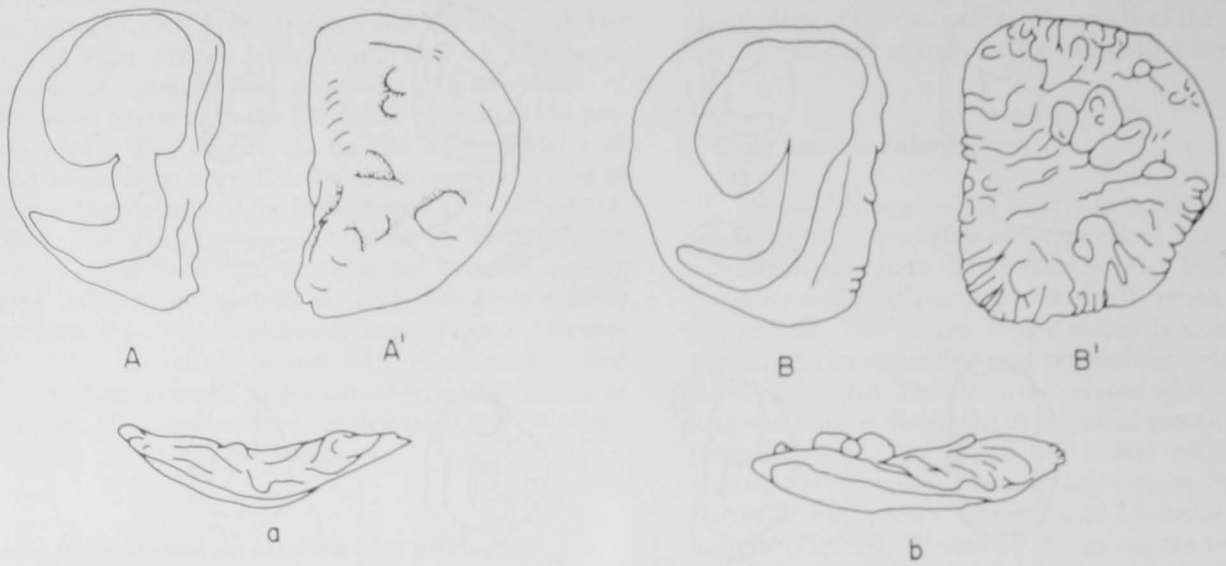


Figure 19.—Sagittae of the *Pogonias* pattern. A, A', a: *Pogonias cromis*; B, B', b: *Aplodinotus grunniens*. A, B: inner surface; A', B': outer surface; a, b: lateral view.

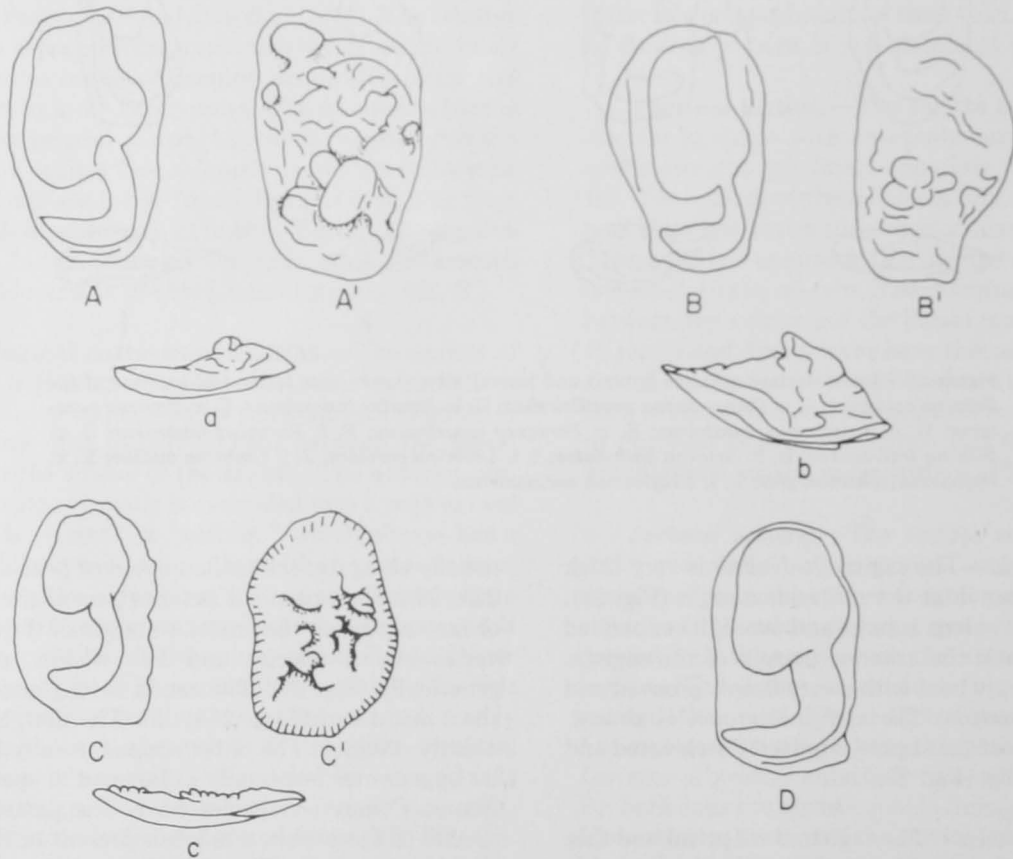


Figure 20.—Sagittae of the *Larimus* pattern. A, A', a: *Larimus fasciatus*; B, B', b: *Larimus breviceps*; C, C', c: *Sciaenops ocellata* (357 mm TL); D: *S. ocellata* (1,100 mm TL). A-D: inner surface; A'-C': outer surface; a-c: lateral view.

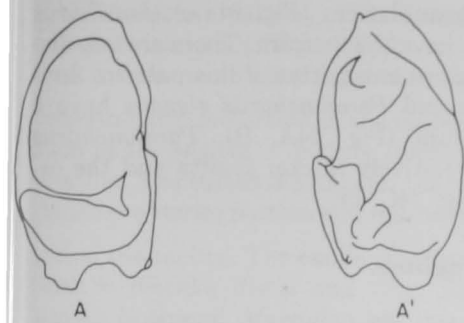


Figure 21.—Sagitta in *Nebris microps*. A, inner surface; A', outer surface; a, lateral view.



Figure 22.—Sagittae of the *Cynoscion* and the *Menticirrhus* patterns. A, A', a: *Cynoscion nebulosus*; B, B', b: *Menticirrhus saxatilis*. A, B: inner surface; A', B': outer surface; a, b: lateral view.

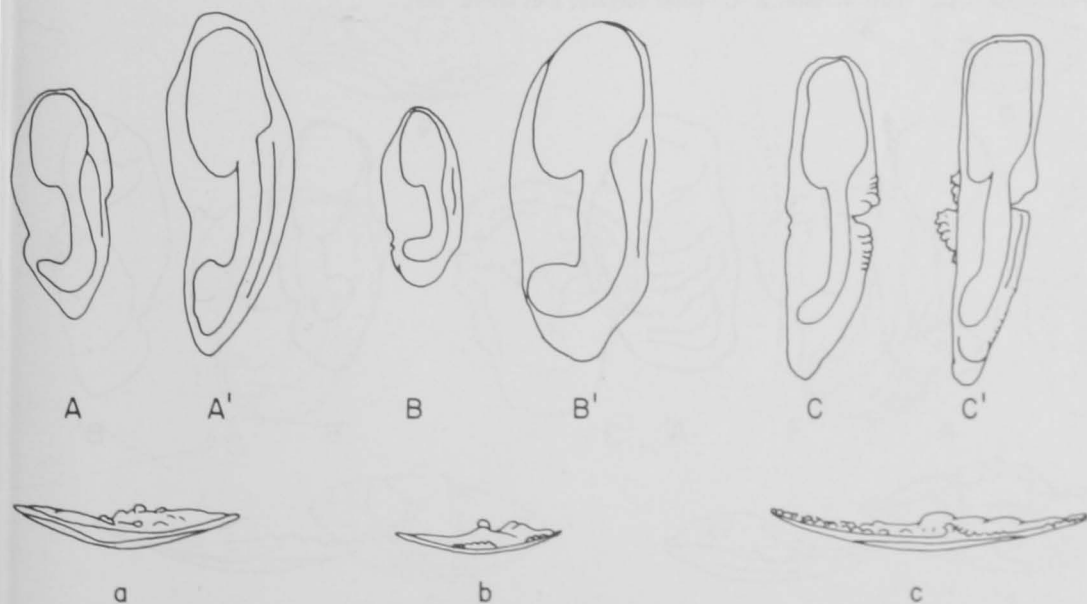
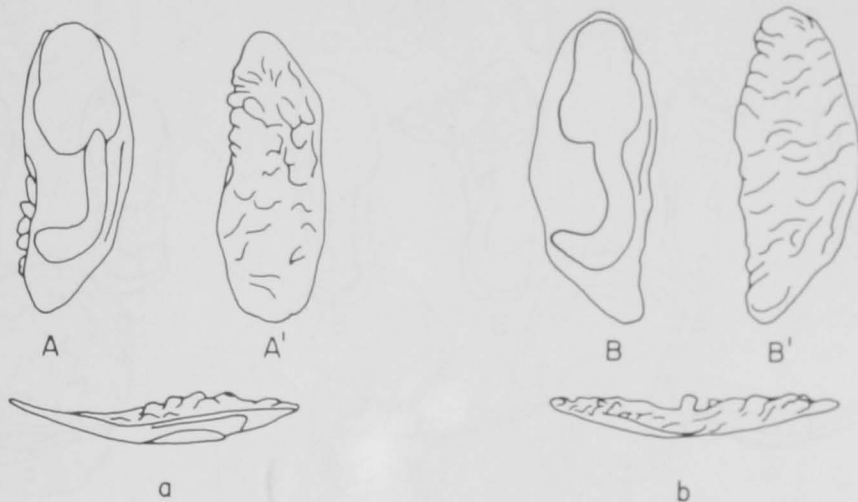


Figure 23.—Specific and ontogenetic variations of sagittae in species of *Cynoscion*: *C. regalis*: A, a, 370 mm TL; A', 516 mm TL; *C. similis*: B, b, 166 mm TL; B', 350 mm TL; *C. virescens*: C, c, 260 mm TL; C', 350 mm TL. A, A', B, B', C, C': inner surface; a, b, c: lateral view.

straight and finely crenulate, and the ventral margin is slightly convex. Laterally, the middle portion is the thickest. The sulcus is elongate, the ostium is pear-shaped (Fig. 22B) and its expanded part does not reach the anterior margin of the sagitta. The cauda is long and J-shaped. The marginal groove is present. The outer surface usually has crests and granulations. *Menticirrhus* species have this pattern.

**Lonchurus pattern.**—The sagitta is moderately thin and elongate (Fig. 24), the ventral margin is usually smoothly convex, and the dorsal margin is slightly concave or crenulate. Laterally, the posterior portion of the sagitta is thicker than the anterior portion. The sulcus on the inner surface is elongate. The ostium is pear-shaped and bent toward the ventral margin of the sagitta anteriorly. The cauda is J-shaped with a rather expanded distal end, close or reaching to the ventral posterior margin of the sagitta. The marginal groove is absent. The

outer surface has granulations (Fig. 24a-c). *Lonchurus* and *Paralonchurus* have this pattern. There are two distinctive forms of sulcus on sagittae of this pattern. *Lonchurus lanceolatus* and *Paralonchurus elegans* have a rather narrow ostium (Fig. 24A, B). *Paralonchurus brasiliensis* has a relatively thicker sagitta and the ostium is broader (Fig. 24C, c).

**Other forms of sagittae.**

**Isopisthus pattern.**—The sagitta is slightly elongate, rather broad and thick posteriorly (Fig. 25A, A', a). The sulcus is elongate; the ostium is round and its expanded part reaches to the anterior margin of the sagitta. The cauda is long and slightly bent at the distal end. The marginal groove is not distinct. The outer surface has crestlike elevations, especially thickened at the posterior half (Fig. 25a). *Isopisthus* has this pattern.

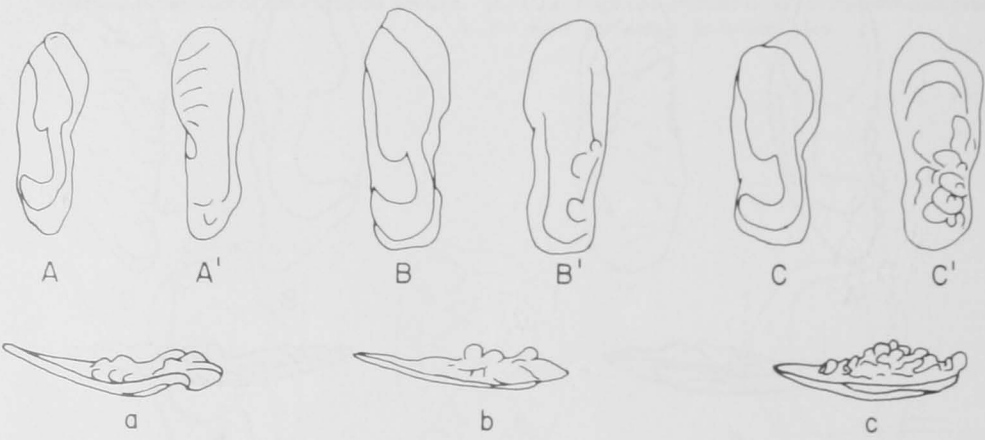


Figure 24.—Sagittae of the *Lonchurus* pattern. A, A', a: *Lonchurus lanceolatus*; B, B', b: *Paralonchurus elegans*; C, C', c: *P. brasiliensis*. A-C: inner surface; A'-C': outer surface; a-c: lateral line.

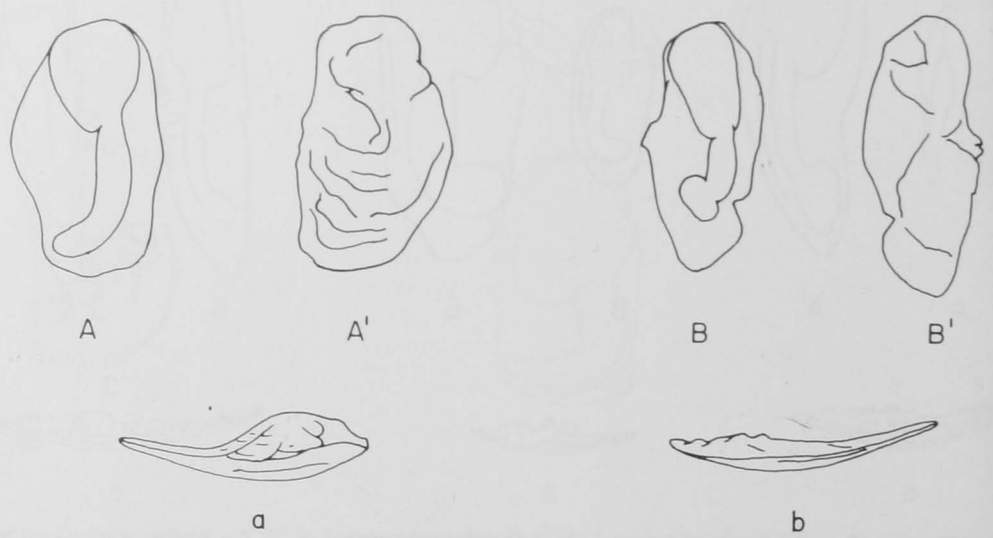


Figure 25.—Sagittae of the *Isopisthus* and the *Macrodon* patterns. A, A', a: *Isopisthus parvipinnis*; B, B', b: *Macrodon ancylodon*. A, B: inner surface, A', B': outer surface; a, b, lateral view.

**Macrodon pattern.**—The sagitta is relatively elongate and thin (Fig. 25B, b', b). The dorsal margin has a deep notch on the posterior half and the ventral margin has a projection in the middle. The anterior portion of the sagitta is slightly thicker than the posterior portion. The sulcus is elongate; the ostium is oval with a broader anterior portion and reaches to the anterior margin of the sagitta. The cauda is rather straight and short with a disclike distal end (Fig. 25B). The marginal groove is absent. *Macrodon* has this pattern.

**Micropogonias pattern.**—The sagitta in *Micropogonias* is very thick and shield-shaped, often with a shelf or flange on the outer surface or on the dorsal margin (Fig. 26). The ostium of the sulcus is large and its expanded part does not reach the anterior margin of the sagitta. The cauda is oblique and bent only slightly towards the ventral margin with a round disclike distal end. The marginal groove is distinct. The sagittal shelf on the outer surface of *M. furnieri* and the lateral flange of *M. undulatus* vary with size and possibly ontogenetically (Fig. 26).

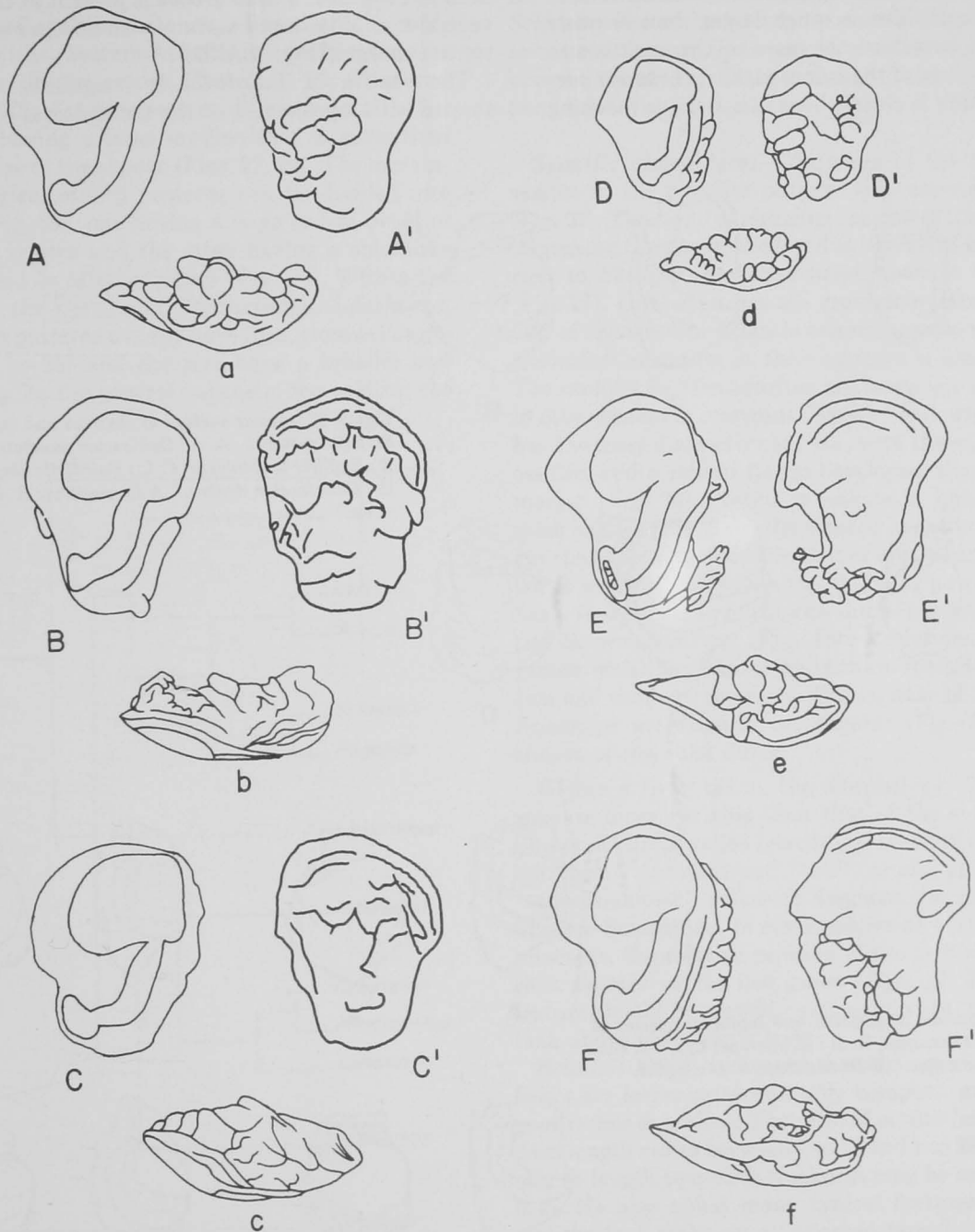


Figure 26.—Variation, possibly ontogenetic, in sagittae of the *Micropogonias* pattern. *Micropogonias furnieri*: A, A', a, 235 mm TL; B, B', b, 295 mm TL; C, C', c, 330 mm TL. *Micropogon undulatus*: D, D', d, 141 mm TL; E, E', e, 250 mm TL; F, F', f, 350 mm TL. A-F: inner surface; A'-F': outer surface; a-f: lateral view.

In summary, sagittae with the *Sciaena*, *Larimus*, and *Nebris* patterns are usually oval in shape and very thick in the middle. The *Pogonias* pattern is usually semicircular in shape and thin. Sagittae with the *Cynoscion*, *Menticirrhus*, *Lonchurus*, and *Macrodon* patterns are usually more elongate and thin. The *Isopisthus* pattern is elongate and thick in the posterior portion. Sagittae with the *Micropogonias* pattern are irregular in shape and very thick.

**Both sagitta and lapillus enlarged.**

**Stellifer pattern.**—Although the anterior portion of the sagitta is reduced in size, it is still larger than in most Perciformes. The lapillus is much larger than in other sciaenids, about two-thirds or more of the sagitta size (Fig. 27). The ostium of the sulcus lacks its anterior portion, and the cauda is clearly bent in a J-shape reaching

almost to the ventral margin of the sagitta. *Bairdiella*, *Odontoscion*, *Ophioscion*, and *Stellifer* have this pattern. There is considerable morphological variation within this otolith pattern (Fig. 27).

*Stellifer* and *Ophioscion* have a parallelogram-shaped sagitta and a suboval lapillus, with both otoliths about the same size (Fig. 27A, A', B, B'). The ostium of the sulcus is short and reaches to the anterior margin of the sagitta. The cauda is bent obliquely towards the ventral margin of the sagitta. A marginal groove is evident along the dorsal margin of the cauda. The whole sagitta appears to be truncated at the middle of the ostium. The lapillus is large, sometimes larger than the sagitta (e.g., *Stellifer*, Fig. 28); a deep groove is present at the anteroventral end of its inner surface with an open end to the ventral margin (Fig. 28A'-D').

The sagitta of *Bairdiella* is irregularly triangular shaped with a projection at the enterodorsal corner dor-

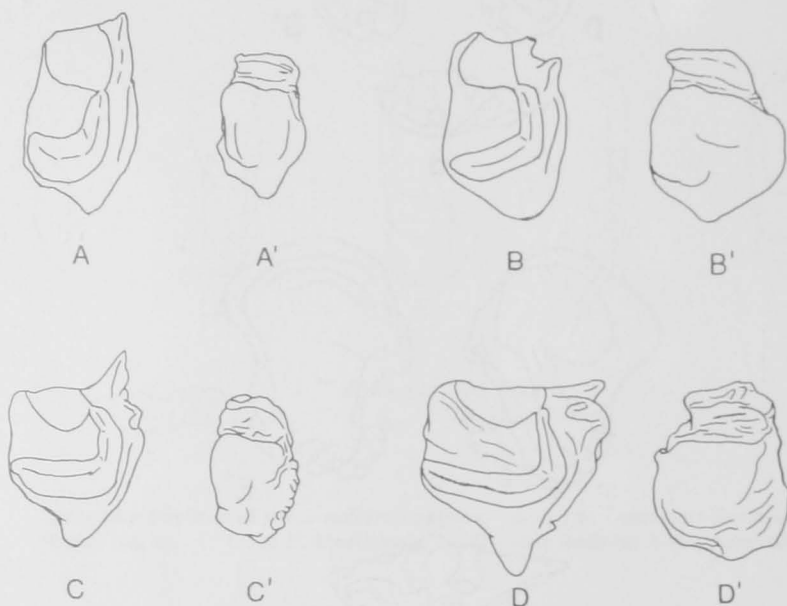


Figure 27.—Inner surface of sagittae and lapilli of the *Stellifer* pattern. A, A': *Ophioscion punctatissimus*; B, B': *Stellifer lanceolatus*; C, C': *Bairdiella chrysourea*; D, D': *Odontoscion dentex*. A-D: sagittae; A'-D': lapilli.

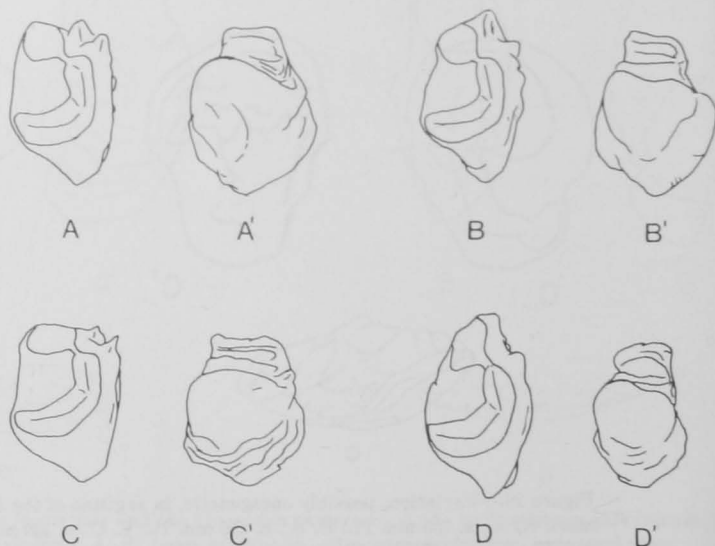


Figure 28.—Inner surface of sagittae and lapilli in species of *Stellifer*: A, A': *S. colonensis*; B, B': *S. microps*; C, C': *S. ras-trifer*; D, D': *S. venezuelae*. A-D: sagittae; A'-D': lapilli.

sally (Fig. 27C). The ostium of the sulcus is very short. The cauda is inverse L (or J)-shaped and broadened at the middle. The marginal groove is well defined. The lapillus is smaller than the sagitta and is irregular in shape (Fig. 27C'). The groove along the anteroventral end of the lapillus opens to the ventral margin.

The sagitta of *Odontoscion* is subtriangular in shape. The ostium of the sulcus is reduced to a small oval-shaped piece at the anterior margin (Fig. 27D). The cauda is long and reaching to the ventral margin. The marginal groove is present on the sagitta. The lapillus is ovoid and its anteroventral groove is distinct (Fig. 27D').

**Groupings of otolith patterns.**—Based on the morphology of otoliths, western Atlantic sciaenids can readily be divided into two groups (Figs. 2, 3, 29; Chao and Miller 1975). The *Stellifer* pattern differs from all other sciaenids by having a large lapillus that is more than one-half the size of the sagitta (Figs. 27, 29). The remaining morphological otolith patterns can be divided into two groups (Fig. 29), one having a more or less ovoid or oval-elongate sagitta and the other having a shieldlike sagitta as found in *Micropogonias* (Fig. 26). Within the former group, the *Cynoscion*, *Menticirrhus*, *Lonchurus*, and *Macrodon* patterns usually have thin, elongate sagittae (Figs. 22 to 25) and the rest have a broader and thicker sagitta. In the general outline of the sagitta, the

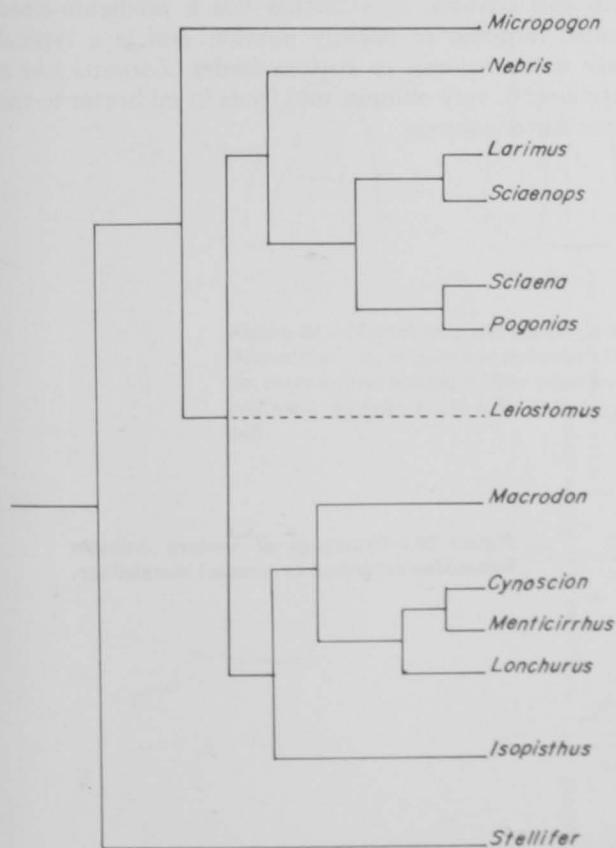


Figure 29.—Groupings of western Atlantic Sciaenidae according to otolith patterns.

*Cynoscion*, *Menticirrhus*, and *Lonchurus* patterns are most similar to each other and have the posterior portion of their sagittae slightly thicker than the anterior portion (Figs. 22, 24). The *Isopisthus* pattern has the posterior portion of its sagittae further thickened (Fig. 25a). The sagitta of *Macrodon* is unique in having the anterior portion of the sagitta thicker than the posterior portion (Fig. 25b). Among the remaining otolith patterns, the *Nebris* pattern (Fig. 21) is unique in the general outline of its sagitta and the morphology of the sulcus (Fig. 29). The *Larimus* pattern has a "rectangular" sagitta (Fig. 20), which differs from the more generalized oval-shaped sagitta of the *Sciaena* and *Pogonias* patterns (Figs. 18, 19, 29). *Leiestomus xanthurus* also differs from other *Sciaena* patterns by having its sagitta (Fig. 18D, d) narrower and thinner. It is probably an intermediate form between the elongate thin and ovoid thick forms of sagittae.

**Specific characters.**—The sizes of the lapillus and sagitta in the *Stellifer* pattern vary among the genera (Fig. 27). The trend of reducing the size of the sagitta and increasing the size of the lapillus is evident from *Ophioscion* to *Stellifer*, and *Bairdiella*, than to *Odontoscion* (Fig. 27). *Cynoscion* has the greatest number of species (12) of any western Atlantic sciaenid genus, and the morphological variation in their sagittae is great (Fig. 23). The otoliths in *Menticirrhus* are relatively smaller than in other genera of sciaenids (Smith 1905). *Micropogonias* has the most distinctive sagitta, with the sagitta further ossified and a lateral flange developed along the dorsal margin (Fig. 26). *Nebris* is unique in having an oval, thick sagitta (Fig. 21) with a notch in the posterior margin that does not resemble that of any other western Atlantic sciaenid. Although the *Pogonias* pattern (Fig. 19) has a semicircular sagitta, the sulcus is similar to that of the *Sciaena* pattern (Fig. 18). Variations among the genera with the *Sciaena* pattern are mainly in the position and shape of the sulci. The sagittae of *Larimus* and *Sciaenops* are slightly rectangular (Fig. 20), but the shapes of the sulci differ.

Within a given taxon, the morphology of the otoliths appears more variable than that of the swim bladder. Chu et al. (1963) relied heavily on the relative position of the "head" (ostium) and "tail" (cauda) sections of the "tadpole-shaped" sulcus to diagnose the subfamilies of Chinese Sciaenidae. In some species of western Atlantic sciaenids, the relative position of the ostium and cauda shift slightly as the fish grows (Figs. 20, 23, 26). This feature should be viewed cautiously when used to group taxa above the generic level.

Schmidt (1968) indicated that the sagitta of sciaenid fishes are large, extraordinarily compact, and often appear rather shapeless. The ratio of otolith length to standard length varies between 1 to 18 and 1 to 28; the ratio of otolith length to otolith thickness may be as high as 1 to 0.45. He also noted many typical features of sciaenid otoliths that make up a "sciaenid type."

Fossil materials of sciaenid otoliths are important in assessing phyletic relationships of modern sciaenids.

John Fitch of the California Department of Fish and Game is currently studying this aspect of sciaenid relationships. Nolf (1976) described sciaenid otoliths of Pliocene and Miocene (néogènes) from Trinidad and indicated that some modern sciaenid species had a wider range of distribution in the past.

### Groupings Based on External Morphology

Prior to Trewavas (1962) and Chu et al. (1963), most recent authors used external morphology to classify sciaenid fishes (see section "A brief history of the study of western Atlantic Sciaenidae"). Characters used were body shape, presence or absence of the mental barbel and/or pores, size of the second anal fin spine, and position of the mouth. Unfortunately these characters are extremely adaptive, evolutionarily plastic, and convergent. They are more indicative of feeding adaptations and habitats than of phylogenetic relationships (Fig. 30). Even so, these characters do show that similar external morphology is often found in closely related taxa. External morphology is also diagnostic at the generic and specific levels. The following discussion assesses the limits and usefulness of these characters.

**Patterns of pore and barbel systems.**—The pores at the tip of the snout and lower jaw (mandible) of sciaenids are the openings of the well-developed cavernous lateral-line canals on the head (Fig. 1). The snout (rostral) pores can be divided into upper pores, those present at the tip of snout, and marginal pores, those present along the edge of the rostral fold (Fig. 1). Usually, there are three or five distinct upper pores, although some genera lack upper pores and some may have more than five as adults.

Typically there are five marginal pores, one median and two pairs of lateral pores (Fig. 31). Some genera have only two marginal pores. The mental (mandibular) pores are most often five (four to six), one median and two pairs of lateral pores (Fig. 32), whereas some genera completely lack mental pores. One or more mental barbels may be present in many western Atlantic sciaenid fishes. The number of pores and barbels is correlated with the mouth position and feeding habitats of the species (Chao 1976; Chao and Musick 1977). Variations are broad among the genera and species (Figs. 33 to 36).

**Structural patterns of snout pores.**—There are four snout pore patterns recognized in western Atlantic Sciaenidae (Fig. 31).

**Two (or no) marginal pores.**—This pattern has no upper pores and the rostral fold is thin and entire without notches (Fig. 31A). *Cynoscion*, *Macrodon*, *Nebris*, and *Plagioscion* have this pattern. They have a very oblique, large mouth and the lower jaw projects in front of the upper, except in *Plagioscion*, which has a slightly oblique and terminal mouth. Fishes with this snout pore pattern and mouth position are midwater to upper water column feeders.

**Five marginal pores.**—This pattern has no upper pores and the rostral fold has notches at the openings of the lateral pores (Fig. 31B). *Aplodinotus* and *Larimus* have this pattern. *Aplodinotus* has a moderate-sized mouth, terminal or slightly inferior, and is a typical lower water column to bottom feeder. *Larimus* has a large mouth, very oblique, and feeds in midwater to the upper water column.

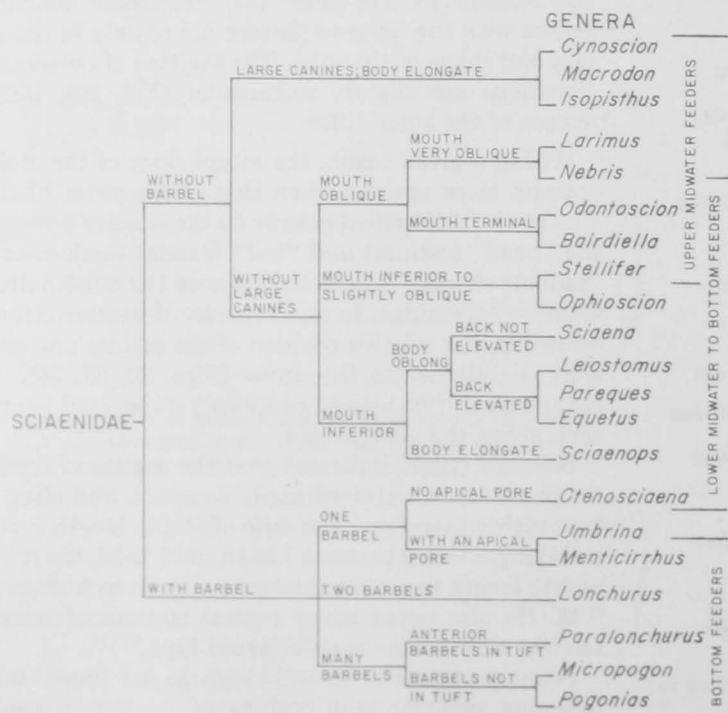


Figure 30.—Groupings of western Atlantic Sciaenidae according to external morphology.

**Five marginal and three upper pores.**—The rostral fold of this pattern is indented at the openings of the marginal pores (Fig. 31C). *Bairdiella*, *Ctenosciaena*, *Menticirrhus*, *Odontoscion*, *Ophioscion*, *Paralonchurus*, and *Stellifer* have this pattern. The position and size of the mouths in this group of fishes suggest that some feed in midwater and some on the bottom. In bottom

feeders such as *Menticirrhus* and *Paralonchurus*, the rostral folds are very deeply indented below the marginal pores (Fig. 33C, D). For the midwater or lower midwater feeders, *Stellifer lanceolatus* and *Ophioscion punctatissimus*, the rostral folds are only slightly indented (Fig. 33A, B). *Ophioscion punctatissimus* also has two minute pairs of upper pores present dorsolaterally to the outer lateral marginal margins pores (Fig. 33B).

**Five (or more) marginal and five (or more) upper pores.**—This pattern usually has five distinct rostral and five marginal pores (Fig. 31D). Sometimes an extra pair or

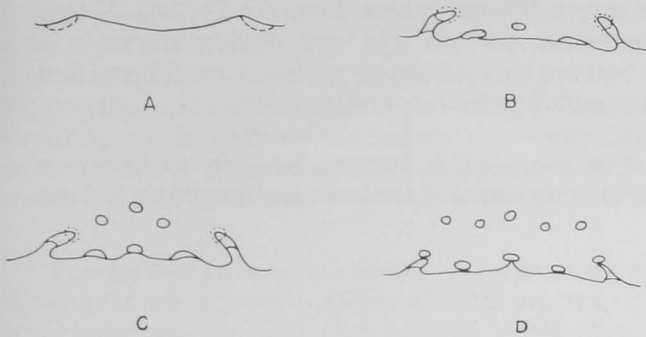


Figure 31.—Snout pore patterns (diagrammatic) of western Atlantic Sciaenidae. A, no upper and two marginal pores; B, no upper and five marginal pores; C, three upper and five marginal pores; D, five upper and five marginal pores.

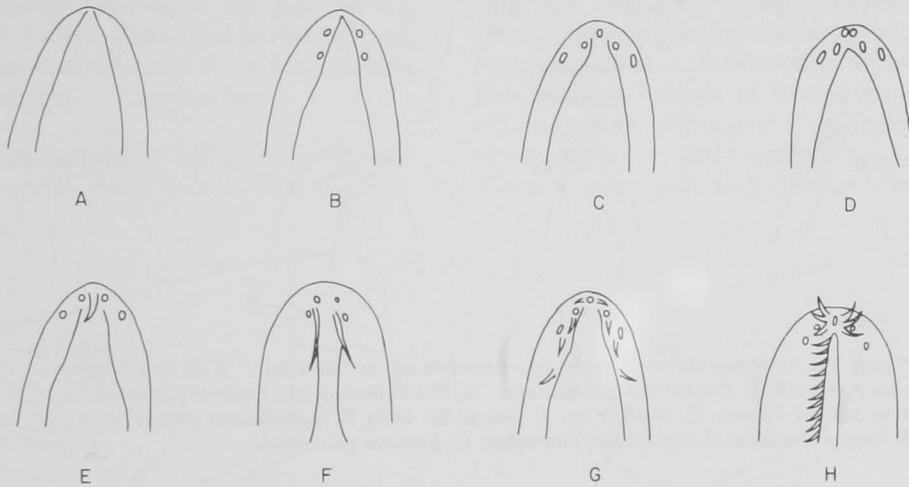


Figure 32.—Mental pore and barbel patterns (diagrammatic) on the lower jaw of western Atlantic Sciaenidae. A, no pore and no barbel; B, four pores and no barbel; C, five pores and no barbel; D, six pores and no barbel; E, four pores and one barbel; F, four pores and two barbels; G, five pores and many barbels, not in tuft; H, five pores and many barbels, anterior three pairs of barbels in tuft.

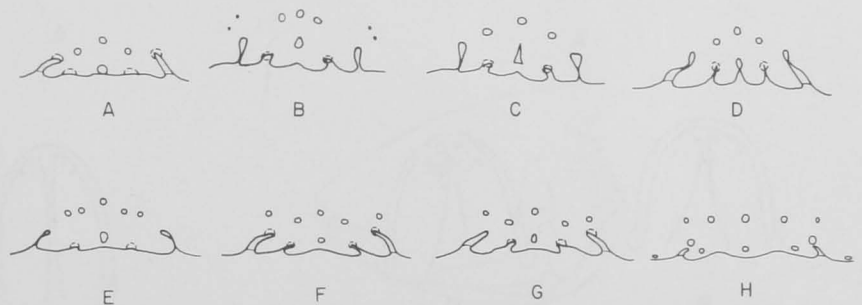


Figure 33.—Diversity in snout pores with five or more marginal pores. A-D, three upper pore pattern; E-H, five upper pore pattern. A, *Bairdiella chrysoura*; B, *Ophioscion punctatissimus* (with additional four minute pores); C, *Paralonchurus elegans*; D, *Menticirrhus americanus*; E, *Pogonias cromis*; F, *Sciaenops ocellata*; G, *Micropogonias undulatus*; H, *Pareques umbrosus* (with seven marginal pores).



two pairs of minute pores are developed lateral to the upper and marginal pores (Fig. 33H). The rostral fold is smooth or slightly notched below (or at) the openings of the marginal pores. *Equetus*, *Leiostomus*, *Lonchurus*, *Micropogonias*, *Pachyurus*, *Pareques*, *Pogonias*, *Sciaena*, *Sciaenops*, and *Umbrina* have this pattern, have a horizontal or inferior mouth, and are typically bottom feeders. Variation within this snout pore pattern is mainly in the presence of additional minute pores (Fig. 33E-H), which may also vary ontogenetically.

**Structural patterns of mental pores and barbels.**—There are seven mental pore and barbel patterns recognizable in western Atlantic sciaenids (Fig. 32). Variations are rather common within genera, especially in speciose genera such as *Stellifer* and *Bairdiella*.

**No pores.**—This pattern has neither pores nor barbels on the lower jaw (Fig. 32A) and is found in *Cynoscion*, *Isopisthus*, *Macrodon*, and *Plagioscion*. All fishes with this pattern have a large oblique mouth and are upper water or midwater feeders, although *Plagioscion* has a nearly terminal mouth.

**Four pores.**—This pattern has two pairs of laterally set pores (Fig. 32B), which may vary in arrangement and size among different genera (Figs. 34A-D, 35A). *Nebris*, *Odontoscion*, *Larimus*, and some *Stellifer* species have this pattern, have a terminal or oblique mouth, and feed in the midwater to upper water column.

**Five pores.**—This pattern has one median pore located at the center of the lower jaw symphysis and two

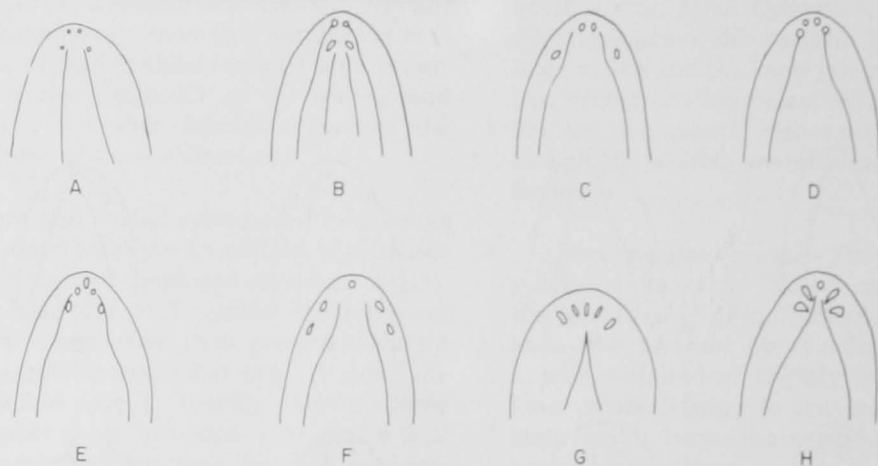


Figure 34.—Diversity in mental pore arrangements on the lower jaw. A-D, four mental pore pattern; E-H, five mental pore pattern. A, *Nebris microps*; B, *Larimus fasciatus*; C, *Odontoscion dentex*; D, *Stellifer* sp. B (see p. 55, key); E, *Aplodinotus grunniens*; F, *Sciaenops ocellata*; G, *Ophioscion punctatus*; H, *Equetus punctatus*.

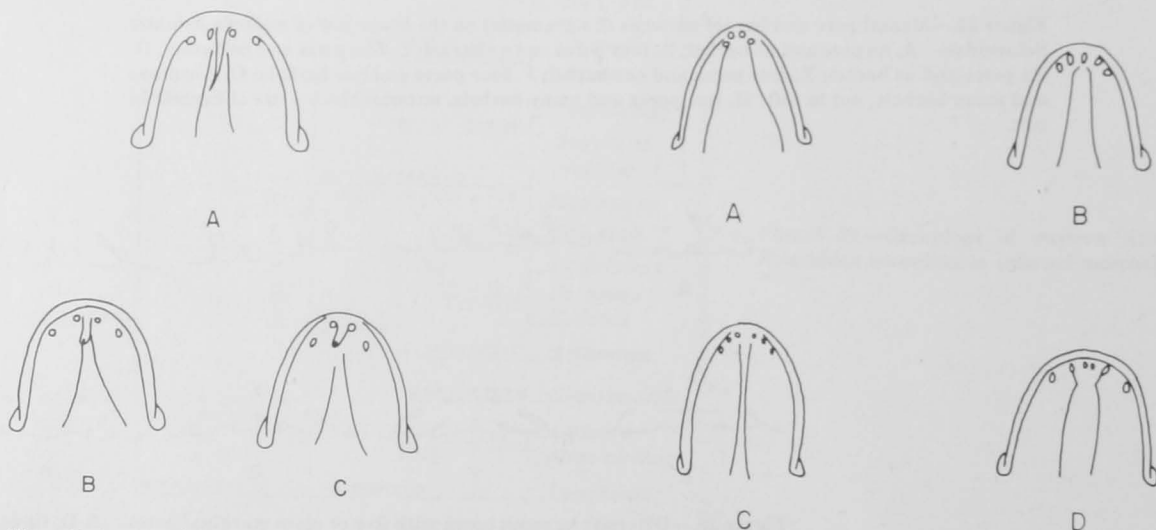


Figure 35.—Diversity in mental pore patterns on the lower jaw in the species of *Stellifer*; A, *Stellifer* sp. B (see p. 55, key), four mental pores; B, *S. stellifer*, five mental pores; C, *S. rastrifer*, six mental pores; D, *S. colonensis*, six mental pores.

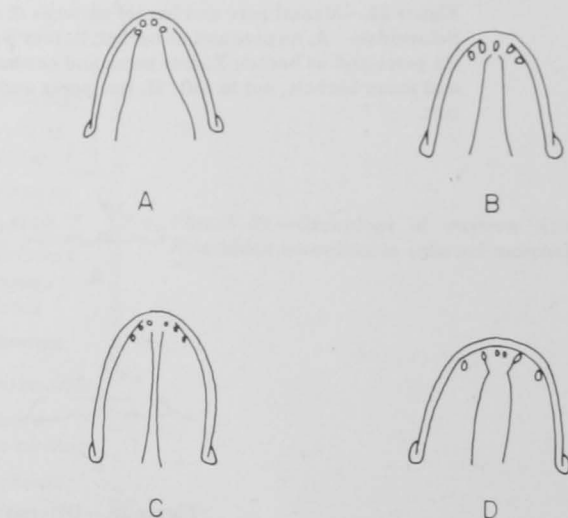


Figure 36.—Western Atlantic Sciaenidae with one mental barbel on the lower jaw. A, *Ctenosciaena gracilicirrhus* (lacks an apical pore); B, *Menticirrhus* and C, *Umbrina* (with an apical pore).

lateral pairs (Fig. 32C). In fact, the median pore (opening) often consists of a pair of closely set pores inside. The arrangement of the five pores varies among genera (Figs. 34E-H, 35B). *Aplodinotus*, *Equetus*, *Leiostomus*, *Ophioscion*, *Pachyurus*, *Pareques*, *Sciaena*, *Sciaenops*, and some species of *Bairdiella* (*B. ronchus* and *B. sanctaeluciae*) and *Stellifer* (*S. microps*, *S. stellifer*, and *S. venezuelae*) have this pattern.

**Six pores.**—This pattern has two median pores and two pairs of lateral pores (Figs. 32D; 35C, D). *Bairdiella chrysoura*, *Stellifer colonensis*, *S. griseus*, and *S. rastrofer* have this pattern. Two median pores may be closely set and appear as the five-pored pattern. Fishes with this pattern of mental pores have a terminal to slightly inferior mouth and feed from lower midwater to the bottom.

**Four (or five) pores and one barbel.**—This pattern has two pairs of lateral pores and a barbel at the anterior tip of the lower jaw (Fig. 32E). *Ctenosciaena*, *Menticirrhus*, and *Umbrina* have this pattern. The morphology of the barbel varies among these three genera (Fig. 36). *Ctenosciaena* has a thin barbel tapering at the end. *Menticirrhus* and *Umbrina* have a short rigid barbel with an apical pore. They have subterminal to inferior mouths and are lower midwater to bottom feeders.

**Four pores and two barbels.**—This pattern has two pairs of lateral pores and a pair of thin barbels originat-

ing on the medial side of each posterior mental pore (Fig. 32F). *Lonchurus* is the only genus with this pattern and has an inferior mouth, typical of bottom feeders.

**Five pores and many barbels.**—This pattern has five pores, one median and four lateral, together with 3 to 16 pairs of minute barbels at the symphyses of the mandibles and along the rami of the lower jaws (Fig. 32G, H). *Micropogonias*, *Paralonchurus*, and *Pogonias* have this pattern. The arrangement of the barbels differs among the genera, especially in *Paralonchurus*. Three pairs of minute barbels form a tuft situated laterally to the median pore, and 12 to 16 pairs of small barbels distributed along the rami of the lower jaw (Fig. 32H). *Micropogonias* and *Pogonias* lack the tufts of barbels at the symphysis of the lower jaw (Fig. 32G). Fishes with this pore and barbel pattern have an inferior mouth, and are typically bottom feeders.

**Generic groupings based on external morphology.**—Western Atlantic sciaenids can be readily separated into two groups by the presence or absence of mental barbels (Fig. 30). The group without barbels can be further divided by mouth position and body shape (Fig. 30). *Cynoscion*, *Isopisthus*, and *Macrodon* differ from other sciaenids without barbels in having an elongate body, an oblique mouth with a pair of enlarged canines at the tip of the upper jaw, and a protruding lower jaw (Fig. 37A). Those species that lack canines can be divided into

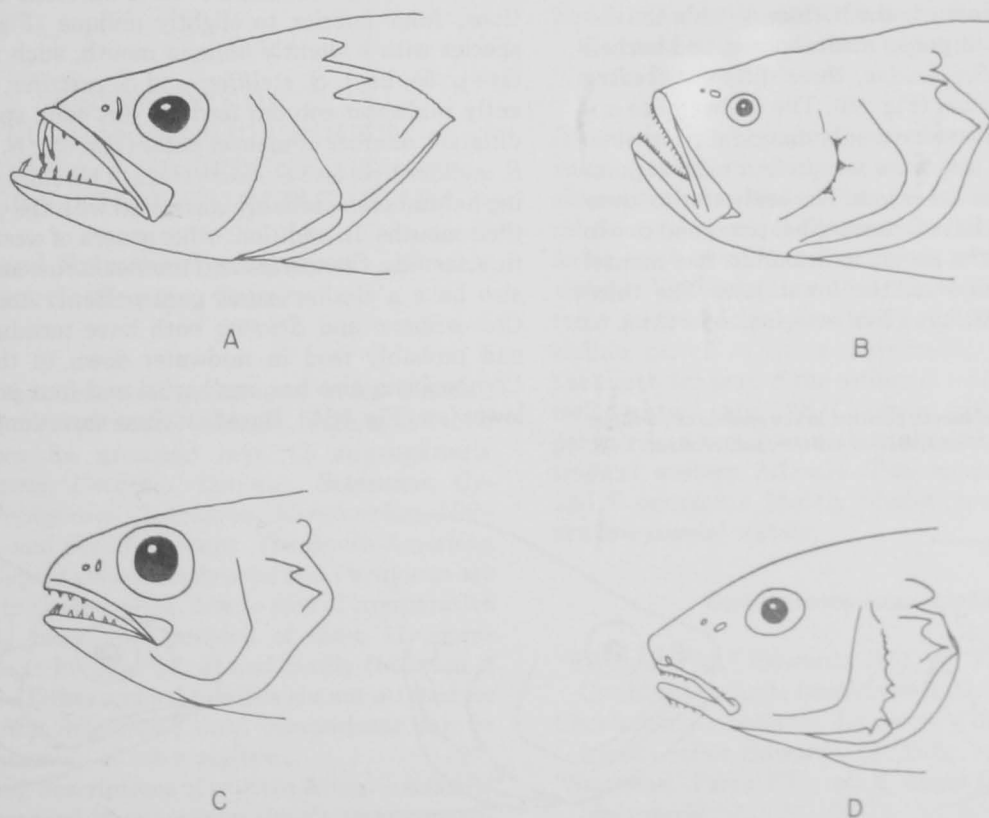


Figure 37.—Four typical mouth positions and dentitions of western Atlantic Sciaenidae. A, *Macrodon ancylodon*; B, *Nebris microps*; C, *Odontoscion dentex*; D, *Micropogonias undulatus*.

groups by their mouth positions and body shapes (Fig. 30). *Nebris* and *Larimus* have a very large and oblique mouth (Fig. 37B). *Bairdiella* and *Odontoscion* both have a terminal mouth (Fig. 37C). The genus *Stellifer* consists of species with oblique (*S. lanceolatus*), subterminal (*S. rastrifer*), and inferior (*S. microps*), mouths (Fig. 38). *Ophioscion*, *Leiostomus*, *Pareques*, *Equetus*, and *Sciaenops* have inferior mouths. *Sciaenops* differs from these fishes by having an elongate body. *Sciaena* is characterized by a nearly terminal and horizontal mouth.

Sciaenids with mental barbel(s) usually have an inferior mouth and can be divided into different categories by the number and/or position of barbels (Fig. 30). *Ctenosciaena* has a thin tapered barbel and a subterminal mouth (Fig. 36A), unique among western Atlantic sciaenids with barbels. *Menticirrhus* and *Umbrina* have an apical pore at the tip of the single rigid barbel (Fig. 36B, C). *Lonchurus* has a pair of long slender barbels at the symphysis of the lower jaw (Fig. 32F). *Paralanchurus* has 3 pairs of minute barbels in a tuft at the symphysis of the lower jaw lateral to the median mental pore and 12 to 16 pairs of small barbels along the rami of the lower jaw (Fig. 32H). *Micropogonias* has 3 to 4 pair of small mental barbels and *Pogonias* has 12 to 13 pairs that never form a tuft at the symphysis of the lower jaw (Fig. 32G).

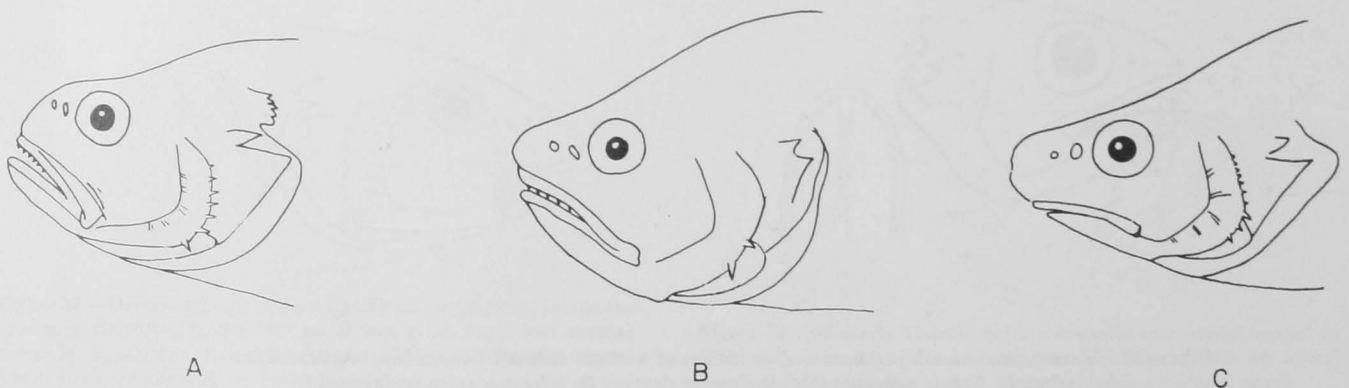
The combination of morphological characters described above reflects habitat or similarities in feeding habits (Chao and Musick 1977). The genera listed at the top of Figure 30 generally feed on the upper water to midwater column and the genera listed near the bottom feed in the lower water column to the bottom. Within the different patterns of snout pores, mental pores, and barbels of western Atlantic Sciaenidae, three different feeding modes may be recognized (Fig. 30). The midwater to upper water column feeders have only marginal pores (two or five) on the snout, and have zero to four mental pores without barbels on the lower jaw. The midwater to lower water column feeders have five marginal pores and two to five upper pores on the snout, and four to five mental pores without barbel(s) on the lower jaw. The third group, bottom feeders, have five marginal and three to

five (or more) upper pores on the snout, and have four to five mental pores and one to many barbels on the lower jaw. The number of pores and barbels seems to increase in feeding niches that are closer to the bottom.

**Specific characters.**—Western Atlantic sciaenids with two marginal snout pores and with neither upper pores nor mental pores (Fig. 31A) such as *Cynoscion* are upper water-midwater column feeders. Although *Nebris* has a very oblique mouth (Fig. 37B) and snout pore arrangement similar to *Cynoscion*, it also has four mental pores (Fig. 34A) and a rounded body with a flat ventral surface. This suggests that *Nebris* is a bottom dweller feeding from the bottom upward. Sciaenid fishes with five marginal pores and no upper pore on the snout are midwater to upper midwater column feeders, such as *Larimus*, which has four mental pores similar to *Nebris* (Fig. 34B). *Larimus*, however, has a compressed body that may not be adapted to a bottom habitat as in that of *Nebris*.

The pattern of five marginal pores and three upper pores (Figs. 31C, 33A-D) is common among different genera, such as *Bairdiella*, *Odontoscion*, *Ophioscion*, *Stellifer*, and *Menticirrhus*. Species of *Menticirrhus* all have four pores and one barbel with an apical pore on the lower jaw, and are bottom feeders. Although the number of mental pores among the species of *Bairdiella* varies from five to six, they all have a terminal mouth and are midwater to lower midwater feeders. Species of *Stellifer* not only have a variable number of mental pores, from four to six (Fig. 35), but also have different mouth positions, from inferior to slightly oblique (Fig. 38). The species with a slightly oblique mouth, such as *S. sp. B* (see p. 55, key), *S. stellifer*, and *S. rastrifer*, are apparently midwater column feeders. But each species has a different number of mental pores (Fig. 35): *S. sp. B* four, *S. stellifer* five, and *S. rastrifer* six. Therefore, their feeding habitats are probably correlated with the positions of their mouths. In addition, other genera of western Atlantic sciaenids, *Ctenosciaena*, *Paralanchurus*, and *Sciaena*, also have a similar snout pore pattern. Among them, *Ctenosciaena* and *Sciaena* both have terminal mouths and probably feed in midwater down to the bottom. *Ctenosciaena* also has one barbel and four pores on the lower jaw (Fig. 36A). Based on these variations, the three

Figure 38.—Three levels of mouth position in the species of *Stellifer*: A, *Stellifer lanceolatus*, oblique; B, *S. rastrifer*, subterminal; C, *S. microps*, inferior.



upper and five marginal snout pore pattern is probably the more generalized among western Atlantic sciaenids with different feeding niches.

Sciaenid fishes with five or more upper and marginal pores (Figs. 31D, 33E-H) are mostly bottom feeders with an inferior mouth. They usually have five pores on the lower jaw with or without mental barbels. *Lonchurus* has four pores and two long tapered barbels on the lower jaw (Fig. 32F).

When comparing the pore and barbel systems of western Atlantic Sciaenidae with the Indo-Pacific (Chu et al. 1963), East Atlantic, and East Pacific sciaenids, the five marginal and three to five upper pores on the snout seem to be generalized in most sciaenids. Also the five pores (or six pores with five openings) on the lower jaw is typical in sciaenids. Sciaenids with a single mental barbel are found in the Indo-West Pacific, on both sides of the Atlantic, and in the eastern Pacific (Trewavas 1964). However, sciaenids with more than one barbel are found only along the Atlantic and Pacific coasts of America, except that *Daysciaena albida* (Cuvier) of the Indian Ocean has a pair of short barbels.

The external characters described above are sometimes variable within a genus and yet similarities are found among different genera. Neither the differences nor the similarities necessarily reflect phylogenetic relationships. These external morphological characters and those mentioned in the key may support the groupings on other criteria. Their usefulness in assessing relationships of western Atlantic sciaenids is usually not above the species level.

## A SYNOPSIS OF THE SUPRAGENERIC GROUPS, GENERA, AND SPECIES OF WESTERN ATLANTIC SCIAENIDAE

### Diagnoses and Primary Synonymy of the Suprageneric Groups, Genera, and Species

Based on the structural patterns of swim bladder, otolith, and pore and barbel systems, western Atlantic sciaenids can be grouped into 11 suprageneric groups: *Sciaena*, *Umbrina*, *Larimus*, *Sciaenops*, *Cynoscion*, *Micropogonias*, *Lonchurus*, *Menticirrhus*, *Nebriis*, *Pogonias*, and *Stellifer* groups. The South American freshwater sciaenid genera *Pachypops* and *Pachyurus* are not included in these groups, due to lack of comparative material. The taxonomic position of these 11 suprageneric groups is between genus and family (between A and D, Fig. 4). Tribes and subfamilies are not utilized for western Atlantic Sciaenidae until comparisons can be made with sciaenids of other regions.

The following descriptions of western Atlantic sciaenid groups are arranged in order from simple to more complex swim bladder patterns. In the description of each group, the diagnoses of the suprageneric group and in-

cluded genera are given and the species are listed for each genus. A primary synonymy is given for each genus and species for nomenclatural purposes. The generic synonymy relies heavily on Jordan (1917-1923) and Norman (1966). Available type-specimens are listed in the synonymy of each nominal species. Where no type-specimens are listed, I am unaware of the existence or location of any.

### *Sciaena* GROUP

*Diagnosis*.—Swim bladder in a simple carrot-shape, without diverticulum (*Sciaena* pattern, Fig. 5); sagitta more or less oval and thick (Fig. 18), lapillus not enlarged; snout with five marginal pores and three to seven upper pores (Figs. 31C, D; 33H); lower jaw with five pores and no barbels (Fig. 32C). There are three genera in this group: *Equetus*, *Paraques*, and *Sciaena*. *Leiostomus* has similar diagnostic characters except that the sagitta of *Leiostomus* is thinner and narrower (Fig. 18D). However, *Leiostomus* is probably more closely related to the *Sciaena* group than to any other western Atlantic sciaenid groups.

### *Equetus* Rafinesque

*Eques* Bloch 1793, pt.7:90 (type-species: *Eques americanus* Bloch, by monotype = *Chaetodon lanceolatus* Linnaeus, preoccupied by *Eques* Linnaeus 1758:459, a genus of lepidopteran insects).

*Equetus* Rafinesque 1815:86 (substitute name for *Eques*, therefore taking the same type-species: *Eques americanus* Bloch).

*Diagnosis*.—Body oblong, compressed, back much elevated, rapidly tapering to a narrow caudal peduncle; sides with broad oblique bands; anterior portion of dorsal fin very long and filamentous. Mouth small and inferior, teeth in villiform bands; gill rakers few, short, and slender. Vertebrae 10 + 15 = 25; no free interneurals anterior to first dorsal fin (McPhail 1961). Swim bladder simple, carrot- or bottle-shaped (Fig. 5C). Sagitta oval, the expanded part of the ostium of sulcus reaching to anterior margin (Fig. 18B, C); snout with five to seven upper pores; lower jaw without barbel. Endemic to the tropical western Atlantic. Two species: *E. lanceolatus* and *E. punctatus*. Mainly inhabit coral reefs, sometimes shallow coastal waters.

### *Equetus lanceolatus* (Linnaeus)

“Ribband Fish” Edwards 1751, pl. 210, middle figure, Caribbean Islands (nonbinominal).

*Chaetodon lanceolatus* Linnaeus 1758:277, Caribbean Islands (after Edwards, pl. 210).

“Serranas” Parra 1787, pl. 2, upper figure, Cuba (nonbinominal).

*Eques americanus* Bloch 1793, pt. 7:91, pl. 347, fig. 1, West Indies.

*Eques balteatus* Cuvier 1829:175 (after Edwards and Bloch).

*Sciaena edwardi* Gronovius (Gray) 1854:53, (West) Indian Sea (after Edwards).

*Equetus punctatus* (Bloch and Schneider)

"Serranas" Parra 1787, pl. 2, lower figure, Cuba (non-binominal).

*Eques punctatus* Bloch and Schneider 1801:105, pl. 3, fig. 2 (based on Parra).

*Pareques Gill*

*Pareques Gill* in Goode 1876:50 (type-species: *Grammistes acuminatus* Bloch and Schneider 1801, by original designation).

**Diagnosis.**—Body oblong, compressed, anterior profile steep, back tapering rapidly to a narrow caudal peduncle; sides with longitudinal stripes; anterior portion of dorsal fin not filamentous. Mouth small, inferior; teeth in villiform bands; gill rakers short and blunt. Vertebrae 10 + 15 = 25; three free interneurals anterior to first dorsal fin (McPhail 1961). Swim bladder simple, carrot-shaped. Sagitta oval, the expanded part of the ostium reaching to anterior margin (Fig. 18E, F), the cauda long, J-shaped. Snout with five to seven upper pores (Fig. 33H); lower jaw without barbel. Tropical eastern Pacific and western Atlantic, about seven species. Three western Atlantic species: *P. acuminatus*, *P. umbrosus*, and one undescribed. Inhabits sandy and muddy bottoms of high salinity waters and coral reefs.

*Pareques acuminatus* (Bloch and Schneider)

"Chaetodon, lineis fuscis, . . ." Seba 1761:72, pl. 26, fig. 33, no locality (nonbinominal).

*Grammistes acuminatus* Bloch and Schneider 1801:184 (after Seba).

*Eques lineatus* Cuvier 1830:169, Brazil (syntypes: MNHN 7475, 135 mm SL; MNHN 43, 137 mm SL).

*Eques pulches* Steindachner 1867:349, Barbados (type: presumably in NHMV, but not found).

*Pareques umbrosus* (Jordan and Eigenmann)

*Eques acuminatus umbrosus* Jordan and Eigenmann 1889:440, Charleston, S.C. (holotype: CAS 18958, 162 mm SL or USNM 25981, 165 mm SL, see remarks).

**Remarks.**—Jordan and Eigenmann (1889) described the subspecies *E. acuminatus umbrosus* based on a specimen from Charleston sent by C. Leslie. Both specimens of CAS 18958 and USNM 25981 were from the same source and fit the original description. Both specimens were also previously labeled as *E. acuminatus*. At present, I am not able to decide which one is the holotype. *Eques*

*acuminatus* and *E. umbrosus* can be separated by their pigmentation pattern and counts (also see "Key to the species of *Pareques*"). The sagittae of these two species differ from each other by features of the sulcus (Fig. 18E, F). *Paraques umbrosus* is a more northerly species distributed from Chesapeake Bay to Florida and also recorded from Texas over sandy mud bottom of inshore and offshore waters; *P. acuminatus* is a more southerly species from Florida to Brazil in coral reef and rocky bottom coastal waters.

*Sciaena Linnaeus*

*Sciaena Linnaeus* 1758:228 (type-species: *Sciaena umbra* Linnaeus, by subsequent designation of International Commission for Zoological Nomenclature 1972, Opinion 988).

**Diagnosis.**—Body elongate, compressed, dorsal profile slightly elevated or evenly arched; anterior portion of dorsal fin not elongated. Mouth horizontal to inferior; teeth in bands; gill rakers short and slender, widely spaced. Vertebrae 25 (11 + 14 in *S. bathytatos* and 10 + 15 in *S. trewavasae*). Swim bladder simple, carrot-shaped (Fig. 5A). Sagittae oval, the expanded part of the ostium reaching to anterior margin (Fig. 18G, H). Snout with three to five upper pores (Fig. 31C, D); lower jaw without barbel. Two species in the western Atlantic, *S. bathytatos* and *S. trewavasae*, inhabiting deeper subtropical waters, and one species in the eastern Atlantic and Mediterranean, *S. umbra*. Some of the six East Pacific nominal species of *Sciaena* probably should be assigned to other genera (Chao).<sup>4</sup>

**Remarks.**—The nomenclature of the genus *Sciaena* was not stabilized until *S. umbra* Linnaeus 1758 was designated as the type-species of the genus under the Plenary Powers of the International Commission for Zoological Nomenclature (1972, Opinion 988). A neotype was designated by Trewavas (1966). The history of the case and synonymies were discussed by Trewavas (1963). This genus is the type-genus of the tribe Sciaenini (Trewavas 1962). The genus *Sciaena* is still not well defined and it may contain more species than currently recognized (Chao and Miller 1975).

*Sciaena bathytatos* Chao and Miller

*Sciaena bathytatos* Chao and Miller 1975:267, fig. 9, Caribbean Sea off Colombia (holotype: USNM 211514, 208 mm SL).

*Sciaena trewavasae* Chao and Miller

*Sciaena trewavasae* Chao and Miller 1975:262, fig. 8,

<sup>4</sup>Chao, L. N. A basis for classifying eastern Pacific Sciaenidae (Teleostei: Perciformes). Manuscr.

Caribbean Sea off Colombia (holotype: USNM 211513, 155 mm SL).

### *Leiostomus* Lacepède

*Leiostomus* Lacepède 1803, 4:439 (type-species: *Leiostomus xanthurus* Lacepède, by monotypy).

*Liostomus* Gill 1862c:93 (invalid emendation of *Leiostomus* Lacepède 1803, therefore taking the same type-species: *Leiostomus xanthurus* Lacepède).

**Diagnosis.**—Body oblong, compressed, back elevated, sides with oblique stripes and a dark humeral spot behind upper end of gill slit; anterior portion of dorsal fin not elongated. Mouth small and inferior; teeth in villiform band; gill rakers short and slender. Vertebrae 10 + 15 = 25. Swim bladder simple carrot-shape (Fig. 5B). Sagitta oval and thin, the expanded part of the ostium reaching to anterior margin and its axis inclined toward the dorsal margin (Fig. 18D). Snout with five upper pores; lower jaw without barbel. Northwestern Atlantic. Monotypic: *L. xanthurus*. Found over sandy and mud bottoms in estuarine and inshore waters.

### *Leiostomus xanthurus* Lacepède

*Leiostomus xanthurus* Lacepède 1803, 4:439, pl. 10, fig. 1, Carolina (syntypes: MNHN 7599, two specimens, 148 and 163 mm SL).

*Mugil obliquus* Mitchell 1814:16, New York.

*Sciaena multifasciata* LeSueur 1822:255, east Florida (length of the type-specimen not reported).

*Leiostomus humeralis* Cuvier 1830:141, pl. 110, New York (holotype: MNHN 9733, one dried stuffed specimen, 146 mm SL).

### *Umbrina* GROUP

**Diagnosis.**—Swim bladder simple carrot-shaped, without diverticula (*Sciaena* pattern, Fig. 5); sagitta oval (*Sciaena* pattern, Fig. 18); snout with five marginal pores and three to seven upper pores (Fig. 31C, D); lower jaw with four pores and one barbel, an apical pore present in *Umbrina*. Two genera in this group: *Ctenosciaena* and *Umbrina*.

### *Ctenosciaena* Fowler and Bean

*Sciaena* (*Ctenosciaena*) Fowler and Bean 1924:15 (type-species: *Sciaena dubia* Fowler and Bean, by monotypy).

**Diagnosis.**—Body oblong, moderately compressed, head moderate and blunt with well-developed cavernous canals. Mouth subterminal to inferior, snout protruding; lower jaw with a barbel tapering to a fine point without an apical pore at the tip (Fig. 36A). Vertebrae 10 + 15 = 25. Sagitta oval, the expanded part of the ostium slightly in contact with the anterior margin (Fig. 18A).

Snout with three upper pores (Fig. 31C). Eastern Pacific and western Atlantic, two species. The western Atlantic species, *C. gracilicirrhus*, inhabits offshore waters over hard sandy bottom.

### *Ctenosciaena gracilicirrhus* (Metzelaar)

*Umbrina gracilicirrhus* Metzelaar 1919:72, fig. 24, Venezuela (holotype: ZMA 113.103, 105 mm SL).

*Sciaena* (*Ctenosciaena*) *dubia* Fowler and Bean 1924:16, Wilkes Exploring Expedition, locality unknown (holotype: USNM 83309, 111 mm SL).

### *Umbrina* Cuvier

*Sciaena* Linnaeus 1758:288 (of Artedi 1738, in part; includes *S. cirrosa*; type-species: *Sciaena umbra* Linnaeus by subsequent designation of International Commission for Zoological Nomenclature 1972, Opinion 988).

*Umbrina* Cuvier 1817:297 (type-species: *Sciaena cirrosa* Linnaeus, by original designation).

*Attilus* Gistel 1848:109 (type-species: *Sciaena cirrosa* Linnaeus, by original designation).

**Diagnosis.**—Body moderately elongate; back slightly arched, ventral profile nearly straight. Head oblong, snout thick and protuberant. Mouth small, horizontal to inferior; teeth in bands, outer row of teeth in upper jaw moderately enlarged. Gill rakers short. Vertebrae 11 + 14 = 25. Swim bladder simple carrot-shape, without diverticula. Sagitta oval, the expanded part of the ostium reaching to anterior margin (Fig. 18 I, J). Snout with five to seven upper pores (Fig. 31D); lower jaw with four pores and a short, thick barbel, the latter with an apical pore (Fig. 36C). Eastern Pacific and both sides of the Atlantic, about nine species. Four species in the western Atlantic: *U. broussonetii*, *U. canosai*, *U. coroides*, and *U. milliae*. Inhabits inshore and offshore waters with sandy or mud bottoms and around coral reefs.

**Remarks.**—The name *Chromis* in the footnote of Lacepède 1802, volume 3, p. 546 was from the sketch of Le Pere Plumier, a missionary in Martinique, for the "grygry" or "grogro," which is *Umbrina coroides* Cuvier 1830. The name *Chromis* is older than *Umbrina* but later than *Cromis* Browne (after Jordan 1917). Also see Gilbert (1966) for more detailed synonymy.

### *Umbrina broussonetii* Cuvier

*Umbrina broussonetii* Cuvier 1830:187, Jamaica (holotype: MNHN 7471, 151 mm SL).

### *Umbrina canosai* Berg

*Umbrina canosai* Berg 1895:56, Montevideo, Uruguay to Mar del Plata Argentina (no type-specimens nor specific localities mentioned in the original description).

*Umbrina coroides* Cuvier

*Umbrina coroides* Cuvier 1830:187, pl. 117, Brazil (holotype: MNHN 5343, 174 mm SL).

*Umbrina milliae* Miller

*Umbrina milliae* Miller 1971:303, fig. 1, Colombia (holotype: USNM 204932, 193 mm SL).

**Menticirrhus** GROUP

*Diagnosis.*—Swim bladders atrophy as the fish grow, only a vestige remains in adult. Drumming muscles absent in both sexes. Sagitta oval, elongate, and relatively small, the expanded part of the ostium not reaching to anterior margin (*Menticirrhus* pattern, Fig. 22B). Snout with three upper pores and five marginal pores, rostral fold deeply indented (Fig. 33D); lower jaw with a short, rigid barbel, knoblike and five pores, the median at tip of barbel (Fig. 36B). Anal fin with only one weak spine. One genus in this group: *Menticirrhus*.

**Menticirrhus** Gill

*Menticirrhus* Gill 1862b:86 (type-species: *Perca alburnus* Linnaeus = *Cyprinus americanus* Linnaeus, by original designation).

*Cirrimens* Gill 1863:17 (type-species: *Umbrina ophiocephalus* Jenyns 1842:45, by original designation).

*Menticirrhus* (*Umbrula*) Jordan and Eigenmann 1889:424 (type-species: *Umbrina littoralis* Holbrook, by subsequent designation of Jordan and Evermann 1898:1469).

*Diagnosis.*—Body elongate, rounded; dorsal profile slightly arched, ventral profile nearly flat. Head conical, low and broad, snout projecting. Mouth small and inferior; teeth in villiform bands. Gill rakers short and tuberclelike. Vertebrae 10 + 15 = 25. Other diagnostic characters as in the group diagnosis. Tropical and temperate eastern Pacific and western Atlantic, nine species. Three species in the western Atlantic: *M. americanus*, *M. littoralis*, and *M. saxatilis*. Inhabits shallow coastal waters with sandy bottoms, juveniles often found in estuaries.

**Menticirrhus americanus** (Linnaeus)

"Alburnus Americanus" Catesby 1743, "Carolina whitening," pl. 12, lower figure, Charleston (pre-Linnaean and nonbinominal, see remarks).

*Cyprinus americanus* Linnaeus 1758:321 (based on Catesby; not *Cyprinus americanus* of Linnaeus 1766:530, a cyprinid, see remarks).

*Perca alburnus* Linnaeus 1766:482, South Carolina (holotype: Linnaean Society of London, no. 111, a dried left side of skin, 282 mm TL, see remarks).

*Umbrina arenata* Cuvier 1830:190, Brazil (syntypes: MNHN 7500, 76.4 mm SL; MNHN 7472, a dried and stuffed specimen, in ethanol, 341 mm TL).

*Umbrina martinicensis* Cuvier 1830:186, Martinique (holotype: MNHN 7498, 193 mm SL).

*Umbrina gracilis* Cuvier 1830:189, Brazil (lectotype: MNHN 44, 156 mm SL, see remarks).

*Sciaena alburnus* (non-Linnaeus) Gronovius (Gray) 1854:108 (Gronovius' specimen; BMNH 1853.11.12.75, a dried skin, 228 mm TL, see remarks).

*Umbrina phalaena* Girard 1859:167, Brazos Santiago, Texas (syntypes: USNM 154721, 88.3 mm SL; other syntypes not located).

*Umbrina januarua* Steindachner 1877:170, Rio de Janeiro (type: not located).

*Remarks.*—The description of "Alburnus Americanus" by Catesby (1743) stated that "under the lip having five or six fleshy barbels, resembling teeth hanging to it on the outside. It had one small fin on the middle of the back." The lower figure of plate 12, "Alburnus" agrees with this description. Except for these features, the general appearance of the figure is a species of *Menticirrhus* but it is impossible to identify it with any of the *Menticirrhus* species. The name *Cyprinus americanus* Linnaeus 1758 is based on Catesby. But in Linnaeus 1766, the 12th edition of "Systema Naturae," he treated the Catesby reference as a synonym of *Perca alburnus* which is based on the D. Garden skin (Linnaean Society of London, no. 111, 282 mm TL). He also employed the name *Cyprinus americanus* (= *Notemigonus bosci* Cuvier and Valenciennes, from Jordan and Eigenmann 1889) within the Cyprinidae on page 530 (1766) based on Garden material but with no reference to his 1758 usage or to Catesby. Linnaeus (1766) appeared to be acknowledging that he had been misled by the plate (Catesby 1743, "Alburnus Americanus," pl. 12) and was clarifying his intentions both for the name *C. americanus* and for the binomen to use for the sciaenid (*Perca alburnus*). A. Wheeler (BMNH, pers. commun.) pointed out that Linnaeus was acting in effect as "first reviser" for *Cyprinus americanus* and also for *Perca alburnus* and suggested that *M. alburnus* (Linnaeus 1766) should be the correct name for this species. Although the earlier usage was in favor of *M. alburnus* (prior to Jordan and Eigenmann 1889), I am in favor of the currently stabilized usage of *M. americanus*. Furthermore, Jordan and Eigenmann (1889) stated that *Cyprinus americanus* was the name Linnaeus gave to the whiting of Catesby and that there could be no doubt that the fish Catesby had in mind was *Menticirrhus americanus*.

A specimen, MNHN 9037, was catalogued as syntype of *Umbrina gracilis* Cuvier 1830, in MNHN, Paris and was identified by Irwin (1970) as *M. littoralis* (Holbrook). It is not a type of *U. gracilis*, because the locality and the donor of the specimen do not agree with the original description of Cuvier (M. Bauchot, MNHN, Paris, pers. commun.). Thus, MNHN 44, is selected as lectotype.

Wheeler (1958) wrote "*Sciaena alburnus* (non-L.)

Gronovius (Gray), 1854" as a synonym of *Menticirrhus americanus* (Linnaeus 1758). This also implied that *S. alburnus* Gronovius (Gray) was not intended to be *Perca alburnus* Linnaeus 1766. In the original description of *Sciaena alburnus*, Gronovius (Gray) 1854, quoted "Perca pinnis dorsalibus distinctis muticis, . . ." from Linnaeus (1766), 12th edition genus 168, no. 6. According to Wheeler (1958), a figure of *S. alburnus* and a specimen (BMNH 11.12.75, a dry skin, 288 mm SL) with Garden's collection number were present in Gronovius' manuscript. Linnaeus (1766) also wrote *Perca alburnus* as "Habitat in Carolina, D. Garden, Whiting." Thus, in my opinion, *Sciaena alburnus* Gronovius (Gray) was intended to be *Perca alburnus* Linnaeus.

#### *Menticirrhus littoralis* (Holbrook)

*Umbrina littoralis* Holbrook 1855:142, South Carolina (holotype: ANSP 11567, 198 mm SL).

#### *Menticirrhus saxatilis* (Bloch and Schneider)

*Johnius saxatilis* Bloch and Schneider 1801:75, New York (holotype: HU 8792, Humboldt-Universität, Berlin, a stuffed skin in poor condition, according to Irwin 1970).

*Sciaena nebulosa* Mitchill 1815:408, pl. 3, New York.

*Menticirrhus focaliger* Ginsburg 1952:97, St. Joseph Bay, Fla. (holotype: USNM 144101, 104 mm SL).

*Menticirrhus atlanticus* McFarland 1963:98, Mustang Island, Texas (nomen nudum).

#### *Larimus* GROUP

*Diagnosis*.—Swim bladder carrot-shaped, with or without a pair of small tubelike diverticula at the anterior end (*Sciaena* pattern, Fig. 5E, F). Sagitta with broader anterior portion and narrower posterior portion, the expanded part of the ostium not reaching to anterior margins (*Larimus* pattern, Fig. 20A, B). Snout with five marginal pores and no upper pores (Fig. 31B), lower jaw with four pores and no barbel (Fig. 34B). *Larimus* is the only genus in this group.

#### *Larimus* Cuvier

*Larimus* Cuvier 1830:145 (type-species: *Larimus breviceps* Cuvier, by monotypy).

*Amblyscion* Gill 1864b:165 (type-species: *Amblyscion argenteus* Gill, by monotypy).

*Monosira* Poey 1881:326 (type-species: *Monosira stahli* Poey, by monotypy).

*Diagnosis*.—Body short and robust, compressed; dorsal profile slightly elevated, ventral profile convex. Head with prominent cavernous canals; snout short. Mouth large and oblique, teeth small, conical in one to two rows on both jaws. Gill rakers, long and slender, more than 25

on first gill arch. Vertebrae 11 + 14 = 25. Other diagnostic characters as in the *Larimus* group. Tropical eastern Pacific and western Atlantic, about seven species. Two western Atlantic species: *L. breviceps* and *L. fasciatus*. Inhabits estuarine and inshore open waters with sandy and muddy bottoms.

#### *Larimus breviceps* Cuvier

*Larimus breviceps* Cuvier 1830:146, pl. 140, Saint Dominique and Brazil, (syntypes: MNHN 7578, 139 mm SL, St. Dominique; MNHN 7636, 156 mm SL, Brazil).

*Monosira stahli* Poey 1881:326, pl. 6, Puerto Rico (holotype: 190 mm long, not located).

#### *Larimus fasciatus* Holbrook

*Larimus faciatus* Holbrook 1855:153, pl. 22, fig. 1, Charleston (type presumably lost).

#### *Nebris* GROUP

*Diagnosis*.—Swim bladder with carrot-shaped main chamber and a pair of diverticula, which almost extend to the tapering end of the main chamber then loop back (Fig. 8) reaching the septum transversum anteriorly (*Nebris* pattern). Sagitta oval, with a notched posterior margin, very thick (Fig. 21); ostium large, its expanded part not reaching to anterior margin; cauda J-shaped, with broad and deeply grooved distal end; snout with only two marginal pores, without upper pores; lower jaw with four minute pores and no barbel. One genus in this group: *Nebris*.

#### *Nebris* Cuvier

*Nebris* Cuvier 1830:149 (type-species: *Nebris microps* Cuvier, by monotypy).

*Cheironebris* Fowler 1944:179 (type-species: *Nebris occidentalis* Vaillant, by monotypy).

*Diagnosis*.—Body elongate, rounded in cross section, tapering posteriorly. Head extremely cavernous, interorbital space very broad, eye very small, more than 10 times in head. Mouth very large, oblique, nearly vertical; teeth small, conical in narrow bands on upper jaw, and two rows of small teeth in lower, the outer row slightly smaller than the inner. Gill rakers long and slender. Vertebrae 12 + 13 = 25. Other diagnostic characters as listed for the group. Tropical eastern Pacific and western Atlantic, two species. One species in the western Atlantic, *N. microps*. Found over sandy to muddy bottoms in coastal and estuarine waters.

#### *Nebris microps* Cuvier

*Nebris microps* Cuvier 1830:149, pl. 112, Surinam (type: in Berlin Museum, not examined).



## *Micropogonias* GROUP

*Diagnosis*.—Swim bladder carrot-shaped with a pair of tubelike diverticula extending anteriorly from the middle of sides to septum transversum. (*Micropogonias* pattern, Fig. 9.) Sagitta very heavy, irregular in shape (*Micropogonias* pattern, Fig. 26), the expanded portion of the ostium not reaching to anterior margin, the cauda oblique with an expanded distal end. Snout with five marginal pores and five to seven upper pores (Fig. 31D); lower jaw with five pores and three to five pairs of minute barbels (Fig. 32G). One genus in this group, *Micropogonias*.

### *Micropogonias* Bonaparte

*Micropogon* Cuvier 1830:213 (type-species: *Micropogon linaetus* Cuvier, in part = *Umbrina furnieri* Desmarest, see remarks; preoccupied by *Micropogon* Boie 1826: 977, Aves).

*Micropogonias* Bonaparte 1831, 52:170 (substitute name for *Micropogon*, therefore taking the same type-species, *M. lineatus* Cuvier in part = *U. furnieri* Desmarest, see remarks).

*Micropogonoides* Trewaves (1977) 33:271 (*lapsus calami*).

*Diagnosis*.—Body elongate, dorsal profile elevated, ventral profile nearly straight. Head conical, preopercular margin with 10 to 14 spines, 2 to 5 strong spines at the angle. Mouth inferior, teeth in villiform bands, outer row teeth in upper jaw slightly enlarged. Gill rakers short. Vertebrae 10 + 15 = 25. Other diagnostic characters as listed for the group. Tropical eastern Pacific and western Atlantic, about five species. Two species in the western Atlantic: *M. furnieri* and *M. undulatus*. Inhabits estuarine rivers and coastal waters with sandy to muddy bottom.

### *Micropogonias furnieri* (Desmarest)

*Umbrina furnieri* Desmarest 1823:182, pl. 17, fig. 3, Havana, Cuba (presumed holotype: MNHN 4968, 109 mm SL, see remarks).

*Micropogon lineatus* Cuvier 1830:215, pls. 119 and 138, in part, swim bladder (lectotype: MNHN 4968, 109 mm SL, Cuba; paralectotype: MNHN 7459, 159 mm SL, Montevideo, see remarks).

*Micropogon argenteus* Cuvier 1830:218, Surinam (holotype: RMNH 685, 300 mm SL, see remarks).

*Corvina crawfordi* Regan 1903:627, Montevideo (holotype: BMNH 1903.10.16.7, 210 mm SL, see remarks).

*Micropogon patagonensis* MacDonagh 1931:409, Richo de San Blas, Argentina (holotype: Museo de la Plata, no. 2.V.31.1, 465 mm SL, not examined, see remarks).

*Micropogon barretoi* MacDonagh 1934:70, Punta Piedras, Argentina (holotype: Museo de la Plata, no. 12.VII.33.15, 423 mm SL, not examined, see remarks).

*Ophioscion woodwardi* Fowler 1937:311, figure on p. 312, Haiti (holotype: ANSP 68257, 108 mm SL).

### *Micropogonias undulatus* (Linnaeus)

"*Perca marina*" Catesby 1743, "Croker," pl. 3, upper figure, Chesapeake Bay (pre-Linnaean and nonbinominal).

*Perca undulata* Linnaeus 1766:483, South Carolina (syntypes: the Linnaean Society of London no. 112, right side of a dried skin, 212 mm SL, and no. 113, left side of a dried skin, 241 mm SL).

*Sciaena croker* Lacepède 1803, 4:309, Carolina (type: presumably in MNHN, but not found).

*Bodianus costatus* Mitchill 1815:417, New York.

*Sciaena opercularis* Quoy and Gaimard 1824:347, baie de Rio de Janeiro (type: reported missing by Roux 1973, also see remarks).

*Micropogon lineatus* Cuvier 1830:215, in part (paralectotype: MNHN 7457, two specimens, 62.8 and 138 mm SL, New York; MNHN 7459, 273 mm SL, Montevideo, also see remarks).

*Remarks*.—The fish genus name *Micropogon* Cuvier 1830 is preoccupied by *Micropogon* Boie 1826, Aves. Although the bird genus name has only been used in synonymys in recent years, the fish genus name has gained wide and stable use since Cuvier 1830. C. G. Gruchy (NMC) and the author had looked into this matter and found the inherent nomenclatural and systematic problems of the bird genus and its family have not been solved. To avoid further complications, we decided to resume the valid substitute name *Micropogonias* (Bonaparte 1831) for fish genus.

Jordan (1917) designated *M. lineatus* Cuvier = *Perca undulatus* Linnaeus as type-species of *Micropogonias*. His reason was that Cuvier's (1830) description on p. 215 mentioned the New York specimens (MNHN 7457, *M. undulatus*) first. Cuvier's (1830) description of *M. lineatus* fits both *M. furnieri* and *M. undulatus*. The syntypes obtained from New York (MNHN 7457) by Milbert are apparently *M. undulatus* (there is also a specimen of *Leiostomus xanthurus*, 87.2 mm SL, in the same jar). The syntype from Cuba (MNHN 4968) was labeled as "type de *Umbrina furnieri* Desmarest," and the specimen illustrated on plate 119 appears to be *M. furnieri*. The oblique streaks of *M. undulatus* usually are not as distinct, particularly the area between the soft portion of dorsal fin and lateral line. MNHN 7459 from Montevideo contains two syntypes, of which the smaller specimen (159 mm SL) appears to be *M. furnieri* and the larger one (273 mm SL) appears to be *M. undulatus*. In this case, MNHN 4968 (109 mm SL) from Cuba is selected as the lectotype of *M. lineatus* and it is likely to be the holotype of *Umbrina furnieri*. Therefore, the type-species of *Micropogonias* is *M. furnieri* (Desmarest).

Some morphometric and meristic characters of the presumed holotype, MNHN 4968, follow:

*Morphometric characters (in mm)*: TL 110; SL 109; snout to anal fin origin 72.6, to dorsal fin origin 40.5, to pectoral fin origin 34.7, to pelvic fin origin 36.0; maximum depth 28.2; head length 33.6; snout length 9.7;

eye diameter 8.5; interorbital width 8.1; pectoral fin lengths 19.5 and 22.5; pelvic fin lengths 16.0 and 19.2; length of anterior (spinous) portion of dorsal fin base 20.2; length of posterior (soft) portion of dorsal fin base 42.7; length of anal fin base 12.5; length of second anal fin spine 13.4; depth of caudal peduncle 9.2.

**Meristic characters:** D X+I, 27; A, II, 8; pectoral rays 18 and 17; lateral gill rakers on the first right gill arch 8 (upper arm) + 15 (lower arm); medial (or inner) gill rakers on the first right gill arch 3 (upper arm) + 10 (lower arm); pored lateral-line scales, left side 52, right side 48; transverse lateral-line scales, from posterior (soft) dorsal fin origin to lateral line 9 (vertical series) and 12 (oblique series), from lateral line to anal fin origin 12 (vertical series) and 15 (oblique series).

The distinguishing characters of the two species of *Micropogonias* (see also "Key to the species of *Micropogonias*") used here are valid only for adult specimens. The sagitta morphology of *M. furnieri* from northern Brazil (Fig. 26A-C) is distinct from that of *M. undulatus* from Chesapeake Bay (Fig. 26D-F). But the sagittae of specimens which key out as *M. undulatus* from the Bay of Campeche, Mexico, are hardly distinguishable from specimens keyed out as *M. furnieri* from the Caribbean coast of Colombia (Fig. 39). Other nominal species of this genus were discussed by Jordan and Evermann (1898), Devincenzi (1924), MacDonagh (1934), and Roux (1973). Among them *Corvina crawfordi* Regan, *Micropogon patagonensis* McDonough, and *M. barretoii* McDonough were described from the mouth of Rio de La Plata or south; morphometric characters were mainly used by the authors for diagnoses. Based on observations of *M. undulatus* from Chesapeake Bay region, Virginia (Chao 1976), such morphological variation is frequent and not a valid basis for species diagnoses. The

true identity of *M. argenteus* Cuvier and *Sciaena opercularis* Quoy and Gaimard is uncertain at present.

Sixteen morphometric and meristic characters were compared in 22 specimens of southern specimens (*M. furnieri*) from Colombia to Uruguay and 24 specimens of the northern species (*M. undulatus*) from Chesapeake Bay to Bay of Campeche. The result of discriminate function analyses indicated one of the Campeche specimens (NMC 76-522, 116 mm SL) was intermediate. All northern specimens can be readily separated from southern ones by color pattern and number of scales (6 to 7 in *M. furnieri* and 8 to 9 in *M. undulatus*) in a vertical series from dorsal fin origin to lateral line (also see section on "Key to the species of *Micropogonias*"). Whether they are species or subspecies of one species requires further study. I suggest that the northern species (or form) *M. undulatus* is present on Atlantic and Gulf of Mexico coasts of U.S.A., south to the Bay of Campeche, Mexico. The southern species (or form) *M. furnieri* is present in the Antilles and on South American coasts.

### Sciaenops GROUP

**Diagnosis.**—Swim bladder carrot-shaped with a pair of short tubelike diverticula at the anterior lateral corners of the swim bladder (*Sciaenops* pattern, Fig. 11). In large specimens, a pair of "saclike" projections which consist of numerous labyrinth chambers (Fig. 11C, D) are present on the dorsal surface of the swim bladder; a pit is present between the third and fourth pleural ribs on both sides of the body wall to receive the paired "saclike" projections. Sagitta rectangular, the expanded portion of the ostium not reaching to anterior margin (*Larimus* pattern, Fig. 20). Snout with five upper and five marginal pores (Fig. 33F); lower jaw with five pores and no barbel (Fig. 34F). *Sciaenops* is the only genus in this group.

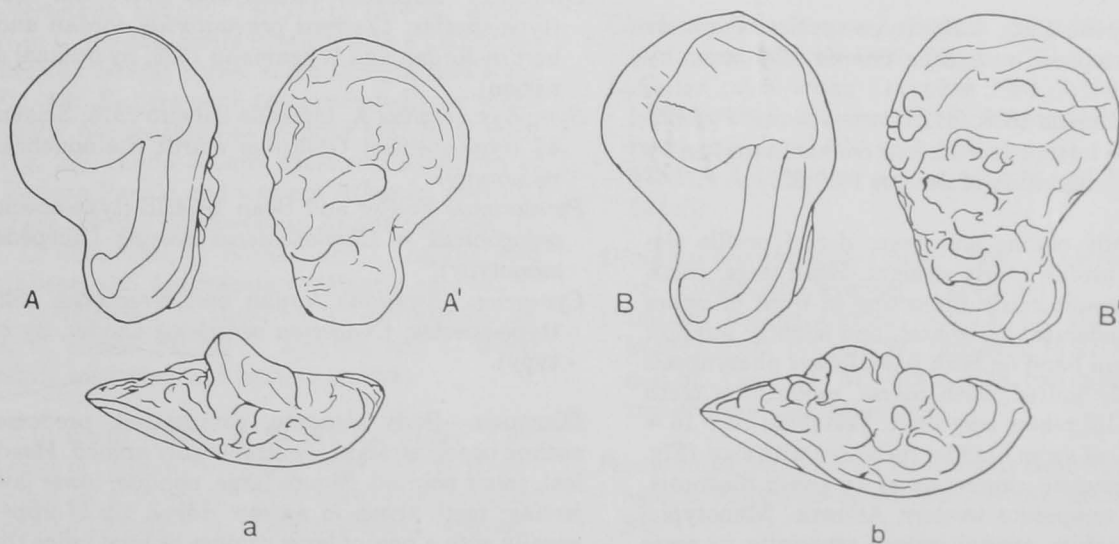


Figure 39.—Sagittae of *Micropogonias*. A, A', a: *M. undulatus*, 205 mm TL, Bay of Campeche, Mexico; B, B', b: *M. furnieri*, 240 mm TL, coast of Caribbean Sea, Colombia. A, B: inner surface; A', B': outer surface; a, b: lateral view.

*Sciaenops* Gill 1864a:30 (type-species: *Perca ocellata* Linnaeus, by monotypy).

*Diagnosis*.—Body elongate, robust, back slightly elevated, ventral surface flat. Head long and low; snout long. Mouth inferior; teeth villiform in bands, those of outer row in upper jaw and inner row in lower jaw slightly enlarged. Gill rakers short. Vertebrae 10 + 15 = 25. Other diagnostic characters as listed for the group. Subtropical northwestern Atlantic. Monotypic: *S. ocellata*. Inhabits estuarine, surf zone and inshore waters with sandy bottoms.

#### *Sciaenops ocellata* (Linnaeus)

*Perca ocellata* Linnaeus 1766:483, South Carolina (syn-types: Linnean Society of London, no. 106, one dried right side skin, 394 mm TL, and no. 107, one dried right side skin, 399 mm TL).

*Lutjanus triangulum* Lacepède 1803, 4:181, figure in vol. 3, pl. 24, fig. 3 (type locality: Sumatra, an East Indian Island, is apparently an error; type specimen: presumably in MNHN but not found).

*Sciaena imberbis* Mitchill 1815:411, New York.

#### Pogonias GROUP

*Diagnosis*.—Swim bladder with very complicated diverticula along the side of main chamber (Fig. 10). Sagitta semicircular, the "tadpole-shaped" sulcus not reaching to the margins (Fig. 19A). Snout with five upper pores and five marginal pores (Fig. 31D); lower jaw with five pores and 12 to 13 pairs of small barbels (Fig. 32G). Monotypic: *Pogonias*.

#### *Pogonias* Lacepède

*Pogonias* Lacepède 1802, 3:137 (type-species: *Pogonias fasciatus* Lacepède = *Labrus cromis* Linnaeus, by monotypy).

*Pogonathus* Lacepède 1803, 5:120 (type-species: *Pogonathus courbina* Lacepède = *Labrus cromis* Linnaeus, by subsequent designation of Jordan 1917:65).

*Diagnosis*.—Body oblong and deep; dorsal profile elevated, ventral profile nearly straight. Head large; snout conical, not conspicuously projecting in front of upper jaw. Mouth moderate, horizontal, and slightly inferior; teeth in villiform band on both jaws. Lower pharyngeals very large, fully united, with coarse, molariform teeth (Fig. 40A, a). Gill rakers very short. Vertebrae 10 + 14 = 24. Complexity of swim bladder increases with size (Fig. 10); other diagnostic characters as in group diagnosis. Tropical and temperate western Atlantic. Monotypic: *P. cromis*. Inhabits coastal waters especially in areas with large river runoffs over sandy and sandy-mud bottoms.

*Labrus cromis* Linnaeus 1766:479, Carolina.

*Pogonias fasciatus* Lacepède 1802, 3:137, figure in vol. 2, pl. 16, fig. 2, Brazil (syntypes: MNHN 7461, one dried stuffed specimen, 103 mm TL; MNHN 7460, one dried stuffed specimen, 181 mm SL).

*Pogonathus courbina* Lacepède 1803, 5:120, Reio de La Plata (from the manuscript of Commerson).

*Mugil grunniens* Mitchill 1814:15, New York.

*Mugil gigas* Mitchill 1814:16, New York.

*Sciaena fusca* Mitchill 1815:409, New York.

#### Cynoscion GROUP

*Diagnosis*.—Swim bladder with a pair of well-developed horns (Fig. 12) from anterolateral corners of main chamber, tapering forward to the back of skull. Sagitta elongate oval with smooth or notched margins. Snout with only two (or no) marginal pores and without upper pores (Fig. 31A); lower jaw without obvious pores or barbels (Fig. 32A). Four genera in this group: *Cynoscion*, *Isopisthus*, *Macrodon*, and a South American freshwater genus, *Plagioscion* (see section on "Freshwater Sciaenidae of America").

#### *Cynoscion* Gill

*Cestreus* Gronovius (Gray) 1854:49 (type-species: *Cestreus carolinensis*, by monotypy, preoccupied by *Cestreus* McClelland 1842).

*Cynoscion* Gill 1872b:81 (type-species: *Otolithus regalis* Cuvier = *Johnius regalis* Bloch and Schneider, by original designation).

*Apsudobranthus* Gill 1863:18 (type-species: *Otolithus two-roe* Cuvier = *Cheilodipterus acoupa* Lacepède 1800, by original designation).

*Archoscion* Gill 1863:18 (type-species: *Otolithus analis* Jenyns 1842, by original designation).

*Cynoscion* (*Buccone*) Jordan and Evermann 1896:394 (type-species: *Cestreus praedatorius* Jordan and Gilbert in Jordan and Eigenmann 1889, by original designation).

*Symphysoglyphus* A. Miranda Ribeiro 1915, Sciaenidae: 43 (type-species: *Otolithus bairdi* Steindachner, by monotypy).

*Paralarimus* Fowler and Bean 1924:18 (type-species: *P. patagonicus* = *Cheilodipterus acoupa* Lacepède, by monotypy).

*Cynoscion* (*Ericcion*) Jordan and Evermann 1927:506 (type-species: *Cynoscion nebulosus* Cuvier, by monotypy).

*Diagnosis*.—Body elongate, compressed, predorsal fin outline nearly straight, ventral evenly arched. Head conical, snout pointed. Mouth large, oblique, lower jaw projecting; teeth sharp in narrow ridges, tip of upper jaw usually with a pair of large canines at least twice the size of other teeth (no obviously enlarged teeth in *C. steindachneri*), tapering from base to tip. Preopercular mar-

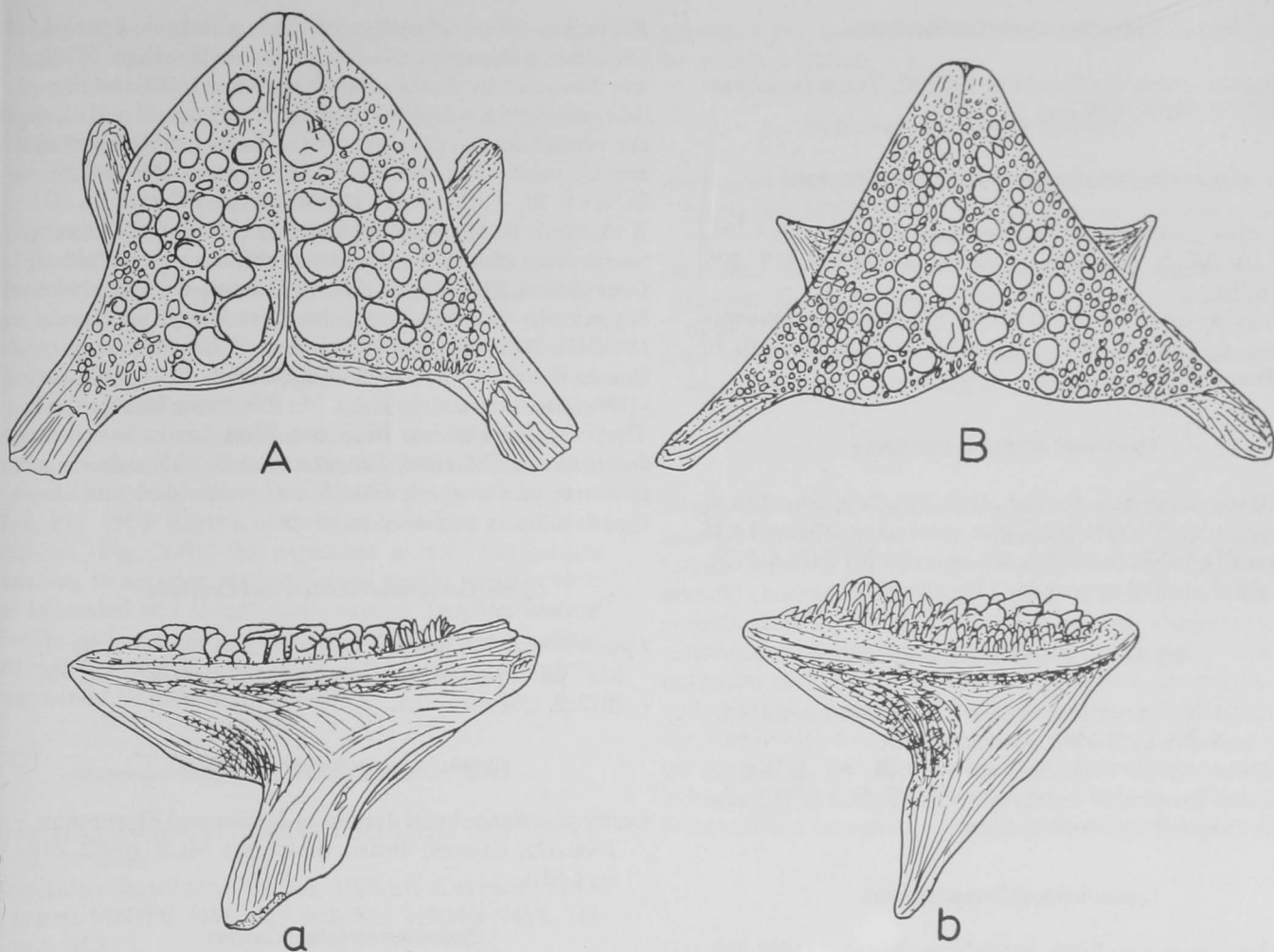


Figure 40.—United lower pharyngeal teeth of *Pogonias cromis* (A, a) and *Aplodinotus grunniens* (B, b). A, B: dorsal view (anterior end to the top of the figure); a, b: lateral view (anterior end to the left of the figure).

gin membranous or ciliate. Gill rakers short to long and slender. Vertebrae usually  $13(12)+12(13)=25$ , except  $15+12=27$  in *C. nothus*. Swim bladder with a pair of anteriorly directed lateral horns, some straight and some curved (Fig. 13). Sagitta oval, the expanded part of the ostium usually not reaching to anterior margin in most species (Fig. 23); cauda usually short and expanded at the end. Eastern Pacific and western Atlantic, about 23 species. There are four northwestern Atlantic species: *C. arenarius*, *C. nebulosus*, *C. nothus*, and *C. regalis*; and eight Caribbean and southwestern Atlantic species: *C. acoupa*, *C. jamaicensis*, *C. leiarchus*, *C. microlepidotus*, *C. similis*, *C. steindachneri*, *C. striatus*, and *C. virescens*. Inhabits estuarine and inshore waters.

**Remarks.**—In Klein (1749), p. 23 and 24, under “Cestres,” species of “Mugil” were described and “Sciaena” was described in a footnote. Type-species of *Sciaena*: *Mugil cephalus* Linnaeus = “Cestres dorso repando” Klein, was subsequently designated by Walbaum (1793), but was invalid because of Linnaeus’ use of *Sciaena* in 1758.

#### *Cynoscion acoupa* (Lacepède)

*Cheilodipterus acoupa* Lacepède 1800, 2:540, Cayenne (holotype: MNHN 5502, 262 mm SL, Surinam).

*Lutjanus cayennensis* Lacepède 1803, 4:196 (syntypes: MNHN 5502, 262 mm SL, Surinam; MNHN A.5617, two specimens, 522 and 567 mm SL, Martinique; MNHN A.4562, two specimens, 278 and 288 mm SL, Brazil).

*Otolithus rhomboidalis* Cuvier 1829:173, Cayenne (based on “Lutjan de Cayenne,” Lacepède).

*Otolithus toe-roë* Cuvier 1830:72, pl. 103 (syntypes: MNHN 5500, 175 mm SL, Surinam; MNHN 4616, 347 mm SL, Cayenne; MNHN A.4518, two specimens, 493 and 485 mm SL, Cayenne).

*Paralarimus patagonicus* Fowler and Bean 1924:18, Patagonia, Argentina (holotype: USNM 83222, 136 mm SL).

*Cynoscion maracaiboensis* Schultz 1949:160, fig. 20, Maracaibo, Venezuela (holotype: USNM 12742, 251 mm SL).

*Cynoscion arenarius* Ginsburg

*Cynoscion arenarius* Ginsburg 1929:83, Texas (holotype: USNM 89385, 245 mm SL).

*Cynoscion jamaicensis* (Vaillant and Bocourt)

*Otolithus jamaicensis* Vaillant and Bocourt 1915:156, pl. 6, fig. 1, Jamaica (holotype: MNHN A.557, 205 mm SL).

*Archiscion petranus* A. Miranda Ribeiro 1915, Sciaenidae: 42, Brazil (type: not located and not listed in P. Miranda Ribeiro 1953).

*Cynoscion leiarchus* (Cuvier)

*Otolithus leiarchus* Cuvier 1830:78, Cayenne, Brazil (syntypes: MNHN 5503, two specimens, 152 and 234 mm SL; MNHN A.2690, 187 mm SL; MNHN A.5422, a dried stuffed specimen, 112 mm SL).

*Cynoscion microlepidotus* (Cuvier)

*Otolithus microlepidotus* Cuvier 1830:79, Surinam (type: presumably in Berlin, not examined).

*Otolithus bairdi* Steindachner 1879:40, pl. 1, fig. 2, Santos (presumed holotype: NHMV 51130, 152 mm SL, donated by Steindachner).

*Cynoscion nebulosus* (Cuvier)

*Labrus squetaegue* var. *maculatus* Mitchill 1815:398, New York (not *Labrus maculatus* Bloch 1793).

*Otolithus nebulosus* Cuvier 1830:79, locality unknown (holotype: MNHN 7527, 233 mm SL).

*Otolithus carolinensis* Valenciennes 1833:475, South Carolina (holotype: MNHN 7507, 335 mm SL).

*Otolithus drummondi* Richardson 1836:70, New Orleans.

*Cynoscion nothus* (Holbrook)

*Otolithus nothus* Holbrook 1855:134, pl. 19, fig. 1, South Carolina (type: presumably lost).

*Cynoscion regalis* (Bloch and Schneider)

*Johnius regalis* Bloch and Schneider 1801:75, New York.

*Roccus comes* Mitchill 1814:26, New York.

*Labrus squetaegue* Mitchill 1815:396, pl. 2, fig. 1, New York.

*Cestreus carolinensis* Gronovius (Gray) 1854:49 (holotype: BMNH 1853.11.12.42, a dried skin, 344 mm TL, not of *Otolithus carolinensis* Valenciennes).

*Otolithus thalassinus* Holbrook 1855:132, pl. 18, fig. 2, Charleston, S.C.

*Otolithus obliquatus* Valenciennes in Sauvage 1879:209, Martinique (lectotype: MNHN 7632, 209 mm SL, also see remarks).

*Remarks.*—The identity of the nominal species, *Otolithus obliquatus* (Valenciennes in Sauvage 1879), was discussed by Jordan and Evermann (1898) and Randall and Cervigón (1968). The higher soft dorsal and anal ray counts in two type-specimens (selected by Randall and Cervigón 1968, MNHN 7632: lectotype 209 mm SL, D. X+I, 30, A. II, 12 and paralectotype 182 mm SL, D. X+I, 28, A. II, 11) were also noted in this study. The vertebrae total 25 in both specimens and the soft portion of their dorsal fins is covered with small cycloid scales beyond the basal half of the fins. These specimens (MNHN 7632) and two specimens of *Leiostomus xanthurus* (MNHN 7600, 106 and 126 mm SL) of Cuvier (1830:143) were collected by M. Plée from Martinique. They are only known from the West Indies by these descriptions. Therefore, I suggest that *O. obliquatus* is a synonym of *C. regalis* (Bloch and Schneider) and the type-locality is probably an error.

*Cynoscion similis* Randall and Cervigón

*Cynoscion similis* Randall and Cervigón 1968:170, fig. 2, Isla de Margarita, Venezuela (holotype: USNM 201382, 284 mm SL).

*Cynoscion steindachneri* (Jordan)

*Cestreus steindachneri* Jordan in Jordan and Eigenmann 1889:372, Curuçá, Brazil (holotype: MCZ 10922, 318 mm SL).

*Cynoscion striatus* (Cuvier)

"Guatucupa" Marcgrave 1648 (translated by Taunay 1941):177, Brazil (nonbinominal).

*Otolithus striatus* Cuvier 1829:173 (after Marcgrave).

*Otolithus guatucupa* Cuvier 1830:75, Montevideo (syntypes: MNHN 7517, two specimens, 358 and 366 mm SL).

*Cynoscion virescens* (Cuvier)

*Otolithus virescens* Cuvier 1830:72, Surinam (type: presumably in Berlin Museum, not examined).

*Otolithus microps* Steindachner 1879:38 (type: presumably in NHMV, but not found).

**Macrodon Schinz**

*Ancylodon* Bosc 1816:497 (type-species: "Lonchures" Schneider = *Lonchurus ancylodon* Bloch and Schneider, by original designation; preoccupied by *Ancylodon* Illiger 1811, Mammalia).

"Ancylodons" Cuvier 1817:299, vernacular name.

*Ancylodon* Oken 1817:1182 (type-species: *Lonchurus ancylodon* Bloch and Schneider, by original designation; not *Ancylodon* Illiger).

*Macrodon* Schinz 1822:482 (substitute name for *Ancylodon* Bosc, therefore taking the same type-species: *L. ancylodon* Bloch and Schneider).

*Nomalus* Gistel 1848, p. VIII (substitute name for *Ancylodon* Bosc, therefore taking the same type-species: *L. ancylodon* Bloch and Schneider).

*Sagenichthys* Berg 1895:52 (substitute name for *Ancylodon* Bosc, therefore taking the same type-species: *L. ancylodon* Bloch and Schneider).

**Diagnosis.**—Body elongate, moderately compressed; dorsal profile slightly arched, ventral profile evenly arched. Head pointed, compressed. Mouth large, oblique; lower jaw projecting in front of upper jaw; teeth in narrow ridge, upper jaw with a pair of very large arrow-headed canines (Fig. 37A); lower jaw with several enlarged arrow-headed canines at the tip, exposed externally when mouth closed. Preopercular margin membranous. Gill rakers slender. Vertebrae 13+12=25. Swim bladder with a pair of anteriorly directed lateral horns (*Cynoscion* pattern, Fig. 12C). Sagitta oval, lateral margins concave or notched (Fig. 25B); the expanded part of the ostium reaching to anterior margin; cauda nearly straight with an expanded end (*Macrodon* pattern). Tropical eastern Pacific and western Atlantic, two species. One western Atlantic species: *M. ancylodon*. Inhabits inshore waters, over sandy to muddy bottoms.

#### *Macrodon ancylodon* (Bloch and Schneider)

*Lonchurus ancylodon* Bloch and Schneider 1801:102, pl. 25, Surinam.

*Ancylodon jaculidens* Cuvier 1830:81, Cayenne (syntypes: MNHN 7451, 212 mm SL; MNHN 7454, 144 mm SL).

*Ancylodon atricauda* Günther 1880:12, Rio de La Plata (type: "5 inches," not found in BMNH).

*Stellifer mecatoris* Delsman 1941:71, fig. 10, Mouth of Amazon River (type: not seen).

#### *Isopisthus* Gill

*Isopisthus* Gill 1863:18 (type-species: *Ancylodon parvipinnis* Cuvier, by monotypy).

*Parapesichthys* Bleeker 1876 (from Kaup's manuscript 1862):335 (type-species: *Isopisthus parvipinnis* Gill = *Ancylodon parvipinnis* Cuvier, by monotypy).

**Diagnosis.**—Body elongate, compressed, dorsal profile nearly straight, ventral profile evenly arched. Head pointed, rather compressed. Mouth large, oblique, lower jaw projecting; teeth in narrow band, tip of upper jaw with a pair of enlarged caninelike teeth. Preopercular margin membranous with fine cilia. Anterior (spinous) and posterior (soft) portions of dorsal fin well separated by a gap. Gill rakers moderately long. Vertebrae 11+14=25. Swim bladder with a pair of tubelike anteriorly directed lateral horns (*Cynoscion* pattern, Fig. 12B). Sagitta nearly oval, the expanded part of the ostium reaching to anterior margin (Fig. 25A); cauda oblique, slightly bent at the end. Tropical eastern Pacific and western Atlantic, two species. One western Atlantic

species: *I. parvipinnis*. Inhabits inshore waters over sandy to muddy bottoms.

#### *Isopisthus parvipinnis* (Cuvier)

*Ancylodon parvipinnis* Cuvier 1830:84, pl. 105, Cayenne (syntypes: MNHN 745, three specimens, 100-140 mm SL).

*Isopisthus affinis* Steindachner 1879:43, pl. 2, fig. 2, Port Alegre, Brazil (syntypes: NHMV 15190, two specimens, 168 and 172 mm SL).

*Isopisthus harroweri* Fowler 1916:402, fig. 3, Colon, Panama (holotype: ANSP 45236, 145 mm SL).

#### *Lonchurus* GROUP

**Diagnosis.**—Swim bladder carrot-shaped with a pair of anterior diverticula, each diverticulum with a short anteriorly directed branch and a long posteriorly directed branch (*Lonchurus* pattern, Fig. 14); sometimes the swim bladder is reduced in size. Sagitta oval elongate to rectangular, the "tadpole-shaped" sulcus elongate; the expanded part of the ostium reaching to anterior margin and the cauda long, J-shaped (*Lonchurus* pattern, Fig. 24). Snout with five marginal pores and three to five upper pores (Fig. 31C, D); lower jaw with two to many pairs of barbels (Fig. 32F, H). Two genera of western Atlantic Sciaenidae in this group: *Lonchurus* and *Paralonchurus*.

#### *Lonchurus* Bloch

*Lonchurus* Bloch 1793, pt. 7:143 (type-species: *Lonchurus barbatus* Bloch, by monotypy).

*Lonchiurus* Bloch (French translation in Laveau), 1797, pt. 10:119 (invalid emendation of *Lonchurus*).

**Diagnosis.**—Body long and rounded; dorsal profile slightly arched, ventral profile nearly flat. Pectoral fin very long. Head conical, low and broader than body; snout projecting. Mouth inferior; teeth conical, in bands. Gill rakers short. Vertebrae 11+18=29. Swim bladder much reduced in size, but retaining typical *Lonchurus* pattern (Fig. 14) with anterior branches of diverticula more prominent, posterior end of the main chamber tapering into a fine point (Fig. 14A). Drumming muscles thin, present only in male. Snout with five upper pores; lower jaw with four pores and two barbels (Fig. 32F), longer than eye diameter. Monotypic: *L. lanceolatus*. Found over sandy and muddy bottom along the coast and in estuarine waters.

#### *Lonchurus lanceolatus* (Bloch)

*Perca lanceolata* Bloch 1788:383, fig. 3, India (= West Indies).

*Lonchurus barbatus* Bloch 1793:144, pl. 360, fig. 1, Surinam.

*Lonchurus depressus* Bloch and Schneider 1801:102, Surinam.

## *Paralonchurus* Bocourt

*Paralonchurus* Bocourt 1869:21 (type-species: *Paralonchurus petersi* Bocourt, by monotypy).

*Polycirrhus* Bocourt 1869:22 (type-species: *Polycirrhus dumerili* Bocourt by monotypy, not *Polycirrhus* Grube 1850, Annelida).

*Polyclemus* Berg 1895:54 (substitute name for *Polycirrhus* Bocourt, non-Grube, therefore taking the type-species: *P. dumerili*).

*Paralonchurus* (*Zonoscion*) Jordan and Evermann 1896:401 (type-species: *Polycirrhus rathbuni* Jordan and Bollman 1889, by monotypy).

*Paralonchurus* (*Zaclemus*) Gilbert in Jordan and Evermann 1896:402 (type-species: *Paralonchurus goodei* Gilbert MS, by monotypy).

**Diagnosis.**—Body elongate, slightly rounded; dorsal profile slightly elevated, ventral profile nearly flat. Pectoral fin long or short. Head broad, nape slightly convex; snout projecting. Mouth small and inferior, teeth in conical bands. Gill rakers short. Total vertebrae 25 or 29 (see "Key to the species of *Paralonchurus*"). Swim bladder well developed (Fig. 14B, C). Drumming muscles present only in male. Sagitta elongate, the expanded part of the ostium reaching to anterior margin; cauda J-shaped (Fig. 24B, C). Snout with three upper pores (Fig. 31C); lower jaw with 12 to 16 pairs of minute barbels, anterior 3 pairs form a tuft at the symphysis of lower jaw, other barbels along the rami of lower jaw (Fig. 32H). Tropical eastern Pacific and western Atlantic, about six species. Two species from the western Atlantic in this genus: *P. brasiliensis* and *P. elegans*. Inhabits estuarine and inshore waters with sandy to muddy bottoms.

### *Paralonchurus brasiliensis* (Steindachner)

*Genyanemus brasiliensis* Steindachner 1875:476, Para, Santos (type: presumably in NHMV, but not found).

*Micropogon ornatus* Günther 1880:13, pl. 7, fig. A, Rio de La Plata (holotype: BMNH 1879.5.14.289, 175 mm SL).

*Paralonchurus rathbuni* Puyo 1949:215, fig. 114 (not *Polycirrhus rathbuni* Jordan and Bollman 1889:162).

### *Paralonchurus elegans* Boeseman

*Paralonchurus elegans* Boeseman 1948:3, Surinam (holotype: RMNH 390, 200 mm SL).

**Remarks.**—*Paralonchurus elegans* and *Lonchurus lanceolatus* have very similar sagittae (Fig. 24) and both have a long black pectoral fin. *Paralonchurus brasiliensis* has a total vertebrae count of 29 as in *L. lanceolatus*. *Paralonchurus brasiliensis* and *P. elegans* both have well-developed swim bladders and many minute barbels on the chin. The interrelationship of these three species cannot be determined without comparative material of the eastern Pacific species of this group. The reduced size of the swim bladder in *L. lanceolatus* (Fig. 14A) has been

viewed as an important diagnostic character (Günther 1860). *Paralonchurus brasiliensis* has been considered to belong in a separate genus, *Polyclemus* as by Berg (1895). The type-species of *Paralonchurus* (*P. petersi*) and *Polyclemus* (*P. dumerili*) are eastern Pacific species. Study of these species will be necessary to clarify the generic status of these fishes.

## *Stellifer* GROUP

**Diagnosis.**—Swim bladder separated into two chambers by a constriction; the anterior chamber yoke-shaped located in front of the septum transversum and the posterior one simple carrot-shaped (*Stellifer* pattern, Fig. 15). A pair of diverticula sometimes present on the anterior chamber posterolaterally. Otoliths with both sagitta and lapillus enlarged (*Stellifer* pattern, Fig. 27). Snout with five marginal pores and three to five upper pores (Fig. 31C, D); lower jaw with four to six pores and without barbels (Fig. 32B-D). Four genera of western Atlantic sciaenids in this group: *Bairdiella*, *Odontoscion*, *Ophioscion*, and *Stellifer*. At present, the generic boundaries of *Bairdiella* and *Odontoscion* are not clear, especially when the eastern Pacific species and genera of this group are considered (Wintersteen and Chao, see footnote 3).

### *Bairdiella* Gill

*Bairdiella* Gill 1862a:33 (nomen nudum).

*Bairdiella* Gill 1862b:83 (type-species: *Bodianus argyroleucus* Mitchell 1815 = *Dipterodon chrysourus* Lacepède 1803, by original designation).

*Corvula* Jordan and Eigenmann 1889:377 (type-species: *Johnius batabanus* Poey, by original designation, see remarks).

*Vacuqua* Jordan and Evermann 1927:506 (type-species: *Corvula macrops* Steindachner, by original designation, see remarks).

**Diagnosis.**—Body oblong, compressed; dorsal profile slightly elevated, ventral profile nearly straight. Head with or without strong spines at angle of preopercular margin. Mouth terminal, slightly oblique; upper jaw teeth conical in a narrow band, outer row moderately enlarged; lower jaw teeth on a narrow ridge, median row slightly enlarged. Gill rakers moderately long and stiff. Vertebrae 12+13 or 11+14=25. Swim bladder in two chambers, without diverticula on anterior chamber (Fig. 15A). Sagitta triangular; ostium incomplete; lapillus more than half the size of sagitta (Fig. 27C). Snout with five marginal and three upper pores; lower jaw with four to six pores, the median pair of pores in six-pored form very closely set (Fig. 32B-D). Tropical eastern Pacific and western Atlantic, about eight species. Four species of western Atlantic Sciaenidae included here: *B. batabana*, *B. chrysourea*, *B. ronchus*, and *B. sanctaeluciae* (also see remarks). Inhabit inshore waters, estuaries, and coral reefs over sandy to muddy bottom.

*Remarks*.—The genera *Corvula* Jordan and Eigenman 1889, and *Vacuoa* Jordan and Evermann 1927 are listed under *Bairdiella* for the convenience of the present study. *Bairdiella batabana* and *B. sanctaeluciae* differ from *B. chrysoira* and *B. ronchus* by lack of strong spines (or serrations) at the preopercular margin and the vertebral arrangement is 12+13 instead of 11+14. These characters are diagnostic within the suprageneric group *Stellifer*. Therefore, *B. batabana* and *B. sanctaeluciae* may be recognized as a separate genus (or subgenus) from other *Bairdiella* species. Jordan and Evermann (1927) distinguished the eastern Pacific sciaenid fish *Corvina macrops* Steindachner, from *Johnius batabanus* Poey by its deeper, symmetrical body and the silvery coloration of *Bairdiella* and related species. These characters are not diagnostic within the genus *Bairdiella*. Study of East Pacific *Bairdiella* and related species will be necessary to clarify the generic status of *Bairdiella* (see footnotes 3 and 4).

#### *Bairdiella batabana* (Poey)

*Johnius batabanus* Poey 1860, 2:184, Batabano, Cuba (holotype: MCZ 21957, 189 mm SL).

*Corvula sialis* Jordan and Eigenmann 1889:379, Key West, Fla. (holotype: USNM 26575, 132 mm SL).

#### *Bairdiella chrysoira* (Lacepède)

*Perca punctata* Linnaeus 1766:482, South Carolina (preoccupied by *Perca punctatus* Linnaeus 1758:291, = *Bodianus fulvus punctatus*; syntypes?: Linnean Society of London, no. 108, a left side dried skin, 144 mm TL, and no. 109, a left side dried skin, 153 mm TL).

*Dipterodon chrysoirus* Lacepède 1803, 4:166, South Carolina (type: presumably in MNHN, but not found).

*Bodianus argyroleucus* Mitchill 1815:417, pl. 6, fig. 9, New York.

*Bodianus exiguus* Mitchill 1815:419, New York.

*Bodianus pallidus* Mitchill 1815:420, New York.

*Homoprion xanthurus* Holbrook 1855:170, pl. 24, fig. 2, South Carolina (not *Leiostomus xanthurus* Lacepède).

#### *Bairdiella ronchus* (Cuvier)

*Corvina ronchus* Cuvier 1830:107 (syntypes: MNHN 95, two specimens, 123 and 149 mm SL, St. Dominique; MNHN 5345, two specimens, 144 and 156 mm SL, Surinam; MNHN 5345, a dried stuffed specimen, 247 mm SL, Maracaibo?).

*Corvina subaequalis* Poey 1875:58, Cuba (holotype: 245 mm TL, not located, also see Robins 1964).

*Sciaena bedoti* Regan 1905:391, pl. 6, fig. 1, Cuba (syntypes: BMNH 1905.3.18.2, 155 mm SL; Museum d'Histoire Naturelle, Geneve 678.1, 222 mm TL, also see Robins 1964).

*Bairdiella verae-crucis* Jordan and Dickerson 1908:17, fig. 1, Vera Cruz (holotype: USNM 61676, 194 mm SL).

*Corvina fulgens* Vaillant and Bocourt 1915:164, pl. 6, fig.

2, U.S.A. (syntypes: MNHN A.975, two specimens, 149 and 150 mm SL).

#### *Bairdiella sanctaeluciae* (Jordan)

*Corvula sanctaeluciae* Jordan 1889:649, Port Castries, St. Lucia (holotype: USNM 4173, 105 mm SL).

#### *Odontoscion* Gill

*Odontoscion* Gill 1863:18 (type-species: *Corvina dentex* Cuvier, by original designation).

*Diagnosis*.—Body oblong, compressed; profile evenly arched. Head conical; snout short, blunt; eye large. Preopercular margin smooth without strong spines. Mouth large, terminal, slightly oblique; enlarged conical teeth in a widely spaced row on both jaws, lower jaw with some tiny teeth outside the large ones, and two larger canine-like teeth at the tip (Fig. 37C). Gill rakers relatively long. Vertebrae 12+12=25. Swim bladder with two chambers, anterior one yoke-shaped in front of septum transversum and posterior one carrot-shaped, without diverticula (Fig. 15A). Sagitta and lapillus both enlarged, only a small oval-shaped ostium left on the sulcus (Fig. 27D). Snout with five marginal pores and three upper pores (Fig. 31C); lower jaw with four pores and no barbel (Fig. 34C). Tropical eastern Pacific and western Atlantic, three species. One species in the western Atlantic: *O. dentex*. Inhabits coral reefs and offshore waters over sandy bottoms.

#### *Odontoscion dentex* (Cuvier)

*Corvina dentex* Cuvier 1830:139, pl. 109, Saint Dominique (holotype: MNHN 144, 114 mm SL).

#### *Ophioscion* Gill

*Ophioscion* Gill 1864b:164 (type-species: *Ophioscion typicus* Gill, by monotypy).

*Ophioscion (Sigmurus)* Gilbert in Jordan and Evermann 1898:1452 (type-species: *Corvina vermicularis* Günther, by monotypy).

*Diagnosis*.—Body robust, dorsal profile elevated, ventral profile slightly convex. Head broad, conical top with prominent cavernous canals; bony interorbital width 3.5 or more in head. Mouth small, inferior, teeth conical in bands. Gill rakers short. Vertebrae 10+15=25. Swim bladder with two chambers, anterior one yoke-shaped and posterior one carrot-shaped, without diverticula (Fig. 15A). Both sagitta and lapillus enlarged; ostium incomplete (Fig. 27A). Snout with three large and two to four minute upper pores, and five marginal pores, rostral fold deeply indented (Fig. 33B). Tropical eastern Pacific and western Atlantic, about 11 species. Three nominal species of this genus from western Atlantic are listed



here: *O. adustus*, *O. panamensis*, and *O. punctatissimus*. Inhabits inshore waters over sandy to muddy bottoms.

#### *Ophioscion adustus* (Agassiz)

*Corvina* (*Sciaena*) *adusta* Agassiz 1831:126, pl. 70, Montevideo (type: see remarks).

*Corvina gilli* (?) Steindachner 1867:335, La Plata (type: not located, see remarks).

#### *Ophioscion panamensis* Schultz

*Ophioscion panamensis* Schultz 1945:134, fig. 8, Fox Bay, Colon, Panama (holotype: USNM 122612, 52 mm SL).

#### *Ophioscion punctatissimus* Meek and Hildebrand

*Ophioscion punctatissimus* Meek and Hildebrand 1925: 644, pl. 68, Panama (holotype: USNM 81766, 131 mm SL, Canal Zone).

**Remarks.**—The soft dorsal and anal fin ray counts of *Corvina adusta* Agassiz (1831) on page 127 (D. X+I, 28; A. II, 9) are different from the Spix figure on plate 70 (D. X+I, 19 or 20; A. II, 7). The descriptions of *Ophioscion adusta* (Agassiz) in Jenyns (1842:42), Günther (1860:289), Berg (1895:52), and Schultz (1945:128) resemble the text description of Agassiz. Jordan and Eigenmann (1889:403) interpreted the specimen (MCZ 22417, 180 mm TL from Fonteboa, Brazil = *O. punctatissimus*) as *O. adusta* of Spix plate 70 and suggested that a new name should be proposed. Jordan and Evermann (1898:1447) added *Stellifer microps* (MCZ 1031, Fonteboa, Brazil) and *O. punctatissimus* (MCZ 21728, Jeremie, Haiti) in their description of *O. adusta*. The descriptions of *O. adustus* (Meek and Hildebrand 1925:639) and *O. panamensis* (Schultz 1945:134) resemble plate 70 of Spix. Furthermore Schultz (1954) interpreted *O. adusta* by a specimen from Uruguay (USNM 86710, 120 mm SL) and suggested that *Ophioscion woodwardi* Fowler (= *Micropogonias furnieri*) is probably a junior synonym of *O. adusta* (the text description of Agassiz 1831). The descriptions of *O. adusta* in A. Miranda Ribiero (1915, Sciaenidae, p. 23), Devincenzi (1924:239), and Dahl (1971:260) are probably *O. punctatissimus* or *Stellifer* species.

Jordan and Eigenmann (1889) reported that the nominal species *Corvina gilli* (Steindachner 1867:335) is similar to *O. adusta* of Spix's plate 70 (Agassiz 1831). The description of *C. gilli* Steindachner from La Plata River seems to be of a sciaenid fish except for the low soft dorsal fin ray count (16). Its identity is unknown.

The type-specimen of *Corvina adusta* was "in Museo Monacensi, 10" longum" (Agassiz 1831). It was probably destroyed in Munich during a bombing attack in April 1944 (Trewavas 1950). The length of the fish (10 in) is also too big for *Ophioscion* or *Stellifer* species. In my opinion, therefore, the text description of *C. adusta* (Agassiz 1831) is most probably a species of *Micropogonias*, al-

though the minute mandibular barbels were not mentioned by these authors (also see section on *Micropogonias*). In addition, four pairs of minute barbels are present on the lower jaw of *O. woodwardi* Fowler (holotype: ANSP 68257). The plate of *C. adusta* (Agassiz 1831) probably fits best the description of *O. panamensis* (Schultz 1945). But the type-specimens of *O. panamensis* (holotype and 13 paratypes in USNM) are all juveniles (23.3 to 52 mm SL). Their identities are doubtful and no specimens have been reported except the types. For the present, *O. panamensis* and *O. punctatissimus* are recognized here and included in the "Key to the genus *Ophioscion*."

#### *Stellifer* Oken

"Stelliferes" Cuvier 1817:283, vernacular name.

*Stellifer* Oken 1817:1182 (type-species: *Bodianus stellifer* Bloch, by original designation).

*Stelliferus* Stark 1828:459 (type-species: *Stellifer capensis* Stark = *Bodianus stellifer* Bloch, by monotypy).

*Homoprion* Holbrook 1855:168 (type-species: *Homoprion lanceolatus* Holbrook, by subsequent designation of Gill 1862b:83).

*Bairdiella* (*Nector*) Jordan and Evermann 1898:1432 (type-species: *Bairdiella chrysoleuca* Günther 1867, by original designation).

*Stellifer* (*Zestis*) Gilbert in Jordan and Evermann 1898: 1439 (type-species: *Stellifer oscitans* Jordan and Gilbert, by original designation).

*Stellifer* (*Zestidium*) Gilbert in Jordan and Evermann 1898:1439 (type-species: *Stellifer illecebrosus* Gilbert, by original designation).

*Stellifer* (*Stellicarens*) Gilbert in Jordan and Evermann 1898:1439 (type-species: *Stellifer zestocarus* Gilbert, by original designation).

**Diagnosis.**—Body robust, back elevated. Head broad, rather flat on top with apparent cavernous canals; interorbital wide, bony interorbital width 3.5 or less in head. Mouth moderate to large, inferior to oblique (Fig. 38); teeth conical or villiform in bands. Gill rakers usually long and slender, some moderate to short. Vertebrae 10+15=25. Swim bladder in two chambers; the anterior chamber yoke-shaped in the head with a pair of diverticula, tubelike or bulblike (Fig. 16), and the posterior chamber simple carrot-shaped. Both sagitta and lapillus enlarged, the ostium on sagitta incomplete (Fig. 28). Snout with five marginal pores, the median one rounded, separate from the rostral fold and arranged rhomboidally with three upper pores at the tip of the snout (Fig. 1B); lower jaw with four to six pores, no barbel (Fig. 35). Tropical eastern Pacific and western Atlantic, about 24 species. Eleven species of western Atlantic sciaenids belong to this genus: *S. brasiliensis*, *S. colonensis*, *S. griseus*, *S. lanceolatus*, *S. microps*, *S. naso*, *S. rastrifer*, *S. sp. A*, *S. sp. B*, *S. stellifer*, and *S. venezuelae*. Inhabits inshore waters of sandy bottoms, also in estuaries and around coral reefs.

*Stellifer brasiliensis* (Schultz)

*Ophioscion brasiliensis* Schultz 1945:128, fig. 6, Santos, Brazil (holotype: USNM 87742, 77 mm SL).

*Stellifer colonensis* Meek and Hildebrand

*Stellifer colonensis* Meek and Hildebrand 1925:623, pl. 46, fig. 1, Mindi, Panama (holotype: USNM 81729, 99 mm SL).

*Stellifer griseus* Cervigón

*Stellifer* sp. Cervigón 1966a:509, fig. 209, Morro de Puer to Santos, Venezuela.

*Stellifer griseus* Cervigón 1966b:1, fig. 1, North Peninsula de Araya (holotype in Museo de Historia Natural La Salle, Venezuela, MHNLS 1.875, 120 mm SL, not examined; paratypes: USNM 200782, two specimens, 108 and 123 mm SL).

*Stellifer lanceolatus* (Holbrook)

*Homoprion lanceolatus* Holbrook 1855:168, pl. 23, Beaufort S.C. (type: presumably lost).

*Stellifer microps* (Steindachner)

*Corvina microps* Steindachner 1864:205, pl. 2, fig. 2, Guiana (type: presumably in NHMV, but not found).

*Ophioscion costaricensis* Caldwell 1958:117, fig. 1, Tortuguero, Costa Rica (holotype: UF 5831, 117 mm SL).

*Stellifer naso* (Jordan)

*Stelliferus naso* Jordan in Jordan and Eigenmann 1889:395, Cachoeira, Brazil (syntypes: USNM 130630, 5 specimens, 68-75 mm SL).

*Stellifer rastrifer* (Jordan)

*Stelliferus rastrifer* Jordan in Jordan and Eigenmann 1889:393, Santos, Brazil (holotype: MCZ 10815A, 128 mm SL).

*Stellifer stellifer* (Bloch)

*Bodianus stellifer* Bloch 1790, pt. 4:55, pl. 231, fig. 1, "Cape of Good Hope" (type-locality is probably in error; since Bloch's specimen was obtained from a Dutch auction, the specimen very likely came from Surinam rather than Africa; also see Jordan and Eigenmann 1889:394).

*Corvina trispinosa* Cuvier 1830:109, Cayenne and Brazil.

*Stellifer mindii* Meek and Hildebrand 1925:626, pl. 66, fig. 2, Mindi Reef, Panama (holotype: USNM 81730, 93.4 mm SL).

*Stellifer venezuelae* (Schultz)

*Ophioscion venezuelae* Schultz 1945:131, fig. 7, Venezuela (holotype: USNM 121749, 140 mm SL).

*Remarks.*—Two additional new species of *Stellifer* (see footnote 3) are included in the section on "Key to the species of *Stellifer*" as *Stellifer* sp. A and *Stellifer* sp. B.

Freshwater Sciaenidae of America

Four genera, *Aplodinotus*, *Pachypops*, *Pachyurus*, and *Plagioscion*, and 22 nominal species of sciaenids are listed here from Atlantic river systems of America. Of these, *Aplodinotus* is the only North American freshwater inhabitant, and the other three genera are endemic to continental South America. Because of lack of sufficient material for the South American genera, the diagnoses of these genera are based mainly on the literature (mainly on Günther 1860; Lütken 1875; Jordan and Evermann 1896; Jordan and Eigenmann 1889; Eigenmann 1912; Starks 1913; Campos 1942; Lowe 1966; Ringuet et al. 1967) and type-specimens. The exact limits of these genera are not clear at present.

*Aplodinotus* Rafinesque

*Aplodinotus* Rafinesque 1819:418 (type-species: *Aplodinotus grunniens* Rafinesque, by monotypy).

*Haploidonotus* Gill 1862d:102 (invalid emendation of *Aplodinotus*, Rafinesque 1819, therefore taking the same type-species: *Aplodinotus grunniens* Rafinesque).

*Eutychelithus* Jordan 1876:242 (type-species: *Corvina richardsoni* Cuvier, by monotypy = *Aplodinotus grunniens* Rafinesque).

*Diagnosis.*—Body oblong, snout blunt, back elevated and compressed. Mouth small, horizontal to inferior; lower pharyngeals very large, completely united (Fig. 40B). Swim bladder simple carrot-shaped (Fig. 5D). Sagitta more or less semicircular, the expanded part of the ostium not reaching anterior margin (Fig. 19B). Snout without upper pores (Fig. 31B); lower jaw without mental barbels. Vertebrae 10+14=24. Freshwater North and Central America. Monotypic: *A. grunniens*.

*Remarks.*—The original description of *Ambledon* Rafinesque (1819:421) included two species of buffalo fish (Catostomidae), *A. bubalus* and *A. niger*. The unique lower pharyngeal teeth of *Aplodinotus grunniens* were wrongly attributed to these fishes. Rafinesque's (1820:24) subsequent replacement of *Aplodinotus* with *Ambledon* does not make *Ambledon* an available name in the Sciaenidae.

*Aplodinotus grunniens* Rafinesque

*Aplodinotus grunniens* Rafinesque 1819:419, Ohio River (no type mentioned in the description).

*Sciaena oscula* LeSueur 1822:252, pl. 13, Lake Erie (holotype: MNHN A.5696, 308 mm SL).

*Sciaena grisea* LeSueur 1822:254, Ohio River (type: "18 to 24 inches in total length," presumably in MNHN, but not found).

*Corvina richardsoni* Cuvier 1830:100, Lake Huron (type: presumably in MNHN, but not found).

*Ambloodon concinnus* Agassiz 1854:307, Tennessee River (lectotype herein designated: MCZ 21970, 251 mm SL).

*Ambloodon lineatus* Agassiz 1854:307, Osage River (syntypes: MCZ 569, two specimens, 198 and 160 mm SL).

*Ambloodon neglectus* Girard 1859:167, Rio Grande del Norte, Rio Bravo (holotype: USNM 639, 84.3 mm SL).

*Remarks.*—Two catalogue numbers, MNHN A.5696 and MNHN 7536, are indicated as "syntypes of *Corvina oscula* LeSueur": MNHN A.5696, a dried stuffed specimen, 308 mm SL, collected by LeSueur from Lake Erie was examined; MNHN 7536 from New Orleans was not found. In Agassiz's (1854) original description no types were mentioned. The MCZ specimens of *A. concinnus* and *A. lineatus* catalogued as types are considered the types.

### *Pachypops* Gill

*Pachypops* Gill 1862b:87 (type-species: *Micropogon trifilis* Müller and Troschel 1848, by original designation).

*Diagnosis.*—Body moderately elongate, dorsal profile elevated and descending nearly straight under soft portion of dorsal fin, ventral profile nearly straight. Head oblong, snout convex and projecting; suborbital region much swollen and translucent. Mouth small, inferior, teeth villiform in narrow bands; maxillae almost entirely concealed under the suborbitals. Preopercular margin slightly serrate. Snout with five upper pores and five marginal pores; lower jaw with five to six pores and three to many barbels. From Cuvier (1830:pl. 138) and Trewavas' (1964) description, the swim bladders of *Pachypops fourcroi* and *P. trifilis* have a pair of anterior appendages each dividing into a longer posterior branch and a shorter anterior one; the anterior branch extending in front of the septum transversum (*Lonchurus* pattern, Fig. 14). The sagitta of a *Pachypops fourcroi* (153 mm SL) is similar to the sagitta of *Pachyurus schomburgkii* (Fig. 18K). Four nominal species are listed here: *P. adpersus*, *P. camposi*, *P. fourcroi*, and *P. trifilis*.

### *Pachypops adpersus* (Steindachner)

*Pachyurus (Lepipterus) adpersus* Steindachner 1880: 123, Rio San Antonio, Brazil (type: presumably in NHMV, but not found).

### *Pachypops camposi* Fowler

*Pachypops camposi* Fowler 1954:252, Rupununi River,

British Guiana (holotype: ANSP 39773, 117 mm SL, labeled as *P. steindachneri*).

### *Pachypops fourcroi* (Lacepède)

*Perca fourcroi* Lacepède 1803, 4:398, no locality (holotype: MNHN 7539, 135 mm SL).

### *Pachypops trifilis* (Müller and Troschel)

*Micropogon trifilis* Müller and Troschel 1848:622, British Guiana (type: not located).

### *Pachyurus* Agassiz

*Pachyurus* Agassiz 1829:125, 127 (type-species: *Pachyurus squamipennis* Agassiz, by monotypy).

*Lepipterus* Cuvier 1830:152 (type-species: *Lepipterus francisci* Cuvier, by monotypy).

*Diagnosis.*—This genus may be divided into at least two groups (or genera) based on the swim bladder. One with a simple carrot-shaped swim bladder (*P. schomburgkii*, Fig. 6B), the other with a pair of tubelike diverticula extending from the anterior corners of swim bladder, tapering back to the end of the main chamber (*P. bonariensis*, Fig. 6A). Because of lack of study material, only common characters are presented. Body moderately elongate, dorsal profile slightly elevated, ventral profile nearly straight or slightly arched. Head conical; snout blunt, swollen, and translucent. Eye moderate to large. Mouth horizontal, inferior or terminal; teeth villiform in bands. Snout with five marginal pores and usually without upper pores, some with three to five upper pores; lower jaw with five pores and no barbel. Sagitta moderate to large. Second spine of anal fin moderate to strong. Eight nominal species are included in this group: *P. biloba*, *P. bonariensis*, *P. francisci*, *P. grunniensis*, *P. lundii*, *P. paranensis*, *P. schomburgkii*, and *P. squamipennis*.

### *Pachyurus biloba* Cuvier

*Corvina biloba* Cuvier 1830:112, no locality (holotype: MNHN 7683, 75.6 mm SL).

### *Pachyurus bonariensis* Steindachner

*Pachyurus (Lepipterus) bonariensis* Steindachner 1870: 126, La Plata, Argentina (NHMV 15181 may be one of the syntypes, 188 mm SL, La Plata, Argentina; CAS specimen, Indiana University 11353, 152 mm SL, Buenos Aires, collected by W. B. Scott and labeled cotype is apparently a mistake).

### *Pachyurus francisci* (Cuvier)

*Lepipterus francisci* Cuvier 1830:152, pl. 113, "Riviere de Saint-Francois," Brazil (type: not located).

*Lepipterus corvina* Reinhardt 1851:30, Rio das Velhas, Brazil (syntypes: ZMK 1 and 2; 336 and 274 mm SL). mm SL).

***Pachyurus grunniens* (Schomburgk)**

*Corvina grunniens* Schomburgk 1860:136, pl. 2, Essequibo River, Comacca Island, British Guiana (not of *Aplodinotus grunniens* Rafinesque).

***Pachyurus lundii* Reinhardt**

*Pachyurus lundii* Reinhardt 1855:108, Rio das Velhas, Brazil (syntypes: ZMK 1 and 2; 336 and 274 mm SL).

***Pachyurus paranensis* Daneri**

*Pachyurus paranensis* Daneri 1956:6, fig. 1, Santa Fe, Argentina (type: not located).

***Pachyurus schomburgkii* Günther**

*Pachyurus schomburgkii* Günther 1860:282, rivers of Brazil (holotype: BMNH 49.11.8.22, 197 mm SL).

*Pachyurus nattereri* Steindachner 1863:10, pl. 3, Rio Branco, Rio Negro, Brazil (type: presumably in NHMV, but not found).

*Pachyurus nattereri* Campos 1942:17 (valid emendation of Steindachner's spelling).

***Pachyurus squamipennis* Agassiz**

*Pachyurus squamipennis* Agassiz in Spix and Agassiz 1831:128, pl. 71, Brazil.

**Remarks.**—Agassiz's spelling of the species name is *squamipennis* and should be used although it has often been spelled as *squamipinnis*. The type-specimen of this species probably was destroyed in Munich during a bombing attack in April 1944 (Trewavas 1950).

***Plagioscion* Gill**

*Plagioscion* Gill 1862b:82 (generic description, no species or type indicated, compared with *Corvina* of Cuvier; type-species: *Sciaena squamosissima* Heckel, by subsequent designation of Jordan and Eigenmann 1889:380).

*Diplolepis* Steindachner 1863:2 (type-species: *Diplolepis squamosissimus* Steindachner = *Sciaena squamosissima* Heckel, by monotypy, preoccupied by *Diplolepis* Geoffroy 1762, cynipid insect and *Diplolepis* Fabricius 1805, calcid insect, quoted from Neave 1939-40; spelled *Diplolepis* on p. 3).

**Diagnosis.**—A freshwater genus of Sciaenidae from South American rivers, some species occasionally in estuaries, rarely marine. Body elongate, dorsal profile

evenly arched, ventral profile nearly straight. Head slightly conical, snout protuberant. Mouth moderate, terminal, slightly oblique, no enlarged caninelike teeth at tip of upper jaw. Scales along lateral line concealed by many smaller scales in some species, appearing as one enlarged scale (Fig. 41). Gill rakers rather long and slender. Swim bladder with a pair of hornlike diverticula, originating from anterior quarter of main chamber and hooked at the distal ends (*Cynoscion* pattern, Fig. 12D). Sagitta suboval, expanded part of the ostium reaching to anterior margin and the cauda deeply curved in a J-shape (Fig. 18L). Nine nominal species are included in this genus: *P. auratus*, *P. heterolepis*, *P. macdonaghi*, *P. microps*, *P. monacantha*, *P. pauciradiatus*, *P. squamosissimus*, *P. surinamensis*, and *P. ternetzi*.

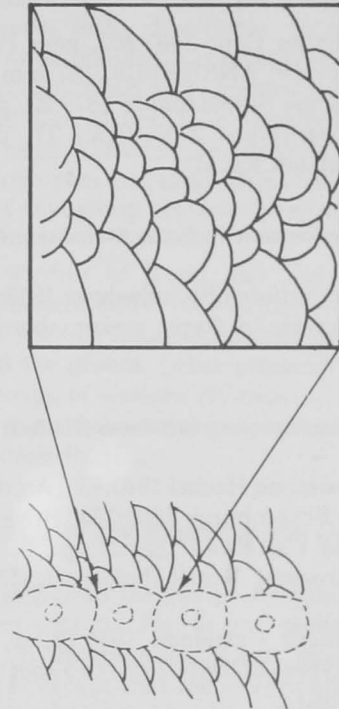


Figure 41.—Portions of lateral line scales of *Plagioscion surinamensis*. The large-scale view shows numerous small scales covering a segment of lateral line; in the small-scale view, the lateral line pores are seen through the small scales.

***Plagioscion auratus* (Castelnau)**

*Johnius auratus* Castelnau 1855:12, pl. 4, fig. 2; Ucayala, Brazil (holotype: MNHN 7622, 203 mm SL).

***Plagioscion heterolepis* (Bleeker)**

*Johnius heterolepis* Bleeker 1873:456, Surinam (syntypes: RMNH 6042, two specimens, 123 and 129 mm SL, these type-specimens are similar to the *Stellifer* group in external appearance. Its true identity is uncertain at present).

*Plagioscion macdonaghi* Daneri

*Plagioscion macdonaghi* Daneri 1954:179, fig. 1, Rio de La Plata (holotype in Coleccion Nacional del Instituto Nacional de Investigacion de las Ciencias Naturales, Brazil, no. 4197, 147 mm TL, not examined).

*Plagioscion microps* Steindachner

*Plagioscion microps* Steindachner 1917:657, pl. 1, fig. 1, Amazon (presumed syntype: NHMV 15180, 206 mm TL, collected by Steindachner in Surinam, may be one of the originally described specimens, 208 and 214 mm TL).

*Plagioscion monacantha* (Cope)

*Corvina monacantha* Cope 1867:402, near Paramaribo, Surinam (holotype: ANSP 11519, 167 mm SL).

*Sciaena magdalenae* Steindachner 1878:22, pl. 1, fig. 1, Magdalena River (types: 270-540 mm TL, presumably in NHMV, but not found).

*Plagioscion pauciradiatus* Steindachner

*Plagioscion pauciradiatus* Steindachner 1917:660, figure on p. 661, Paramaribo (type: presumably in NHMV, but not found).

*Plagioscion squamosissimus* (Heckel)

*Sciaena squamosissima* Heckel 1840:438, Amazon.

*Sciaena rubella* Schomburgk 1860:133, British Guiana.

*Johnius courvina* Castelnau 1855:11, pl. 5, fig. 1, Rio Crixas, Rio Arognay, Brazil (holotype: MNHN 7503, 366 mm TL).

*Johnius amazonicus* Castelnau 1855:12, pl. 4, fig. 1, Amazon (syntypes: MNHN 7504, two specimens, 96.3 and 145 mm SL).

*Plagioscion surinamensis* (Bleeker)

*Pseudosciaena surinamensis* Bleeker 1873:458, Surinam (holotype: RMNH 5995, 88.1 mm SL).

*Plagioscion ternetzi* Boulenger

*Plagioscion ternetzi* Boulenger 1895:523, Paraguay (syntypes: BMNH 1895.5.17.1-2, two specimens, 88.4 and 263 mm SL).

**Phylogenetic Relationships of the Genera and Suprageneric Groups**

The morphological patterns of swim bladders, otoliths, and external features of western Atlantic sciaenid fishes (Table 1) are considered here to assess phylogenetic rela-

tionships. In the following discussion, relationships will be discussed among genera within the groups, then among suprageneric groups. The adaptive characters are indicated and their phyletic significance are also discussed. The dendrogram (Fig. 4) indicates similarities of these sciaenid genera but may not express the actual phylogeny. Study of sciaenids in other areas, particularly the eastern Pacific (see footnote 4), is needed to test the relationships hypothesized here.

**Relationships of the Genera Within the Suprageneric Groups**

**Sciaena GROUP**

Members of this group all have a simple swim bladder (*Sciaena* pattern, Fig. 5) and a thick sagitta (*Sciaena* pattern, Fig. 18). The shape and position of the sulcus varies among the genera and species. *Equetus* and *Paraques* are very similar in having an elevated dorsal profile and dark stripes on the side. They are mainly coral reef and coastal dwellers. *Sciaena* usually lives in deeper offshore water (Chao and Miller 1975) than other sciaenids. Members of the *Sciaena* group have enclosed inferior mouths except for *Sciaena* with a subterminal and slightly inferior mouth. Habitat diversification of this group is greatest among all western Atlantic suprageneric groups of sciaenids.

**Umbrina GROUP**

This group is most similar to the *Sciaena* group, in having a simple swim bladder (*Sciaena* pattern, Fig. 5) and a thick sagitta (*Sciaena* pattern, Fig. 18). These fishes also have a barbel at the tip of lower jaw (Fig. 36A, C). The mental barbel of *Ctenosciaena* is flexible and tapered at its tip without an apical pore, whereas that of *Umbrina* is rigid and short with an apical pore. Also, the mouth of *Ctenosciaena gracilicirrhus* is subterminal, and that of *Umbrina* is inferior. These morphological differences may be attributed to an adaptation of *C. gracilicirrhus* to deeper waters habitats than *Umbrina*. The sagittae of *C. gracilicirrhus*, *S. trewavasae*, and *U. milliae* are most similar among fishes of *Sciaena* pattern sagittae (Fig. 18A, G, J) suggesting a relationship between the *Sciaena* and *Umbrina* groups (Fig. 4).

*Leiostomus* is similar to members of the *Sciaena* group, but it has a much thinner sagitta (Fig. 18D). In addition, the ostium of its sulcus is inclined toward the dorsal margin (to the right of Fig. 18). The kinship of this genus is tentatively put with the *Sciaena* and *Umbrina* groups.

**Pogonias GROUP**

The North American freshwater *Aplodinotus grunniens* and western Atlantic *Pogonias cromis* have a similar thin and semicircular sagitta (*Pogonias* pattern,

Fig. 19). Both of their lower pharyngeal bones are fully united into a triangular plate (Fig. 40). The uniting suture of the lower pharyngeals is apparently weaker in *P. cromis*. Although the swim bladder of *A. grunniens* is a simple carrot-shape (*Sciaena* pattern, Fig. 5D) and that of *P. cromis* has very complicated diverticula (*Pogonias* pattern, Fig. 10) in adults, they may still be most closely related to each other (Fig. 4).

### Cynoscion GROUP

Genera of this group have a similar swim bladder *Cynoscion* pattern, Fig. 12). *Macrodon* and *Cynoscion* are most similar to each other in external morphology, except that the large canines in *Macrodon* have arrow-headed tips and several large canines are present at the tip of lower jaw (Fig. 37A). *Isopisthus* differs from all other western Atlantic sciaenids in having a space between the anterior (spinous) and posterior (soft) portions of dorsal fin, but its general body shape resembles *Cynoscion*. The South American freshwater genus *Plagioscion* has a terminal horizontal mouth, and lacks enlarged canines. Its body shape is deeper and is not as fusiform as other genera of this group. This may be an adaptation to the freshwater habitat, whereas, the fast swimming and fusiform *Cynoscion*, *Isopisthus*, and *Macrodon* may be adapted to open water habitats. The sagittae of the genera in the *Cynoscion* group differ from each other (Figs. 23, 25). *Macrodon ancylodon* has a thin elongate sagitta (Fig. 25B) similar to *Cynoscion* (Fig. 23), but the general outline and the sulcus differ. In *Plagioscion surinamensis* (Fig. 18L) and *Isopisthus parvipinnis* (Fig. 25A), the sagittae have a similar thickened posterior half. Sciaenidae usually have a thick sagitta; therefore, this similarity is not indicative of generic relationships. *Plagioscion* may be more closely related to the *Cynoscion* group than to other sciaenid fishes (Fig. 4).

### Lonchurus GROUP

*Paralonchurus* and *Lonchurus* show a sequence of reduction in swim bladder size (Fig. 14). *Lonchurus lanceolatus* has the most reduced swim bladder (Fig. 14A) and weak drumming muscles only in male. It is a coastal and estuarine dweller. Its habitat is similar to that of *Menticirrhus* which has only a vestige of the swim bladder remaining in adults. The reduced swim bladder of *L. lanceolatus* also shows a basic two-horned structure, which resembles that of the *Cynoscion* group (Fig. 12). *Paralonchurus* usually has a well-developed swim bladder, but the relative size in *P. elegans* is slightly reduced (Fig. 14B), especially in female specimens. They inhabit deeper inshore waters than does *Lonchurus*. In comparing the sagitta (Fig. 24) and external morphology of *Lonchurus* and *Paralonchurus*, the similarities among *L. lanceolatus*, *P. brasiliensis*, and *P. elegans* indicate that they are most closely related to each other. Other eastern Pacific *Paralonchurus* species are most important to define the boundaries and relationships of this supra-

generic group (or tribe). In addition, the South American freshwater scianid genus *Pachypops* may also belong to this group, based on the swim bladder of *P. fourcroyi* (Fig. 14D). The few species examined from this genus all have inferior mouths and three to many pairs of barbels.

### Stellifer GROUP

Genera of this group all have a two-chambered swim bladder (Fig. 15) and an enlarged lapillus (Fig. 27). The genus *Stellifer* has a pair of diverticula posterolaterally on the anterior chamber of the swim bladder (Fig. 16). Morphological variation of the swim bladder diverticula is most important in assessing species relationships within *Stellifer*. *Ophioscion* has a sagitta and lapillus shaped similarly to *Stellifer* (Fig. 27A, B), and the body shape, cavernous head, and swim bladder position are similar. *Ophioscion* lacks diverticula on the anterior chamber of the swim bladder, but is otherwise similar to *Stellifer* (Fig. 4). *Bairdiella* and *Odontoscion* (Fig. 37C) have a terminal mouth and lack apparent cavernous canals on the head. *Odontoscion* inhabits clear-water reefs and has large eyes and large caninelike teeth (Fig. 37C0). Genera of this group are mainly estuarine.

Osteological studies of Topp and Cole (1968) on *Sciaenops* and Mohsin (1973) on four *Cynoscion* species from the Gulf of Mexico are also useful in assessing relationships within the genera. Other presently monotypic suprageneric groups of western Atlantic sciaenids may contain more genera from other geographic regions, especially the eastern Pacific.

### Relationships of the Suprageneric Groups

The *Sciaena* and *Umbrina* groups are similar in swim bladder (*Sciaena* pattern, Fig. 5) and otolith (*Sciaena* pattern, Fig. 18) morphology. Their external morphology is similar except that the *Umbrina* group has a mental barbel (Fig. 36A, C). Members of both groups are mainly bottom feeders with inferior mouths. The genus *Sciaena* of the *Sciaena* group and the genus *Ctenosciaena* of the *Umbrina* group have entered deeper waters and both have a relatively larger subterminal mouth to feed in midwater. The cluster of *Sciaena* and *Umbrina* groups are in turn most closely related to the *Larimus* group (Fig. 4). The species of *Larimus* have a basic simple swim bladder (Fig. 5E, F). A pair of anterior projections found on the swim bladder of *L. breviceps* appear to be a modification of the *Sciaena* swim bladder pattern. The sagitta of *Larimus* species (Fig. 20A, B) has a unique outline, and the ostium is much larger and does not reach to the anterior margin of the sagitta. The lack of upper pores on the snout (Fig. 31B) and four minute mental pores (Fig. 34B) in *Larimus* are adaptive characters correlated with its large oblique mouth and upper water column feeding habits (Fig. 30; Table 1).

Among the suprageneric groups, members of both *Pogonias* and *Sciaenops* have a complicated swim blad-

der as adults (Figs. 10, 11), but the structural patterns are different and their sagittae also differ (Figs. 19, 20C, D). Although *Pogonias* and *Sciaenops* have a similar inferior mouth and inhabit inshore coastal and estuarine waters, the body shape of *Sciaenops* is more elongate and less compressed than *Pogonias*. This may be an adaptation of *Sciaenops* to the shallow-water surf zone habitat. They are probably most closely related to the *Larimus*, *Sciaena*, and *Umbrina* groups, but these relationships could be drawn at the tribal level (between lines C and D, Fig. 4). The suprageneric groups included in this cluster (Z, Fig. 4) show a basic carrot-shaped swim bladder with diverticula present or absent. Their sagittae are basically suboval and most members are bottom feeders. In this cluster of suprageneric groups, the trend of swim bladder development in western Atlantic sciaenids is clearly demonstrated from the simple *Sciaena* pattern with independent drumming muscles in the male to the complex *Pogonias* pattern with intrinsic drumming muscles in both sexes. Furthermore, the ontogenetic development of the swim bladder in *Pogonias cromis* (Fig. 10) and *Sciaenops ocellata* (Fig. 11) may also reflect the phylogenetic development of the swim bladder, from simple (primitive) to complex (advanced) with diverticula developing on the swim bladder from the anterior to the posterior end.

The *Menticirrhus* and *Lonchurus* groups resemble each other in the trend of reduced swim bladders (Figs. 14, 17) in adults. The sagittae are elongate and thin (Figs. 22B, 24). Both groups have inferior mouths and barbels. Their body shapes are elongate and rounded. The flat ventral side of the body is an adaptation for inhabiting the bottom habitats or specifically the surf zone (Table 1). Whether these similarities should be interpreted as phylogenetic relationships or merely ecological convergence is not clear at present, but their close kinship is apparent. The *Menticirrhus* group also has a pored single barbel (Fig. 36B) similar to that of *Umbrina* (Fig. 36C), but this probably should be viewed as ecologically convergent for bottom feeding rather than as phylogenetically important.

Other suprageneric groups of western Atlantic sciaenids may not be as closely related as the groups already discussed. Further clustering of the taxa (between lines A and B, Fig. 4) is more difficult due to the limitations of a regional study. There are gaps, especially in assessing the relationships of the *Micropogonias* and *Nebris* groups. *Nebris microps* has a pair of well-developed anterior diverticula on its swim bladder (Fig. 8) and a very thick oval sagitta (Fig. 21). *Micropogonias* species have a pair of posteriorly originating tubelike diverticula on their swim bladders (Fig. 9) and rather thick, shieldlike and irregular sagitta (Fig. 26). At present, I think that *Nebris* is more closely related to the Z cluster (Fig. 4) than is *Micropogonias*. The clustering is based mainly on the position of the diverticula. The swim bladder diverticula of *Micropogonias* are developed more posteriorly than in the *Nebris* group. Both of them have a sagitta different from the members of the Z cluster (Fig. 4; also see Table 1).

Grouping of the *Cynoscion* group with the *Menticirrhus* and *Lonchurus* groups (Y cluster, Fig. 4) is based on the basic shape of the main chamber of the swim bladder (in the *Cynoscion* and *Lonchurus* groups) and their elongate thin sagittae (in all). Although the members of the *Lonchurus* group have a pair of posteriorly directed diverticula on their swim bladders (Fig. 14), the main chambers have two well-developed anterior branches resembling those of the *Cynoscion* group (Fig. 12). Especially in the reduced form of *Lonchurus lanceolatus* (Fig. 14A), the anterior branches remain unchanged. This cluster (Y) is a convenient grouping and may not reflect phyletic relationships (also see Table 1).

The X and Y clusters on Figure 4 are more closely related to each other phyletically than to the *Stellifer* group, because they all have a single chambered swim bladder and only the sagitta enlarged (Table 1). The swim bladder of the *Stellifer* group has an additional chamber (Fig. 15) in front of the main carrot-shaped chamber. This yoke-shaped anterior chamber is located in front of the septum transversum and its anterior end reach the skull. The sagitta of the *Stellifer* group is reduced in size and the lapillus is enlarged (Fig. 27). The sequences of sagitta reduction and lapillus enlargement are evident among modern genera of the *Stellifer* group. The unique swim bladder and otolith characters of the *Stellifer* group have not been reported in sciaenid fishes of geographic regions other than the New World (Wirtler and Chao, see footnote 3). The Indo-west Pacific sciaenid genera, *Johnius* and *Wak* are characterized by "T-shaped" swim bladder but lack a constriction (Chao et al. 1963). Their sagittae also show a reduction at the anterior portion of the ostium. Possible phyletic links of the *Stellifer* group with *Johnius* and *Wak* are not clear at present.

In conclusion, western Atlantic Sciaenidae can be readily divided into two groups. One group is characterized by a swim bladder with two chambers and with two pairs of enlarged otoliths (lapillus and sagitta). The other group is characterized by a single chambered swim bladder and only one pair of enlarged otoliths (sagitta). Further divisions are based mainly on swim bladder structure, secondly on the morphology of the sagitta and thirdly on external morphology.

Swim bladder structure may be graded from simple to complex. Such a gradation is also reflected in the ontogenetic changes of several species such as *Pogonias cromis* (Fig. 10) and *Sciaenops ocellata* (Fig. 11). The primitive condition of the swim bladder (simple *Sciaenops* pattern) exists in juveniles and adults of many species. Further development of the swim bladder is determined by the development of the diverticula from the anterior to the posterior end of the main chamber. Whether the reduction in size or loss of the swim bladder in adults of the *Menticirrhus* and *Lonchurus* groups (Figs. 7, 14) is attributed to phylogenetic relationships or ecological convergence is undetermined at present.

The general morphologies of the sagitta and its sulcus were used to determine relationships of different taxa especially at the generic level. In the primitive condition

the sagitta is thick and the sulcus opens to the anterior margin of the sagitta, i.e., the expanded part of the ostium reaches the anterior margin (*Sciaena* pattern, Fig. 18). This is the most generalized pattern in many groups of western Atlantic sciaenids.

The external morphology of the western Atlantic Sciaenidae, especially the mouth positions and body shapes, are more diverse than in any other perciform family in the region. These characters are more or less adaptive and plastic, but may be used to supplement other characters in assessing the relationships of the western Atlantic sciaenids.

Biochemical characters of parvalbumins have been studied by Sullivan et al. (1975) and Rao et al.<sup>4</sup> to assess the systematic relationships of some sciaenid species

from the Atlantic American coast. Biochemical data should contribute much to the current knowledge of phylogenetic relationships of western Atlantic Sciaenidae.

Four genera of Sciaenidae—*Aplodinotus*, *Pachyurus*, *Pachypops*, and *Plagioscion*—may live in freshwater for their entire life history. Fossil otoliths of *Plagioscion* and *Pachypops* were described from Pliocene and Miocene deposits in Trinidad (Nolf 1976). This suggests that the freshwater sciaenids were widely distributed and may have originated in marine or estuarine environments. The modern freshwater sciaenids are endemic to the Atlantic drainages of the New World. Knowledge of their taxonomy and biology is rather sparse. Further studies on these freshwater sciaenids and on eastern Pacific sciaenids (Chao, see footnote 4) should supplement the present study, and only when this is done, shall we have adequate evidence for phylogenetic groupings.

Based on the morphology of otoliths (Schmidt 1968; Nolf 1976), the family Sciaenidae is most similar to Lutjanidae, Pomadasyidae, Sparidae, and other closely related perciform fish families.

<sup>4</sup>Rao, K. V. R., C. L. Mahajan, L. Pennell, B. Sullivan, J. Bonaventura, and C. Bonaventura. The structure and evolution of parvalbumins. II. Differential rates of evolution among sciaenid isoparvalbumins. Manuscript.

## KEY TO THE GENERA AND SPECIES OF WESTERN ATLANTIC SCIAENIDAE (WITH FRESHWATER AMERICAN GENERA)

- 1a. Lower jaw with one or more barbels (Fig. 32E-H) . . . . . 2
- 2a. Only one barbel at tip of lower jaw . . . . . 3
  - 3a. Anal fin with one spine; body elongate fusiform, and rounded in cross section; swim bladder absent or rudimentary in adult . . . . . *Menticirrhus*
  - 3b. Anal fin with two spines; body compressed, not fusiform; swim bladder well developed in adult . . . . . 4
    - 4a. Barbel stout and rigid, its tip rounded and perforated with an apical pore (Fig. 36C); mouth distinctly inferior; body with longitudinal stripes and vertical bars, without a well-defined black spot at pectoral fin base . . . . . *Umbrina*
    - 4b. Barbel slender and flexible, its tip tapering and without an apical pore (Fig. 36A); mouth slightly inferior, subterminal; body uniform in color, a very distinct and well-defined black spot at pectoral fin base. [D. X+I, 20-24; A. II, 7-9; gill rakers short, (7-9)+(13-17)=21-25] . . . . . *Ctenosciaena gracilicirrhus*  
(Central and South America from Honduras to Brazil)
- 2b. Two or more barbels on lower jaw . . . . . 5
  - 5a. Barbels only present on tip of lower jaw . . . . . 6
    - 6a. Lower jaw with two barbels only (Fig. 32F); eye small, 9 to 12 times in head length; pectoral fins very long, jet black, upper rays filamentous, reaching to caudal peduncle; swim bladder atrophied in adult (Fig. 14A); estuarine and marine. [D. X-XI+I, 37-39; A. II, 7-9; gill rakers short, (4-6)+(11-13)=15-18] . . . *Lonchurus lanceolatus*  
(Venezuela to Brazil)
    - 6b. Lower jaw with three to many barbels; eye large, 3 to 5 times in head length; pec-



- toral fins pale, upper rays not reaching beyond vent; swim bladder well developed in adult; freshwater and sometimes estuarine . . . . . *Pachypops*  
(Freshwater South America)
- 5b. Barbels present at tip and a series of small barbels along rami (medial edges) of lower jaw . . . . . 7
- 7a. Pairs of small barbels along rami of lower jaw, not in tuft at tip of lower jaw (Fig. 32G); eye diameter about 5 times in head length, second anal fin spine strong and long, more than two-thirds the length of first anal fin ray . . . . . 8
- 8a. Preopercular margin strongly serrate; body covered with relatively small scales, 50 to 56 pored scales along lateral line; body silvery with pinkish cast, with many oblique stripes along the scale rows, swim bladder with a pair of tubelike diverticula (Fig. 9) . . . . . *Micropogonias*
- 8b. Preopercular margin smooth; body covered with relatively large scales, 41 to 46 pored scales along lateral line; body gray to dark, juveniles with 4 to 5 broad vertical bars; swim bladder very complex with many interconnected diverticula (Fig. 10). [D. X+I, 19-23; A. II, 5-7; gill rakers short, (4-6)+(12-16)=16-21] . . . . . *Pogonias cromis*  
(Gulf of Maine to Gulf of Mexico and southern Brazil to Argentina)
- 7b. Three pairs of barbels in a tuft at tip and more than 10 pairs barbels along rami of lower jaw (Fig. 32H); eye diameter about 9 times in head length, second anal fin spine weak and short, less than half the length of first anal fin ray . . . . . *Paralonchurus*
- 1b. Lower jaw without barbel (Fig. 32A-D) . . . . . 9
- 9a. Mouth strongly oblique, tip of lower jaw projecting beyond upper jaw, preopercular margin smooth without strong spines (Fig. 37A, B) . . . . . 10
- 10a. Eye very small, 8 to 11 times in head length (Fig. 37B); body rounded in cross section. [D. VII+I, 31-32; A. II, 9-10; gill rakers long and slender, (5-9) + (14-15) = 20-24] . . . . . *Nebris microp*  
(Costa Rica to Brazil)
- 10b. Eye moderate to large, 3 to 6 times in head length (Fig. 37A); body compressed in cross section . . . . . 1
- 11a. Body elongate and fusiform; teeth conical, set in narrow ridges on both jaws, usually with a pair of enlarged caninelike teeth at the tip of upper jaw; anal fin spines small, inconspicuous; swim bladder with a pair of large hornlike diverticula anteriorly (Fig. 12) . . . . . 1
- 12a. Anterior (spinous) and posterior (soft) portions of dorsal fin well separated, with a gap in between; anal fin base about equal to the length of soft dorsal fin base; anal fin rays 16 to 20. [D. VII+I, 18-20; gill rakers moderately long, (2-3)+(7-9)=9-12] . . . . . *Isopisthus parvipinnis*  
(Panama to southern Brazil)
- 12b. Anterior (spinous) and posterior (soft) portion of dorsal fin, with a deep notch in between, but not separated by a gap; soft dorsal fin base much longer than anal fin base; anal fin rays 7 to 12 . . . . . 1
- 13a. Large caninelike teeth with arrow-headed tips present on both upper and lower jaws (Fig. 37A); lower jaw canines exposed externally when mouth closed. [D. X+I, 27-29; A. II, 8-9; gill rakers slender, (2-3)+(7-9)=9-12] . . . . . *Macrodon ancylodor*  
(Venezuela to southern Brazil)

13b.	Large canines, if present, only at tip of upper jaw, none in lower jaw and tips never arrow-headed . . . . .	<i>Cynoscion</i>
11b.	Body short and robust; teeth minute, set in one to two rows on both jaws; without caninelike teeth; anal fin spines large, conspicuous; swim bladder simple or with a pair of small projections at the anterior end (Fig. 5E, F) . . . . .	<i>Larimus</i>
9b.	Mouth not strongly oblique, tip of lower jaw usually not projecting beyond upper jaw, if so the preopercular margin with strong spines (Figs. 37C, 38) . . . . .	14
14a.	Preopercular margin usually serrate, sometimes strongly with one or more spines at the angle . . . . .	15
15a.	Scales along lateral line considerably enlarged but almost entirely concealed by small scales (Fig. 40); swim bladder with one chamber and a pair of anterior horns (Fig. 12D); lapillus (small earstone) small, less than 10% the size of sagitta (large earstone); freshwater and estuarine . . . . .	<i>Plagioscion</i> (Freshwater and estuarine South America)
15b.	Scales along lateral line about same size as adjacent rows; swim bladder with two chambers, anterior one yoke-shaped and separated by a constriction from main posterior chamber (Fig. 15); lapillus (small earstone) large, more than 50% the size of sagitta (larger earstone) (Fig. 27); marine and estuarine . . . . .	16
16a.	Interorbital width usually more than 1.5 times of eye diameter, tip of anterior swim bladder chamber terminating subcutaneously, frequently visible on superficial inspection in adult and juvenile under the upper end of operculum. Mouth inferior to terminal; snout usually projecting; dorsal view of head blunt, cavernous . . . . .	17
17a.	Anterior chamber of swim bladder with a pair of variably developed posterior diverticula (Fig. 16); bony interorbital width 3.5 or less in head . . . . .	<i>Stellifer</i>
17b.	Anterior chamber of swim bladder without posterior diverticula; bony interorbital width 3.5 or more in head . . . . .	<i>Ophioscion</i>
16b.	Interorbital width usually less than 1.2 times of eye diameter, tip of anterior swim bladder chamber visible externally only in juvenile under the upper end of operculum. Mouth terminal; snout not projecting; dorsal view of head tapered, not cavernous . . . . .	<i>Bairdiella</i>
14b.	Preopercular margin without obvious serrations, sometimes ciliated but never with spines at the angle . . . . .	18
18a.	Mouth small, horizontal, inferior; snout projecting in front of upper jaw; lower jaw included . . . . .	19
19a.	Body short, deep; dorsal profile strongly elevated at nape . . . . .	20
20a.	Body silvery with faint oblique stripes along the oblique scale rows dorsally; a dark spot above upper angle of gill slit; gill rakers 30 or more on first gill arch. [D. IX-XI+I, 29-35; A. II, 12-13; gill rakers (8-12) + (20-24) = 30-36] . . . . .	<i>Leiostomus xanthurus</i> (United States Atlantic and Gulf of Mexico coasts to Bay of Campeche, Mexico)
20b.	Body pale to dark brown; with dark longitudinal stripes and/or oblique bars on sides, gill rakers less than 20 on first gill arch . . . . .	21
21a.	Height of anterior (spinous) portion of dorsal fin much greater	

- than head length; body pale brownish with three oblique bars on sides; third bar running from nape to caudal fin; dorsal fin with more than 45 soft rays . . . . . *Equetus*
- 21b. Height of anterior (spinous) portion of dorsal fin less than head length; body pale brown to dark brown with longitudinal stripes on sides; dorsal fin with less than 40 soft rays . . . . . *Pareques*
- 19b. Body elongate, dorsal profile not strongly elevated at nape . . . . . 22
- 22a. Snout with peculiar conical appearance from the preorbital region being swollen and enlarged; maxillary almost entirely concealed under snout; freshwater . . . . . *Pachyurus*  
(Freshwater South America)
- 22b. Snout rounded, not swollen, maxillary not concealed under snout . . . . . 23
- 23a. Body elongate; one or more large dark spots (larger than eye) on the base of caudal peduncle and/or side of body in adult. [D. X+I, 23-25; A. II, 7-9; gill rakers (4-5)+(7-9)=12-14] . . . . . *Sciaenops ocellata*  
(United States Atlantic and Gulf of Mexico coasts to northern Mexico)
- 23b. Body robust; color uniform, no black spot on caudal peduncle nor on side of body. [D. IX-X+I, 27-33; A. II, 7; gill rakers 6+(10-12)=16-18]; freshwater . . . . . *Aplodinotus grunniens*  
(Freshwater, Canada to Guatemala)
- 18b. Mouth large, moderately oblique, terminal or subterminal; lower jaw not included . . . . . 24
- 24a. A row of enlarged caninelike teeth present on both jaws; a distinct black blotch at pectoral fin base. [D. XI-XII+I, 23-26; A. II, 8-9; gill rakers long, (5-9)+(14-17)=19-25] . . . . . *Odontoscion dentex*  
(Florida, Antilles, along South American coast to Brazil)
- 24b. Without enlarged caninelike teeth on jaws; no distinct blotch at pectoral fin base . . . . . *Sciaena*  
(Colombia and adjacent Caribbean Sea)

### Key to the Species of *Bairdiella*

- 1a. Preopercular margin with distinct strong spines at the angle, vertebrae 11+14=25; length of second anal fin spine less than 2.2 times in head . . . . . 2
- 2a. Second anal fin spine very strong, about the length of first soft ray; preopercular margin with strong spinelike serrations. [D. X+I, 21-26 (usually 23-25); A. II, 7-9 (usually 8); gill rakers slender, (6-10)+(15-18)=21-27 (usually 24-25)] . . . . . *B. ronchus*  
(Antilles and from Honduras to Brazil)
- 2b. Second anal fin spine not as strong, about two-thirds the length of first soft ray; preopercular margin with distinct strong spines. [D. X-XI+I, 19-23; A. II, 8-10 (usually 9); gill rakers slender, (7-8)+(14-16)=22-24] . . . . . *B. chrysourea*  
(U.S. Atlantic and Gulf of Mexico coasts)
- 1b. Preopercular margin with only weak serrations, no spines at the angle, vertebrae 12+13=25; length of second anal fin spine more than 2.5 times in head . . . . . 3
- 3a. Mouth slightly inferior; side with distinct stripes on scale rows; length of second anal fin spine

- 2.5-3.0 times in head; D. X+I, 25-29; A. II, 8; gill rakers rather short, (5-6)+(13-16)=18-22  
 ..... *B. batabana*  
 (Southern Florida to Antilles)
- 3b. Mouth terminal; side without stripes; length of second anal fin spine 3.2-3.6 in head; D. X-XI  
 +I, 22-24; A. II, 9; gill rakers moderately long, (7-8)+(16-18)=23-26 ..... *B. sanctaeluciae*  
 (Antilles, Honduras to Guyana, and occasionally in Florida)

### Key to the Species of *Cynoscion*

- 1a. Scales on body cycloid ..... 2
- 2a. Posterior (soft) portion of dorsal fin covered with small scales beyond basal half of fin. [Lower  
 jaw with a row of enlarged and widely spaced teeth; D. X+I, 22-25 (usually 23-24); A. II, 8-10  
 (mostly 9); gill rakers (2-3)+(6-8)=8-11; 150 to 160 scales in transverse row above lateral line;  
 anterior horns of swim bladder long and straight (Fig. 13A)] ..... *C. microlepidotus*  
 (Colombia to Brazil)
- 2b. Posterior (soft) portion of dorsal fin with only one or two rows of small scales at base ..... 3
- 3a. Dorsal fin with 20 to 24 soft rays; lower jaw teeth uniform in size, closely set; A. II, 10-12  
 (mostly 11); gill rakers (2-3)+(5-8)=7-11; 115 to 125 scales in transverse row above lateral  
 line; anterior horns of swim bladder strongly curved (Fig. 13D, D') sagitta without a notch  
 on ventral margin ..... *C. leiarchus*  
 (Venezuela to Brazil)
- 3b. Dorsal fin with 27-31 soft rays; lower jaw teeth with a row slightly enlarged, widely set;  
 A. II, 7-9 (mostly 8); gill rakers (1-3)+(6-8)=7-11; 120-130 transverse scale rows above  
 lateral line; anterior horns of swim bladder slightly curved; sagitta with a notch on ven-  
 tral margin (Fig. 23C) ..... *C. virescens*  
 (Honduras to Argentina)
- 1b. Scales on body ctenoid ..... 4
- 4a. More than 20 gill rakers on first gill arch. [D. X+I, 18-21; A. II, 8-9; gill rakers long, (7-9)+  
 (14-17)=21-26] ..... *C. striatus*  
 (Brazil to Argentina)
- 4b. Less than 20 gill rakers on first gill arch ..... 5
- 5a. Dorsal fin usually with 22 or fewer soft rays; anal fin usually with 8 soft rays. [D. X+I,  
 17-23; A. II, 7-9; gill rakers (2-6)+(8-10)=10-16; posterior (soft) portion of dorsal fin with  
 only one to two rows small scales at base; caudal fin rhomboidal in adult] ..... *C. acoupa*  
 (Nicaragua to Argentina)
- 5b. Dorsal fin usually with more than 22 soft rays; anal fin usually with 9 or more soft  
 rays ..... 6
- 6a. Posterior (soft) portion of dorsal fin covered with small scales up to or beyond basal  
 third of fin, especially on membranes between anterior rays ..... 7
- 7a. Caninelike teeth absent at the tip of upper jaw; pectoral fins usually shorter  
 than pelvic fins, 2 times or more in head length. [D. X+I, 21-24; A. II, 10-12;  
 gill rakers (3-5)+(8-10)=11-15] ..... *C. steindachneri*  
 (Guyana to Brazil)
- 7b. A pair of large caninelike teeth present at the tip of upper jaw; pectoral fins  
 longer than pelvic fins, less than 2 times in head length ..... 8

- 8a. Side of body with small dark spots forming distinct oblique streaks above lateral line; D. X+I, 24-29; A. II, 10-13 (usually 12); gill rakers (4-5)+(10-12)=14-17 . . . . . *C. regalis*  
(Gulf of Maine to Florida, U.S.A)
- 8b. Side of body pale without distinct spots, sometimes with faint streaks above lateral line . . . . . 9
- 9a. Anal fin with 10 to 12 soft rays (usually 11). [D. IX-X+I, 25-29; gill rakers (3-4)+(9-10)=12-14 (or more); soft portion of dorsal fin covered with small scales up to basal half of fin] . . . . . *C. arenarius*  
(Gulf of Mexico coast, U.S.A to Bay of Campeche, Mexico)
- 9b. Anal fin with 8 to 10 soft rays (usually 9) . . . . . 10
- 10a. Soft portion of dorsal fin covered with small scales up to (or beyond) three-fourths of fin height; total vertebrae 25; D. X+I, 23-27; gill rakers (2-3)+(7-10)=9-13 . . . . . *C. jamaicensis*  
(Lesser Antilles and Panama to Argentina)
- 10b. Soft portion of dorsal fin covered with small scales less than two-thirds of soft dorsal fin height; total vertebrae 27; D. X+I, 26-31; gill rakers (3-4)+(8-10)=11-14 . . . . . *C. nothus*  
(Chesapeake Bay to Texas, U.S.A to Bay of Campeche, Mexico)
- 6b. Posterior (soft) portion of dorsal fin with only one to two rows small scales at base [caudal fin truncate in adults] . . . . . 11
- 11a. Sides of body scattered with large dark spots; D. IX-X+I, 24-28; A. II, 9-12; gill rakers (2-3)+(7-9)=9-12 . . . . . *C. nebulosus*  
(New York to Florida and Gulf of Mexico coast, U.S.A. to northern Mexico)
- 11b. Side of body without dark spots; D. IX-X+I, 24-29; A. II, 8-10; gill rakers (3-4)+(6-9)=9-12 . . . . . *C. similis*  
(Venezuela to Brazil)

### Key to the Species of *Equetus*

- 1a. Body with two narrow longitudinal stripes above and below the third oblique bar; dorsal, anal, and caudal fins dark brown with white spots; pectoral fin dark brown. [D. XI-XII+I, 45-47; A. II, 6-8; gill rakers short, 5+(10-13)=15-18] . . . . . *E. punctatus*  
(Bermudas, Florida, Antilles; and Panama to Brazil)
- 1b. Body without narrow longitudinal stripes; broad oblique bars with distinct white margins; pectoral, dorsal, and anal fins pale. [D. XII-XIII+I, 47-55; A. II, 6; gill rakers short, (5-6)+(10-13)=14-18] . . . . . *E. lanceolatus*  
(Bermudas, North Carolina to Florida, western Gulf of Mexico, Antilles; and Venezuela to Brazil)

### Key to the Species of *Larimus*

- 1a. Body dark gray above and silvery below without vertical bars on the sides; D. X+I, 26-28; gill rakers slender, longer than eye diameter, (9-11)+(19-22)=28-33 . . . . . *L. breviceps*  
(Caribbean Islands to Brazil)
- 1b. Body dark with 7 to 9 vertical bars on the sides; D. X+I, 24-27; gill rakers slender, about equal to eye diameter, (11-13)+(22-25)=34-36 . . . . . *L. fasciatus*  
(U.S. Atlantic and Gulf of Mexico coasts)

### Key to the Species of *Menticirrhus*

- 1a. Breast scales not uniform in size, those towards head notably smaller than scales along lateral line; molariform teeth present on pharyngeal plates; pectoral fins short, not reaching beyond tip of pelvic fins; gill rakers in adult usually three or more on the lower limb of first branchial arch; color plain silvery gray. [Young fish (less than 100 mm SL) with only a vestige of swim bladder. D. IX-X+I, 19-26; gill rakers short, (3-5)+(0-8)=3-12] . . . . . *M. littoralis*  
(U.S. Atlantic coast, Gulf of Mexico and Caribbean coast to Brazil)
- 1b. Breast scales uniform in size; about as large as those along lateral line; no molariform teeth on pharyngeal plates; pectoral fin reaching to or beyond tip of pelvic fin; gill rakers in adult tuberculate or absent on the lower limb of first branchial arch; side with dark oblique bars . . . . . 2
- 2a. Anal fin rays usually 7(6-8); depressed spinous portion of dorsal fin seldom extends past base of second soft ray in dorsal fin; longest dorsal spine 16.2-24.1% of SL; young fish (less than 100 mm SL) with only a vestige of swim bladder. [D. IX-X+I, 20-26; gill rakers short, (2-3)+(0-7)=2-10] . . . . . *M. americanus*  
(U.S. Atlantic coast, Gulf of Mexico and Antilles, Caribbean coast to Argentina)
- 2b. Anal fin rays usually 8(7-9); depressed spinous portion of dorsal fin often extends past base of second soft ray in dorsal fin; longest dorsal spine 24.6-38.9% of SL; young fish (less than 100 mm SL) with well-developed swim bladder. [D. IX-X+I, 22-27; gill rakers short, (3-5)+(0-7)=3-12; a longitudinal dark stripe usually present below lateral line posteriorly . . . . . *M. saxatilis*  
(U.S. Atlantic and Gulf of Mexico coasts to Yucatan, Mexico)

### Key to the Species of *Micropogonias*<sup>6</sup>

- 1a. Dark spots on scales above lateral line forming distinct continuous streaks particularly below the posterior (soft) portion of dorsal fin; 6 or 7 scales between dorsal fin origin and lateral line in vertical series. [D. X+I, 26-30 (usually 26-28); A. II, 7-8; gill rakers short, (7-9)+(12-15)=21-25] . . . . . *M. furnieri*  
(Antilles, Venezuela to Argentina)
- 1b. Dark spots on scales above lateral line not forming distinct continuous streaks below the posterior (soft) portion of dorsal fin; 8 or 9 scales between dorsal fin origin and lateral line in vertical series. [D. X+I, 26-30 (usually 28-29); A. II, 7-9 (usually 8); gill rakers short, (8-10)+(14-18)=22-29] . *M. undulatus*  
(Cape Code, Mass., to Bay of Campeche and maybe from southern Brazil to Argentina)

### Key to the Species of *Ophioscion*<sup>7</sup>

- 1a. Dorsal fin with 20 to 21 soft rays; pored lateral line scales 47-49; gill rakers (7-9)+14=21-23 . . . . . *O. panamensis*  
(Only known from types, Panama)
- 1b. Dorsal fin with 23 to 24 soft rays; pored lateral line scales 52-53; gill rakers (7-8)+(13-16)=20-24  
. . . . . *O. punctatissimus*  
(Panama to Brazil)

### Key to the Species of *Paralonchurus*

- 1a. Pectoral fin short and pale, not extending beyond the tip of pelvic fin; eye diameter moderate (about 5 times in head); soft dorsal with 28-31 rays; body with vertical dark stripes and dark humeral spot above pectoral fin origin; vertebrae 11+18=29; gill rakers short, (3-5)+(6-9)=10-14 . . . . . *P. brasiliensis*  
(Venezuela to Argentina)

<sup>6</sup>This key is based on types, specimens examined, and literature descriptions of Jordan and Eigenmann (1889), Jordan and Evermann (1898), Meek and Hildebrand (1925), MacDonagh (1934), Cervigón (1966a), and Roux (1973). Scale counts failed to key out species in several cases, but color patterns were useful in all cases. The morphology of sagittae (Figs. 26, 41) is useful within limits (also see Remarks on *Micropogonias* in the "Synopsis section").

<sup>7</sup>Also see Remarks on *Ophioscion* in the "Synopsis section."

- 1b. Pectoral fin very long and jet black, reaching to anal fin origin; eye diameter small (about 9 times in head); soft dorsal 31-33 rays; body uniform brown; vertebrae  $10+15=25$ ; gill rakers very short,  $(3-4)+(4-8)=7-11$  . . . . . *P. elegans*  
(Surinam to Brazil)

**Key to the Species of *Pareques***

- 1a. Body with a broad oblique bar running from the base of anterior (spinous) portion of dorsal fin to pelvic fins; only one longitudinal stripe present at the midline of sides, reaching almost to the tip of caudal fin. [D. X+I, 38-39; A. II, 7; gill rakers short,  $(5-6)+(12-13)=17-19$ ] . . . . . *Pareques* sp.  
(Gulf of Mexico)
- 1b. Body without oblique bar; usually several distinct longitudinal stripes present on sides . . . . .
- 2a. Side with 7 to 10 narrow longitudinal stripes narrower than pupil; young with an anteriorly directed, V-shaped dark bar connecting the orbits across top of the head; depressed anterior (spinous) portion of dorsal fin usually not reaching base of the fourth soft ray. [D. IX-X+I, 38-40; A. II, 7; gill rakers short  $(4-6)+(10-12)=15-18$ ] . . . . . *P. umbrosus*  
(Chesapeake Bay to Florida and Gulf of Mexico coast, U.S.A.).
- 2b. Side with 3 to 5 broad longitudinal stripes wider than pupil; and narrow stripes in between them; young with a straight dark bar connecting the orbits across the top of the head; depressed anterior (spinous) portion of dorsal fin usually reaching base of sixth soft ray. [D. VIII-IX+I, 37-41; A. II, 7-8; gill rakers short,  $(5-6)+(9-14)=14-20$ ] . . . . . *P. acuminatus*  
(Chesapeake Bay to Gulf of Mexico, U.S.A., south to Bay of Campeche, Mexico; Antilles; and Honduras to Brazil).

**Key to the Species of *Sciaena***

- 1a. Dorsal fin with 24-26 soft rays; gill rakers  $(6-7)+(13-15)=19-21$  . . . . . *S. trewavasae*  
(Colombia and adjacent Caribbean Sea)
- 1b. Dorsal fin with 21-23 soft rays; gill rakers  $(7-9)+(14-19)=22-27$  . . . . . *S. bathytata*  
(Colombia and adjacent Caribbean Sea)

**Key to the Species of *Stellifer***

- 1a. Preopercular margin with two or three strongly developed spines at the angle . . . . .
- 2a. Propercular margin with three strong spines (occasionally four); gill rakers  $(12-14)+(20-25)=32-38$ ; D. XI+I, 18-20; A. II, 8. [Pectoral fin about 28.5 to 31% of SL (72-106 mm SL specimens)] . . . . . *S. stellifer*  
(Venezuela to Brazil, one record from Puerto Rico)
- 2b. Preopercular margin with two strong spines; gill rakers on first arch 40 or more. [D. XI-XII+I, 21-24; A. II, 8-9] . . . . .
- 3a. Gill rakers  $(16-21)+(23-30)=40-49$  (rarely more than 50); tip of lower jaw with a dark band inside dentary teeth; interorbital width usually less than 2.8 in head; pectoral fin length usually less than 30% of SL . . . . . *S. rastrifer*  
(Venezuela to Brazil)
- 3b. Gill rakers  $(20-23)+(32-36)=52-59$ ; tip of lower jaw without a dark band inside dentary teeth; interorbital width usually more than 2.8 in head; pectoral fin length usually more than 30% of SL . . . . . *S. griseus*  
(Venezuela and Trinidad)

\*Manuscript species of L. Woods (FMNH) and G. Miller (NMFS, Miami).

- 1b. Preopercular margin with four or more strongly developed spines at the angle . . . . . 4
- 4a. Gill rakers 37 to 41; snout 4.1 to 4.5 in head length; roof of mouth black, [D. XI+I, 23-24; A. II, 8-9] . . . . . *Stellifer* sp. A  
(Venezuela, Wintersteen and Chao, see footnote 3)
- 4b. Gill rakers 36 or fewer; snout 3.2 or less in head length; roof of mouth pale . . . . . 5
- 5a. Gill rakers 28 or fewer; upper jaw gape length<sup>9</sup> 2.8 or more in head length, mouth more or less ventral in position; when mouth closed, snout projecting in front of premaxillae (upper jaw) . . . . . 6
- 6a. Scales on top of head mostly cycloid; pelvic fins moderately long, its tip reaching (or almost) to vent; with a medial row of slightly enlarged teeth on lower jaw; swim bladder with tubular diverticula (Fig. 16C, D) . . . . . 7
- 7a. Gill rakers (7-9)+(13-16)=20-24; D. X-XI+I, 19-21; A. II, 8-10 (usually 9); diverticula on swim bladder short, digitlike (Fig. 16C) . . . . . *S. microps*  
(Colombia to Brazil, and West Indies)
- 7b. Gill rakers 8+(14-16)=22-24; D. X+I, 22; A. II, 9; diverticula on swim bladder very long, U-shaped (Fig. 16D) . . . . . *S. brasiliensis*  
(Brazil)
- 6b. Scales on top of head ctenoid; pelvic fins relatively short, tip falling far short of vent; without an enlarged medial row of teeth on lower jaw; swim bladder with bulb or bean-shaped diverticula (Fig. 16A) . . . . . 8
- 8a. Pelvic fin 5.3 to 6.0 in standard length, its tip ends slightly anterior to the tip of pectoral fin; eye 3.7 to 4.1 in head; gill rakers (8-9)+(15-16)=23-25 [D. XI+I, 20-22; A. II, 8] . . . . . *S. naso*  
(Venezuela to Brazil)
- 8b. Pelvic fin 6.8 in standard length, its tip ends much anterior to tip of pectoral fin; eye 4.6 to 5.3 in head; gill rakers (9-10)+(16-19)=26-28 [D. XI-XII+I, 21-22; A. II, 8 (rarely 9)] . . . . . *S. venezuelae*  
(Venezuela)
- 5b. Gill rakers 29 or more; upper jaw gape length (see footnote 9) 2.6 or less in head length, mouth more or less oblique and terminal in position; when mouth closed, snout equal to or projecting slightly in front of premaxillae (upper jaw) . . . . . 9
- 9a. Underside of lower jaw with 4 pores; gill arch dark; gill rakers at the corner distinctly longer than the filaments; posterior diverticula of the anterior swim bladder chamber short, pear-shaped [head cavernous, but not spongy to touch, tip of upper lip on horizontal with or above ventral margin of eye; snout usually not projecting beyond upper lip; D. XI+II, 20; gill raker (11-12)+(18-21)=30-33; eye 5.5-6.3 times in head] . . . . . *Stellifer* sp. B.  
(French Guiana and Northern Brazil; Wintersteen and Chao, see footnote 3)
- 9b. Underside of lower jaw with 6 pores; gill arch pale; gill rakers at the corner about equal or short of the filaments; posterior diverticula of the anterior swim bladder chamber small, knoblike . . . . . 10
- 10a. Head extremely cavernous, spongy to touch, tip of upper lip on horizontal with or above ventral margin of eye; snout usually not projecting beyond upper lip; D. XI-XII+I, 20-24; gill rakers (10-13)+(22-23)=32-36; eye 4.7-5.5

<sup>9</sup>Upper jaw gape length is measured from the tip of premaxillary to the corner of mouth (junction of premaxillary and dentary bones).



times in head . . . . . *S. lanceolatus*  
(Chesapeake Bay to Gulf of Mexico coasts, U.S.A.)

10b. Head cavernous, but not spongy to touch; tip of upper lip usually on horizontal line with or well below ventral margin of eye; snout projecting slightly beyond upper lip; D. XI+I, 23-24; gill rakers (10-12)+(19-22)=29-33; eye 5.5-6.2 times in head . . . . . *S. colonensis*  
(Panama, Puerto Rico and Haiti)

### Key to the Species of *Umbrina*

- 1a. Anal fin rays 7 or 8; mental (chin) barbel short; total gill rakers 19 to 20 . . . . . 2
- 2a. Eye larger, about 9.8 to 10.7% of SL; caudal peduncle circumferential scales 22; mental barbel with an apical pore; D. X+I, 24-25; A. II, 7; gill rakers (8-9)+(12-13)=20-22 . . . . . *U. canosai*  
(Southern Brazil to Argentina)
- 2b. Eye smaller, about 5.9 to 6.2% of SL; caudal peduncle circumferential scales 18 or 19; mental barbel with a pore on the middle anterior surface; D. X+I, 22-23; A. II, 8; gill rakers (7-8)+(11-13)=19-20 . . . . . *U. milliae*  
(Offshore Colombia and adjacent Caribbean seas)
- 1b. Anal fin rays 6; mental (chin) barbel relatively long and slender; total gill rakers 13 to 15 . . . . . 3
- 3a. Scale rows beneath spinous dorsal fin and longitudinal stripes approximately parallel to lateral line; scales in diagonal series from dorsal fin origin to lateral line 5 or 6; stripes on body less distinct; D. X+I, 23-26; gill rakers (5-7)+(7-10)=13-15 . . . . . *U. broussonetii*  
(Antilles)
- 3b. Scale rows beneath spinous dorsal fin and longitudinal stripes situated at an angle of about 30° to lateral line; scales in diagonal series from dorsal fin origin to lateral line usually 8, sometimes 7; stripes on body distinct; D. X+I, 26-31 (except for specimens from western Gulf of Mexico, which have slightly lower counts, 24-26); gill rakers (5-7)+(7-10)=13-15 . . . . . *U. coroides*  
(Gulf of Mexico to Brazil)

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