Fishes of the Western North Atlantic

This series of volumes, several of which are now available, presents authoritative studies of the anadromous, estuarine, and marine fishes presently known to frequent the western North Atlantic from Hudson Bay southward to the Amazon. For many years to come, these studies will rank as primary references for both amateur and professional persons interested in fishes and as significant working tools for students of the sea.

Shortly after Part One was published, the eminent ichthyologist, Carl Hubbs, said, "The first volume of FISHES OF THE WESTERN NORTH ATLANTIC sets a very high standard—perhaps so high a standard as to render difficult the completion of subsequent volumes by authors less well equipped than Henry Bigelow and associates in courage, energy, time, meticulousness, experience, library facilities and willingness to sacrifice much else for this one grand task. . . . In several ways this volume has been successfully adapted, in line with the policy set for the series, for the use and interest of sportsmen and general naturalists as well as ichthyologists. Features that lead to this desirable end . . .. include the excellent summaries of natural history information, the limited treatment of internal and particularly microscopical anatomy, the simplified keys, the complete coverage of the species in the clear-cut illustrations."

The over-all arrangement accords with our present knowledge of systematics, and each account is comprehensive in treatment, excellently illustrated, fully documented, and completely indexed. In addition to the descriptive details and discussion of orders, suborders, families, genera, and species, the keys and synopses relate distinguishing characters that facilitate identification. Details, aside from the description itself, include (when known) the color, size, development, habitat, general habits, food, parasites, predators, sporting qualities, range, abundance, and commercial importance. The accurate detailed illustrations, which aid particularly in identification, have been prepared by competent zoological artists, and for many species the indispensable illustration of the adult is supplemented by figures of developmental stages and by enlarged drawings of diagnostically important characters.

This series is especially useful as it brings together much information usually found only in many inaccessible publications. The annotated References direct the interested reader to more detailed information.

These volumes are published by the Sears Foundation at Yale University, with an editorial board composed of prominent students of the sea. Contributors of the individual sections have been selected as recognized authorities on their various groups.

Iselin

Fishes of the Western North Atlantic

Part Three of Fishes of the Western North Atlantic continues to provide the comprehensive and informative accounts of fishes that distinguish the first two volumes in this series.

This volume includes studies of nearly 100 species in 35 genera of "Bony Fishes."

Each account combines a critical review of published knowledge with original study and research, resulting in distinctive contributions to ichthyological literature not found elsewhere. These accounts, following precedent, have been written with the purpose of being useful to both amateur and professional ichthyologist, to people casually or vitally interested in the general phenomena of marine life, to sportsmen whose objectives are pleasure and relaxation, and to fishermen whose livelihood depends upon a knowledge of fishes.

The contributions on the sturgeons and gars bridge the gap between studies of the cartilaginous fishes, treated in Parts One and Two, and studies of the soft-rayed bony fishes that follow. To the sportsman, the widely renowned gamefish—salmon, trout, tarpon, ladyfish, and bonefish—will be of particular interest. To the amateur and professional fisherman, the shads, anchovies, menhaden and other herrings, sardines, charrs, smelt, and capelin will be of particular interest. To the ichthyologist and other students of marine biology, all contributions in this and other volumes will be essential adjuncts to future research and study.

The contributions in this volume were prepared by the following well-known students of ichthyology: H. B. Bigelow, M. G. Bradbury, J. R. Dymond, J. R. Greeley, the late S. F. Hildebrand, G. W. Mead, R. R. Miller, L. R. Rivas, W. C. Schroeder, R. D. Suttkus, and V. D. Vladykov.

Published by the Sears Foundation for Marine Research at the Bingham Oceanographic Laboratory, Yale University.

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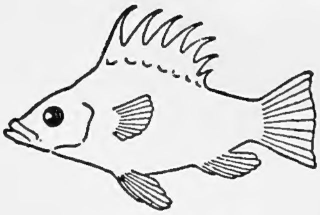
Fishes of the Western North Atlantic

MEMOIR
SEARS FOUNDATION FOR MARINE RESEARCH
Number I

Fishes of the Western North Atlantic



PART THREE

Soft-rayed Bony Fishes

Class Osteichthyes

Order Acipenseroidei, *Order* Lepisostei

Order Isospondyli, *Suborder* Elopoidea

Suborder Clupeoidea, *Suborder* Salmonoidea

NEW HAVEN 1963

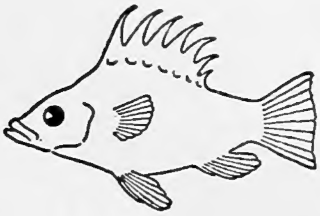
SEARS FOUNDATION FOR MARINE RESEARCH, YALE UNIVERSITY

PRINTED IN DENMARK FOR
SEARS FOUNDATION FOR MARINE RESEARCH
BINGHAM OCEANOGRAPHIC LABORATORY
YALE UNIVERSITY

Yngve H. Olsen, *Editor*

Bianco Luno's Printing, Copenhagen, Denmark

Fishes of the Western North Atlantic



Authors

HENRY B. BIGELOW
Museum of Comparative Zoology

MARGARET G. BRADBURY
Hopkins Marine Station

JOHN R. DYMOND
University of Toronto

JOHN R. GREELEY
New York Conservation Department

SAMUEL F. HILDEBRAND
U.S. Fish and Wildlife Service

GILES W. MEAD
Museum of Comparative Zoology

ROBERT R. MILLER
The University of Michigan

LUIS R. RIVAS
University of Miami

WILLIAM C. SCHROEDER
Woods Hole Oceanographic Institution

ROYAL D. SUTTKUS
Tulane University

VADIM D. VLADYKOV
University of Ottawa

NEW HAVEN, 1963

SEARS FOUNDATION FOR MARINE RESEARCH, YALE UNIVERSITY

Editorial Board

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Suborder Salmonoidea, Composite Authorship

Preface

THE SYSTEMATIST has divided the Superclass Pisces into two major groups: the elasmobranchs with an internal supporting skeleton of cartilage only, and bony fishes with a skeleton consisting of true bone in greater or lesser amount, or some derivation of it. Parts 1 and 2 of this series have already treated the sharks, skates, and rays, which comprise the elasmobranchs. With publication of Parts 3–5, this series enters the realm of bony fishes, by far the larger and more diverse of the two groups. The fishes treated here, commonly referred to as "soft-rayed bony fishes," include the anadromous sturgeons and gars, the wide-ranging and numerous groups of herring-like isospondylids, the little-known giganturoids, the broad assemblage of iniomes, and finally the strange-looking lyomerids. The Introduction and Table of Contents for each volume provide detailed information as to the subjects treated by the various authors.

The diverse shapes and characters of the forms detailed in these volumes, well known to the ichthyologist and many students of oceanography, constitute a notable display of the devious developments and modifications that have occurred in the course of evolutionary changes throughout time. This is also quite apparent to the average reader from a mere glance at the illustrations. Certainly none among nature's multiplicity of creatures is more bizarre than the oddly shaped hatchet fish with its tubular eyes and luminous organs, or the pelican fish with its long eel-like body and an enormous mouth that allows it the unusual ability to devour prey larger than itself. Indeed, so unusual and diverse are many of the groups treated here that even the trained systematist is put to it even to approximate their correct position on the ichthyological tree. Parallel with their diverse development in form, we also find pronounced modifications in their mode of life and habitat, as in the anadromous sturgeons and gars who have assumed the capacity to live in both fresh and salt water, and the deep-sea creatures who have adjusted to life at great depths under tremendous pressure where no sunlight penetrates.

In Parts 3–5, as in the two previous volumes, our objectives have remained the same—to provide for both professional and nonprofessional readers "critical reviews and revisions of each group rather than perfunctory compilations or mere reprintings of previously published works." The extent to which these objectives are fulfilled in each section will be determined by the usefulness of the account to both groups of readers.

With multiauthorship, instead of dual authorship as in the case of Parts 1 and 2, and with wide variation in both subject matter and available material, treatment and emphasis vary extensively according to authorship. All of the papers in these three Parts have been edited by me to a greater or lesser extent, except the Family Sternoptychidae in Part 4, which is published as it was submitted by the Editors-in-Chief.

All of these volumes should prove to be of considerable value in one way or another to the ichthyologists and to other students of the sea. To the average reader, and to sport and commercial fishermen in particular, Part 3 will be of special interest, for here is contained a large accumulation of facts about the tarpon, ladyfish, bonefish, shad, salmon, and trout, all of which are sportsmen's favorites, and about the sturgeon, anchovy, herring, pilchard, sardine, smelt, menhaden, and shad, many of which are important to man either directly as table food or indirectly as food for the larger inhabitants of the sea that are of economic value to man.

As in the case of Parts 1 and 2, the geographic area for these studies has been arbitrarily defined as that extending from the vicinity of Hudson Bay, just below the fringe of the Arctic, southward to the tropical latitudes of the Amazon, and seaward more or less to the mid-Atlantic, including Bermuda and all of the Caribbean archipelago. Although most of the accounts in these volumes treat fishes that spend at least part of their life-span in waters ranging from brackish to maximum salinities, a few, known at present from fresh water only, have been included when, in the author's opinion, they are likely to be taken in brackish or saline situations at some future date.

The format, general organization, and arrangement of the included material have been modified from Parts 1 and 2 only insofar as the subject matter and the demands of economy dictated. In Parts 1 and 2 there was excessive footnoting, and this has been eliminated largely by the use of numbered references. Long museum and institutional names have been replaced by the abbreviations listed in the Introduction for each Part.

It is regrettable that a number of deep-sea groups—particularly the isospondylous Alepocephalidae and Searsiidae and the iniomous Myctophidae and Neoscopelidae—are represented in their respective positions by only interim accounts, inasmuch as the detailed studies could not be completed for these volumes. The genus *Cyclothone*, though treated in somewhat more detail than the groups just noted, also awaits further study. It is hoped that these missing sections can be incorporated in the following Parts. While these volumes were in preparation, a comprehensive study of the Searsiidae by A. E. Parr has appeared in DANA Report No. 51, 1960, to which the reader is referred in lieu of a detailed account here.

It is of interest to note that the contents of these three volumes were originally intended for inclusion in Part 3 only, a commentary indicating quite clearly the impossibility of predicting the ultimate total number of volumes for this series. Because of the redistribution of the subject matter into three volumes, the sections on *Bony Fishes* and *Class Isospondyli* in Part 3, prepared originally when only one volume was assumed, now obtains for all three volumes. Of particular importance in these sections are the Keys—to Orders in *Bony Fishes*, and to Suborders and Families in *Class Isospondyli*.

The Keys and other material in these two sections have not been repeated in Parts 4 and 5.

Despite the ever-increasing progress of ichthyology, and of oceanography in general, and despite the impressiveness of the contents in these volumes, the ichthyologist, and anyone else for that matter who becomes acquainted with the contents here, cannot avoid being impressed with the great gaps in our knowledge of fishes, particularly with regard to the deep-sea groups in Parts 4 and 5. For all the study, observation, and exploration throughout the centuries, our present knowledge is indeed meager when compared to what is unknown. Taxonomic descriptions aside, our knowledge of the deep-sea fishes is limited primarily to speculation—to what may be surmised from their shape and color, stomach contents, or location of capture. Of many shallow-water forms we know little more. And even of those that have been subjects of extensive investigation, such as the salmon and some of the commercially important herring-like groups, much of what is known appears to be contradictory or debatable.

Many species are as yet unknown, and of those now known, many are still represented by only one or a few specimens, these often damaged. Not until larger and more extensive collections are assembled will it be possible to clarify the inter-relationships of many species and groups, to obtain a more complete knowledge of distribution in area and depth, and much other important information. For the great majority of deep-sea fishes, the records of depth distribution are sparse or crude at best, a lack that stems largely from the fact that most of the deep-sea collections have been taken with open nets rather than closing nets. With the former device, one knows only that a collected specimen frequented some level of the water column between the surface and the estimated fishing depth of the net. Even with the closing net, exact depth is questionable because of uncertainties in determining the wire angle. Add to this the fact that the scientific expeditions that have explored the depths have been few and widely dispersed. Considerable areas of all oceans, more so in some than in others, still remain unexplored.

Even as the present volumes constitute a tribute to the expeditions and countless investigators who have contributed to our present knowledge of fishes, so do they reemphasize, by what is not known, the need for earnest and continued expansion of marine exploration and investigation, particularly at a time when exploration of the "sea" beyond our atmosphere holds the stage. Especially notable in Parts 4 and 5, dealing mainly with the deep-sea isospondylids and iniomes, are the contributions of the OREGON, SILVER BAY, and COMBAT, whose surveys, sponsored by the U.S. Fish and Wildlife Service, have provided a wealth of study material. Similarly, the contributions of specimens obtained from stomach contents during investigations of the tuna and other commercially important fish have enhanced many accounts; in fact, a number of species, presumably fast-swimming forms that are consistently successful in evading the slow-moving nets, are known only from such a source. Hand in hand with more extensive collecting must go technical development of gear such as closing nets, devices for accurate measurement of wire angle, underwater luminescent and photographic equipment, and a long list of other essentials. For experimental work at sea, fully equipped floating laboratories are needed to study live specimens at the source. And perhaps most important of all is the need for an increasing number of well-trained marine biologists and technicians.

The Sears Foundation extends its gratitude to Henry Bigelow and Giles Mead for their various contributions in bringing these three volumes to fruition, particularly for harvesting the manuscripts. To those authors who have given their generous cooperation in achieving uniformity in the presentation of the material and in supplying additional information, I extend special thanks. Many of the authors have acknowledged the help and cooperation of individuals and institutions; to them, and particularly to the many who have been omitted, I add the gratitude of the Sears Foundation. It is also a special privilege to note the continued interest and confidence of Henry Sears, who has generously aided in the financing of these volumes, and to acknowledge financial support of various author investigations by the National Science Foundation. In the past two or three years, the Editorial Board has been expanded by the addition of Daniel Cohen, Giles Mead, and Daniel Merriman to its roster; to them and to the older members of the Editorial Board, the Sears Foundation is grateful for many and varied services.

Finally, it is with no small regret that I note the discontinuance of Albert Parr's active participation in the functions of the Sears Foundation and in the publication of these *Memoirs* and the *Journal of Marine Research*, both of which were conceived and brought into being as a result of his sincere and deep interest in all things marine and of his keen perception of the need for vehicles to distribute the thoughts and scientific observations of an expanding oceanographic community. The results seen in the publications themselves speak for his contribution far more significantly than mere words

YNGVE H. OLSEN
Editor

May 1963

Introduction

PART 3 OF THIS SERIES deals with the more primitive groups of soft-rayed bony fishes. The volume commences with a characterization of the class Osteichthyes (bony fishes) and comparison of this group with the class Chondrichthyes (elasmobranchs), followed by a characterization of the subclass Actinopterygii and a key to the various orders dealt with here and in Parts 4 and 5: Acipenseroidei, Lepisostei, Isospondyli, Giganturoidei, Iniomi, and Lyomeri, all of which were originally to be included in this volume. The characterization and discussion of the Isospondyli concludes with a short key to the suborders and an extensive key to the external characters of all the families of the orders noted above; this, then, also applies to Parts 4 and 5 as well as to this volume. Because of the large number of groups in the Isospondyli, only part of the families, mostly shallow-water, are included in this volume; the rest, mainly deep-sea, are relegated to Part 4. Thus, in addition to the sturgeons and gars, this volume includes accounts of the tarpon, ladyfish, bonefish, the numerous anchovies, the herring, menhaden, shad, sardine, pilchard, gizzard shad, round herring, salmon, trout, and smelt.

The geographic area covered extends from Hudson Bay southward to the Amazon and seaward more or less to the mid-Atlantic, with Bermuda and the Caribbean areas included. For the most part, only fishes living in brackish water or salt water have been included.

Unfortunately, the accounts of the Alepocephalidae and Searsiidae could not be completed for inclusion in this volume. These are therefore represented by brief interim accounts that contain enough information for general identification of specimens in this category.

In these volumes, museum and institutional names have been abbreviated according to the following list:

AM — Amsterdam Museum, Holland
AMNH — American Museum of Natural History
ANSP — Academy of Natural Sciences of Philadelphia
BLBG — Biological Laboratory, U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries, Brunswick, Georgia
BMNH — British Museum (Natural History), London
BNM — Bergens Museum, Norway

BOC — Bingham Oceanographic Collection, Yale University
BU — Boston University
BrU — Brown University
CAS — California Academy of Sciences
CF — Carlsberg Foundation, Copenhagen
CFG — California Division of Fish and Game
CM — Carnegie Museum
CNHM — Chicago Natural History Museum
CU — Cornell University
FSM — Florida State Museum
IJ — Institute of Jamaica, B. W. I.
IRSNB — Institut Royal des Sciences Naturelles de Belge, Belgium
LMNH — Leiden Museum of Natural History, Holland
MCZ — Museum of Comparative Zoology, Harvard University
MMF — Museu Municipal do Funchal, Madeira Islands
MHNBA — Museo de Historia Natural de Buenos Aires, Argentina
MNHN — Muséum National d'Histoire Naturelle, Paris
MOM — Musée Océanographique, Monaco
MRAC — Musée Royal d'Afrique Central, Tervuren
MSNF — Museo di Storia Naturale, Firenze
NHR — Naturhistoriska Riksmuseum, Stockholm
NYZS — New York Zoological Society
POFI — Pacific Oceanic Fishery Investigation, U.S. Fish and Wildlife Service (Bureau of Commercial Fisheries), Honolulu, Hawaii
ROMZ — Royal Ontario Museum of Zoology, Canada
SIO — Scripps Institution of Oceanography
SU — Natural History Museum, Stanford University
TU — Tulane University
UCLA — University of California at Los Angeles
UF — University of Florida
UI — University of Indiana
UL — University of Louisville
UMIM — University of Miami Ichthyological Museum
UMML — University of Miami Marine Laboratory
UMMZ — University of Michigan Museum of Zoology
USNM — United States National Museum
UT — University of Texas
UW — University of Washington
VOM — Vanderbilt Oceanographic Museum
WHOI — Woods Hole Oceanographic Institution
ZMA — Zoological Museum, Amsterdam
ZMC — Zoological Museum, Copenhagen

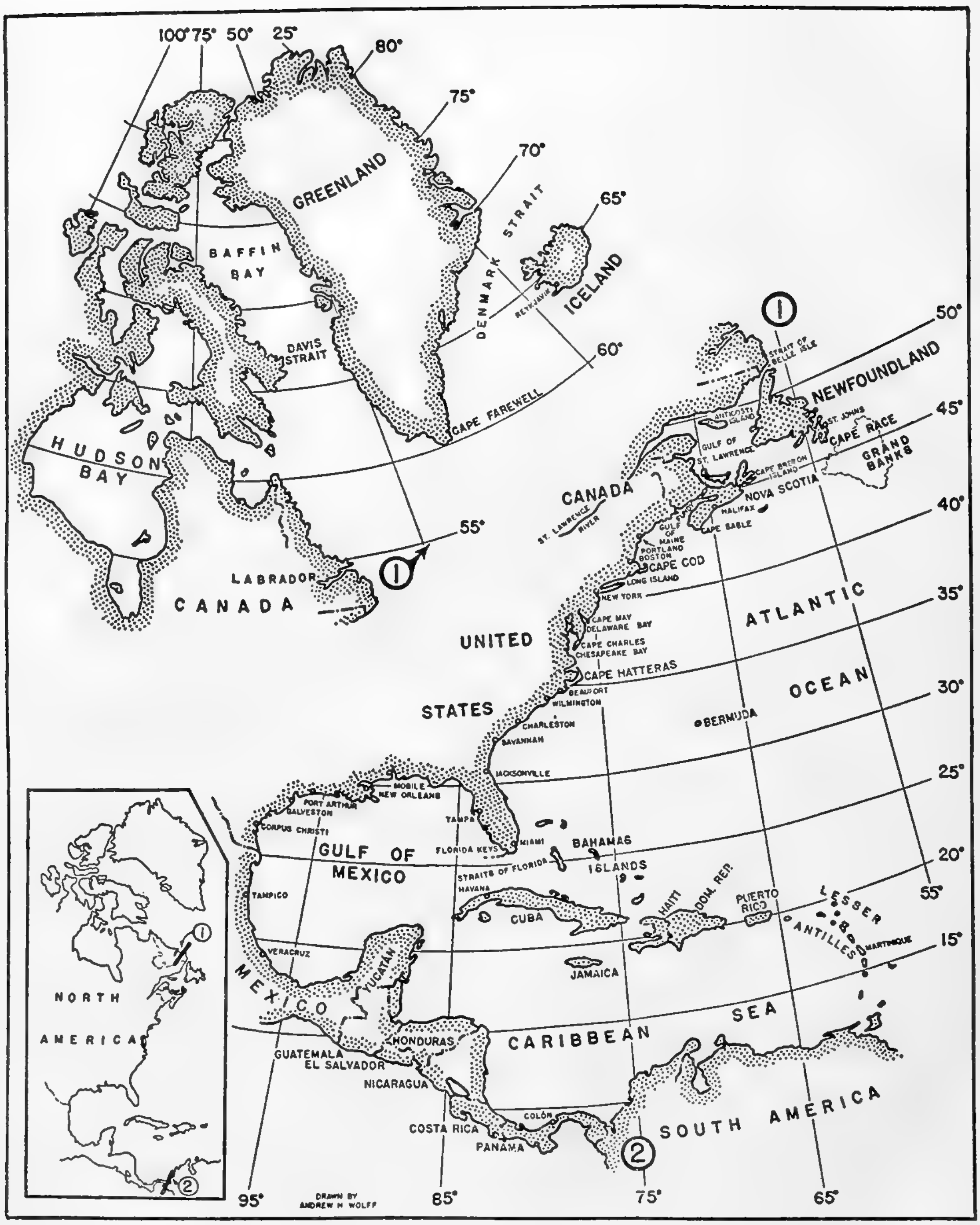
Of the other abbreviations used in this volume, the following require explanation here:

SL — standard length
FL — fork length
hl — head length
m.w. or m.w.o. — meters of wire or meters of wire out, used in lieu of depth of capture when discussing the catches of nets fished at indeterminate depths and not equipped with closing devices.

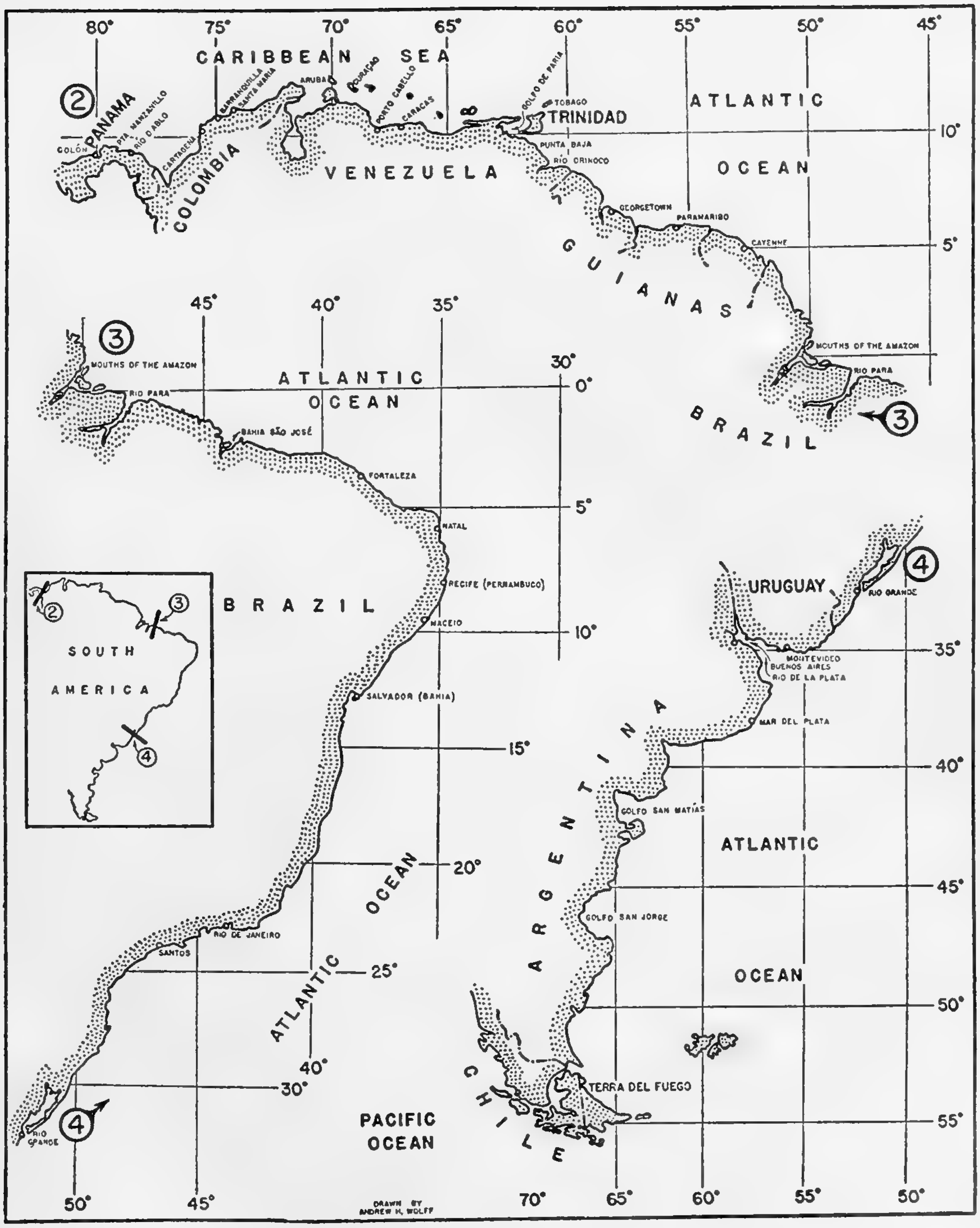
Finally, acknowledgment with gratitude is extended to all of the authors who contributed to this volume and to the institutions that supported their work; to the Sears Foundation for Marine Research, Yale University, and to Mr. Henry Sears for his assistance in financing publication; to the National Science Foundation for funds to finance part of the cost of research (through grant NSF G 7123); and to the numerous ichthyologists and many others who have contributed information for this volume.

HENRY B. BIGELOW
Editor-in-Chief

March 1963



North America



South America

Bony Fishes

Superclass, Class, Subclasses, and Orders

HENRY B. BIGELOW
Museum of Comparative Zoology
Harvard University

ACKNOWLEDGMENTS

With grateful acknowledgment for many helpful criticisms and suggestions from William W. Anderson, U. S. Fish and Wildlife Service; Frederick H. Berry, U. S. Fish and Wildlife Service; Rolf L. Bolin, Hopkins Marine Station; Daniel M. Cohen, U. S. Fish and Wildlife Service; Myvanwy M. Dick, Museum of Comparative Zoology, Harvard; Robert H. Gibbs, Boston University; Joseph Gregory, Peabody Museum of Natural History, Yale; N. B. Marshall, British Museum (Natural History); Giles W. Mead, Museum of Comparative Zoology, Harvard; James E. Morrow, University of Alaska; George S. Myers, Natural History Museum, Stanford University; Yngve H. Olsen, Bingham Oceanographic Laboratory, Yale; Alfred S. Romer, Museum of Comparative Zoology, Harvard; Bobb Schaeffer, American Museum of Natural History; William C. Schroeder, Woods Hole Oceanographic Institution; Leonard P. Schultz, U. S. National Museum; Royal D. Suttkus, Tulane University; John Tee-Van, New York Zoological Society; Ethelwynn Trewavas, British Museum (Natural History); Vladimir Walters, University of California; and Norman J. Wilimovsky, University of British Columbia.

Superclass PISCES

Both the cartilaginous fishes (*8*) and the bony fishes have been grouped together under the name Pisces by Goodrich (*45*) as a Grade intermediate between Branch and Subgrade, by Berg (*4*) as a Series intermediate between Superclass and Class, and by Bertin and Arambourg (*31*) as a Superclass. This last arrangement, with Pisces ranked as a Superclass, is accepted here to embrace both cartilaginous fishes (Chondrichthyes) and bony fishes (Osteichthyes). The cyclostomes, not regarded here as fishes in the usual sense, are considered a separate Branch (Agnatha) of the vertebrate Subphylum Craniata.

Bertin and Arambourg (*31*: 1956) have expanded the Superclass Pisces to include the fossil Placodermi (including the Acanthodii and the Athrodiri); this ancient group, however, was only remotely related to either the living cartilaginous fishes or the living bony fishes. See Romer (*73*: 38–59) for an account of the placoderms and their evolutionary pattern.

Class OSTEICHTHYES

Characters of Living Members. The internal skeleton contains true bone in greater or lesser amount, especially in the regions of the skull, the jaws, and the pectoral arch. In most the jaws are well developed, but in a few they are greatly reduced. The palatopterygoid part of the upper jaw-complex is fused solidly with the lower surface of the skull in the Dipnoi (lungfishes) but not in the others, with one exception (*15*: 273). The teeth are usually embedded in the bone (but see p. 6 for exceptions). In a few there is a spiracular opening between the jaws and the hyoid arch (polypteroids and some acipenseroids). The external opening of each nostril is typically double but is single in a few (p. 6); the nasal sac ends blindly in most but opens internally into the mouth in some. There is only one external gill opening on each side, and the two openings are often united across the throat; the common chamber into which the internal gill clefts open is roofed over by a dermal opercular flap supported in most cases by a series of opercular bones. A typical bony fish has four or five pairs of gill arches (the fifth the smallest) and four to six pairs of internal gill clefts.[1]

The majority has two sets of paired fins—pelvic and pectoral. The pectoral girdle is well developed and is attached at its upper end to the temporal region of the skull in the great majority (see p. 6 for exceptions). The endoskeletal support of the pectoral and pelvic fins consists of either one or two series of short basal elements;[2] in the typical pectoral fin these elements are in parallel or fan-like arrangement (Actinopterygii in general, p. 11), with the outer part of the fin supported by fin rays; but in some there is a jointed midrib with either a series of short side branches on each side, as in the Dipnoi, or a terminal fan of jointed rays (Fig. 2), as in the living coelacanth *Latimeria*

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[1] According to Tchernavin (*84*: 284), there are six gill clefts in *Eurypharynx* (gulper eel).

[2] The basalia of the pectorals are fused in *Dallia* to form a single plate; in *Lophius* there are only two; and in general they are much reduced in the pelvics.

(*31*: 2567, 2570, fig. 1840). The marginal parts of both the single and paired fins are supported, at least in part, by jointed (segmented) and usually branched rays which are either bony or fibrous in composition; in some the rays are apparently single,[3] but in the great majority each ray consists of a right-hand and left-hand half, the halves closely pressed together (Fig. 1). In a great majority the dorsal, caudal, and anal fins are separated, one from the next, but in some these fins are continuous around the tip of the tail.

In a great majority the scales are wholly of mesodermic origin and are embedded in the skin below the epidermis. The outer surface of the scales consists of a simple calcified layer in most but of an enamel-like substance (ganoine) in a few. In most the scales persist throughout life and grow as the fish grows, generally without increase in number or modification except as they may be replaced when accidentally lost. However, in some of the goby-like fishes, additional scales are normally interpolated with growth[4] in the region of the caudal peduncle.

The anal, genital, and urinary tracts open separately to the exterior in most but into a common cloacal pouch in a few. Some of the members of most of the major groups have a swim bladder developed as a diverticulum from the dorsal side of either the oesophagus or the stomach; a few (Dipnoi, polypteroids) have a functional lung (or lungs) developed as an outpocketing from the ventral side of the pharynx.[5]

The notochord is persistent and unconstricted from end to end in a few, but in most it is sharply constricted in its passage through the vertebral centra, often to thread-like proportions, if it is not obliterated altogether.

Nomenclature.[6] The name Osteichthyes, proposed by Howes (*34*: 78, 87), has been adopted by Goodrich (*45*: 210) and by numerous subsequent students, including Berg (*3*: xv), Goodrich,[7] Romer (*73*: 75), Schultz and Stern (*77*: 227), Matsubara (*47*: 78, 154), and Bertin and Arambourg (*31*: 1978, 2068). It is equivalent to the Class Pisces of Linnaeus (*46*), except that Linnaeus excluded the genera *Acipenser* (sturgeons) and *Lophius* (anglerfishes); it is also equivalent to the Subclasses Lophobranchii plus Potomabranchii of Bonaparte (*10*: add. 13), with the addition of the lungfishes, which were unknown to Bonaparte;[8] it also equals: the combined Subclasses Dipnoi, Teleostei, and Ganoidei of Müller (*53*: 201–204); the Class Pisces as restricted by Jordan (*39*: 108) and by Regan (*71* [1929]: 305); the Teleostomi of Stensiö;[9] the Classes

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[3] The situation in this respect is not known for either the coelacanths or the Dipnoi.

[4] Steindachner and Döderlein (*81*: 269) have reported this for *Cepola;* Koumans (*43*: 267–279) has described in detail and pictured clearly a similar situation for *Oxyeleotris.* Furthermore, J. R. Dymond (personal communication) states that he has found in salmon and trout "....what appear to be rows or partial rows [of scales] that appear to have been developed later than the rows above and below"; and Hubbs (*36*: 82) has reported an increase, caused by parasites, in the number of scales in the genus *Platygobius.*

[5] Millot and Anthony (*31*: 2584) have reported a vestigial lung ("poumon degenere") of large size in the living coelacanth *Latimeria.* For a general survey of the relation between swim bladder and lung of living fishes, see Romer (*74*: 344–345, 347–350).

[6] See Myers (*54*: 31–40) for nomenclature of terms that have been used for the higher categories of fishes.

[7] Ref. (*30*: xvii); considered a Subgrade of Class Pisces.

[8] Ref. (*10*: 16); name Dipnoa used for Amphibia.

[9] Ref. (*82*: iii); taxonomic rank not stated.

Dipnoi and Teleostomii, combined, of Berg (*4*); the Teleostea of Fowler (*27*: 53); and the Class Osteichthyes of Bertin and Arambourg (*31*: 1978).

The Class Osteichthyes as defined above includes all of the living groups of fishes apart from the elasmobranchs (sharks and batoids) and chimaeroids. The cyclostomes are not regarded here as "fishes" in the usual sense of the word.

Bony Fishes (Osteichthyes) Compared with Cartilaginous Fishes (Chondrichthyes). All living bony fishes differ fundamentally from all living cartilaginous fishes in that the internal skeleton of the former consists of true bone in greater or lesser amount, or of some derivation of true bone, whereas the skeleton of living elasmobranchs and chimaeroids contains no true bone. Bony fishes differ to an even greater extent from the cyclostomes in that the former have well-developed jaws and (typically) two olfactory organs. The bone of the Osteichthyes represents in part the ossification of the primary skeletal cartilages by the action of bone-forming cells from without (for details, see Goodrich, *45*: 65–67); but in part, especially in the regions of the skull and pectoral arch, it consists of so-called membrane bone, which is not preformed in cartilage. In neither case is it derived from calcifications of the kind that stiffen the cartilaginous skeletons of elasmobranchs and chimaeroids.

Due to the presence of bone, the skull of all living bony fishes is marked by sutures,[10] which is not so in the cranium or brain case of living cartilaginous fishes. However, this seems an appropriate place to note that in fossil placoderms, which are only remotely related to the bony fishes, the internal skeleton was more or less bony; many of them were more or less completely armored with bony plates, and their skulls showed sutures corresponding to those in Osteichthyes. Also, many of the fossil Agnatha, of which the cyclostomes of today are commonly regarded as degenerate descendants, were variously encased in bony armor, and at least in some cases their skulls were marked with sutures.[11]

Hardly less diagnostic for most of the living bony fishes, including the living coelacanths,[12] is the presence (typically) in some part of their fins of segmentally jointed rays[13] (mostly branched) which are either bony or fibrous. These are the soft rays known to every student of fishes. Even among the living Dipnoi (lungfishes), some of the fin rays (hair-fine in this group and of doubtful homology) are segmented, though most of them continue unsegmented throughout life, thus resembling superficially the horny rays (ceratotrichia) of sharks (for details, see Goodrich, *28*: 480–482). In the fossil Dipnoi, however, all of the fin rays were segmented.

No living elasmobranch or chimaeroid has in its fins any structures that correspond structurally to the segmented fin rays of bony fishes. Thus the horny fin rays of sharks are not jointed, and they grow inward from the outer margin of the fin, not outward

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[10] The bony neurocranium of the extinct palaeoniscoids, a primitive group of bony fishes, is not marked with sutures (Stensiö, *83*; Rayner, *65*: 287).

[11] For a readable account of these ancient groups, see Romer (*73*: 25, 38).

[12] For the fin rays of *Latimeria*, see Millot and Anthony (*31*: 2567, 2570, fig. 1840).

[13] The fin rays are not jointed in the lyomerids, the trachypteroids, the stylophoroids, and perhaps in other groups as well.

from its base as the fin rays grow in actinopterygian fishes,[14] and presumably in coelacanths. Although the radial cartilages that support the wing-like pectoral and pelvic fins of skates and rays recall in appearance the jointed fin rays of bony fishes, they are a part of the internal skeleton; and they are single whereas the soft rays of bony fishes are double (p. 3; Fig. 1).

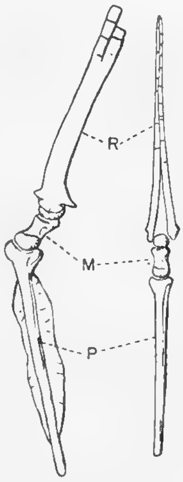

Figure 1. Soft dorsal fin ray of *Esox lucius* (pike) with its skeletal support; Left-lateral view; Right-front view. R ray; P basal segment, and M median segment of supporting radial. After Goodrich, emended somewhat.

Although the fin rays of the Dipnoi, which are intermediate between elasmobranchs and actinopterygian bony fishes in this respect, are jointed, they resemble the horny fin rays of elasmobranchs and chimaeroids in their growth inward from the outer edge of the fin instead of outward from the base, in their arrangement in two series, and in their seemingly single nature.[15]

The contrast between bony and cartilaginous fishes is further blunted by the presence of hair-thin unjointed horny rays like those of the elasmobranchs in the so-called adipose dorsal fin of certain bony fishes (salmons and catfishes)[16] and in the free edges of the rayed fins of other bony fishes.[17]

All of the other differences that have been proposed as alternative between bony and cartilaginous fishes are beset with exceptions. For example, it has been cited repeatedly that the dermal fold, which roofs the common branchial cavity (into which the internal gill clefts open), is supported in bony fishes by a series of opercular bones, whereas in the only living cartilaginous fishes that have a corresponding dermal flap (chimaeroids) it is supported by a series of cartilaginous rays only. The polyodontids (paddlefishes), however, have only vestiges of the opercular bones; in the giganturoids, in some stomiatoids, and in some eels they are ossified but little; and in the lyomerids (an eel-like group of deep-sea fishes with enormously distensible mouths) and in the lophobranchs they are lacking altogether.[18]

Below the gill covers, the great majority of bony fishes has a series of parallel branchiostegal rays, but these rays are lacking in the elasmobranchs, chimaeroids, Dipnoi, acipenseroids, and deep-sea Lyomeri.

The scales of bony fishes are deeply implanted in the skin, are wholly of mesodermal origin, and they usually persist throughout the life of the fish (for exceptions, see ftn. 4);

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[14] For the development of soft rays (leptotrichia) in the actinopterygians, see especially Pennant (*63*: 190–195) and Bertin (*31*: 735).

[15] For the structure, growth, and homologies of the fin rays of the different major groups of living fishes, see especially Goodrich (*28*: 480–491), Eaton (*25*: 195–200), and Bertin (*31*: 731–736).

[16] According to Dr. George S. Myers (personal communication), what appear to be ossified spines are developed in the adipose fin of some African catfishes, and with age in some characids of the genus *Serrasalmus;* also the loricariid and calichthyid catfishes have the adipose fin supported by an initial bony spine.

[17] For a review of early literature on this subject with accounts and illustrations of these rays in the adipose fin of salmon and trout, see Valette St. George (*88*: 187–192, pl. 15); for a more recent review, see Goodrich (*28*: 473–477).

[18] For a discussion of the evolution of the operculum in different groups of fishes, fossil and living, see Eaton (*24*: 42–46).

in elasmobranchs and chimaeroids the so-called placoid scales are tooth-like in structure, have an extensive pulp cavity, and are tipped with an enamel-like substance of ectodermic origin. Furthermore, the scales of a shark are not only short-lived but increase in number as it grows. Although the presence of bony-fish scales is positively diagnostic for those fishes that have them, their absence is not negatively diagnostic, for it is common knowledge that scales are wholly lacking in some bony fishes. Furthermore, certain groups of the bony fishes have placoid denticles of the elasmobranch type on their bony scales, e. g. the polypteroids, the lepisosteids (gars), and some ostariophysids (catfishes); and some of this last group have placoid denticles on their fin spines as well.[19] Denticles, believed to be placoid in nature (an interpretation calling for verification), have also been described for the snouts of young *Xiphias* (swordfish) and young *Istiophorus* (sailfish) (*13*: 321, pls. 1, 2); and Dr. Ethelwynn Trewavas informs us that they are present on the sucking disc of remoras as well (personal communication).

It has been stated repeatedly that, whereas the teeth of elasmobranchs are simply implanted in the gums, those of most bony fishes are set in the bone. The polyodontids (paddlefishes), however, and certain Salariinae (blennies) parallel the elasmobranchs in this respect, their teeth having no special connection with the jaw bones; and the teeth in *Plecoglossus* (related to the salmonoids) are attached to the jaws by connective tissue only (*14*: 437).

The nasal openings are single on either side among the elasmobranchs in general and among the chimaeroids, but among bony fishes they are double (typically) on each side. However, some bony fishes, e. g. pomocentrids and cichlids, have only one nasal opening on each side. On the other hand, it has been discovered recently that each nasal opening in one genus of torpedo rays (*Diplobatis*) is divided into two (*58*: 482, fig. 2; *7*: 562, 563, fig. 7).

Various texts have emphasized the mode of suspension of the pectoral girdle as a diagnostic feature: it is attached to the skull in typical bony fishes; it is not connected at all to the axial skeleton in living sharks and chimaeroids; and it is attached to the anterior part of the vertebral column in batoids. However, among bony fishes, the pectoral girdle has lost its attachment to the skull in the deep-sea giganturoids and saccopharyngoids, in the amphipnoids (a group that is eel-like in appearance but differs widely from the true eels in anatomy), and in the Apodes (eels) as a whole; and in some Apodes (Muraenidae) the pectoral girdle is lacking altogether. On the other hand, the girdle is attached by a ligament to the third or fourth vertebra in the Opisthomi.[20]

The presence of either a swim bladder or a functional lung is diagnostic for such of the bony fishes as have either, unless a small diverticulum from the dorsal side of the oesophagus, observed in embryos of certain sharks by Miclucho-Maclay (*49*: 448, pl. 5), represents the rudiment of a swim bladder. But the absence or presence of a

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[19] For illustrations conveniently available of placoid denticles among bony fishes, see especially Goodrich, in Lankester (*45*: 231, fig. 201; 289, fig. 262; 291–292, figs. 264, 265). For a recent account, with references and excellent illustrations of these denticles among living catfishes, see Ørberg (*56*: 487, figs. 4C, 4D).

[20] An Order of eel-shaped freshwater fishes of doubtful affinity, known from tropical Africa, the Euphrates, and southern Asia north to Peking (*68*: 219).

swim bladder is not a feature of much direct service to the systematist, for groups that differ widely in other respects may agree in lacking the swim bladder, and vice versa.[21]

In some families, even where most of the genera have a swim bladder, others do not. Familiar examples of such families are the Blenniidae (blennies), the Polynemidae (threadfins), and the Scombridae (mackerels); in the last group the chub mackerel (*Pneumatophorus*) has a swim bladder while the common mackerel of the North Atlantic (*Scomber*) has none (Starks, *92*: 223).

It has long been emphasized that, while the gill folds of elasmobranchs and chimaeroids are attached to the interbranchial septa outward nearly to their tips, those of the higher groups of bony fishes are free from the septa for most of their lengths. These extremes, however, are bridged on the one hand by the Dipnoi, where the gills reach only slightly beyond the septa, and on the other hand by the polypteroids, acipenserids (sturgeons), and lepisosteids (gars), where they extend only a little farther outward. Furthermore, most of the bony fishes lack functional respiratory folds on the anterior (hyoidean) wall of the first gill pouch, such as are characteristic of elasmobranchs and chimaeroids; but the acipenserids and lepisosteids are exceptions to this rule, as is the living coelacanth *Latimeria* (Millot and Anthony, *31*: 2584).

The ventral or pleural ribs between the adjoining surfaces of the peritoneum and body wall are diagnostic for such of those bony fishes as have them, for the ribs of the living cartilaginous fishes[22] that have any lie in the horizontal septum that separates the musculature of the trunk into an upper and lower division.[23] Many bony fishes, however, lack ribs of any sort: the lophobranchs (*26*: 28–30), for example, the giganturoids (*70*: 57), the stylophorids (*80*: 21), and some trachypteroids (genus *Agrostichthyes*) (information from Vladimir Walters). The tetraodontids (swellfishes), the diodontids (porcupinefishes), and the ostraciodontids (trunkfishes), among the plectognaths, lack ribs (*76*: 8, 10; *41*: 325, pls. 15, 16), while their relatives, the Balistidae (triggerfishes) and Aleuteridae (filefishes), have ventral ribs.[24] It is also evident from a glance at the skeleton of *Lophius* (anglerfish) that it is ribless, as are the Ogcocephalidae (batfishes), by personal observation, and *Rhynchoceratias* (*60*: 13), among pediculate fishes.

So-called dorsal ribs are not peculiar to the elasmobranchs alone, for the polypteroids, salmonids (salmons), some clupeids (herrings) (*26*: 209), Esocoidea (pikes) (*4*: 242, 429), and balistids (triggerfishes) among the plectognaths (*41*: 304) have both ventral ribs and ribs that occupy the dorsal position. However, it appears that

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[21] N. B. Marshall contributes the information (personal communication) that the major groups of bathypelagic fishes, such as stomiatoids, deep-sea salmonoids, and Miripinnati, can be characterized by the structure of the swim bladder.

[22] The chimaeroids and some of the rays are ribless.

[23] But these ribs are considered by Emelianov (*26*: 244) to be homologous in their development with the pleural ribs of bony fishes.

[24] Regan (*66*: 285, 286, fig. 56) interpreted the rib-like bones of the Balistidae and Triacanthidae as intermuscular in nature and "not bordering the abdominal cavity." But it seems clear from Kashkaroff's account (*41*: 303, 325, pls. 12–14) and from our own dissections that they are true ventral ribs and do embrace the body cavity.

these dorsal ribs may not be homologous, embryologically, with those of the elasmobranchs (*26*: 215–217).

A spiral valve in the intestine, which is universal in elasmobranchs and chimaeroids, is well developed in the living coelacanths (*50*: 426, 2582, Millot and Anthony), in the Dipnoi, and in the polypteroids alone among bony fishes; but it is represented in vestigial form in the acipenserids (sturgeons) and polyodontids (paddlefishes). A structure that more or less suggests the elasmobranch spiral valve has been reported also as occurring in *Chirocentrus*, an Indo-Pacific genus falling among the clupeoids (*18*: 160, pl. 565; *45*: 116, fig. 77A, Goodrich), in *Argentina silus* (the common herring smelt of the North Atlantic),[25] in *Salmo gairdneri* (rainbow trout), *Thymallus* (grayling), and the Coregonidae (whitefishes) among the salmonids (information from Daniel Cohen), in *Macropinna* among the Argentinoidea (*15*: 282), in the young of the characid genus *Curinata* (information from G. S. Myers), and in *Alepocephalus* (*18*: 172, 176). But the so-called spiral valve of these isospondylous fishes probably is not homologous with the spiral valve of elasmobranchs and chimaeroids.[26]

On the males of living cartilaginous fishes among which internal fertilization in the female is universal, a copulatory organ commonly called a clasper is developed in connection with each pelvic fin. But the male copulatory organ of the few bony fishes whose eggs are fertilized internally is single (typically) and has no connection with the pelvic fins, being developed either from the genital papilla on the urogenital orifice, or in connection with the anal fin, or as a special structure on the chest. However, the phallostethids (Indo-Australian freshwater fishes of the Order Percesoces) are an exception, for their "much modified pelvic fins and girdle" join in the formation of the copulatory organ (*2*: 478).

Finally, such of the bony fishes as pass their lives in salt water maintain their body fluids in osmotic balance with the surroundings in one way, elasmobranchs in another. In each case it is a problem of maintaining the concentration of salts in the blood at a level lower than that of the surrounding sea water; the osmotic pressure in the body fluids of marine teleosts is only about 40°/₀ of that of sea water.[27] Elasmobranchs solve this problem by retaining in their blood and tissues much of their nitrogenous wastes in the form of urea; thus they raise the total concentration of materials in solution to a level that is nearly as high as, or even higher than, that of the surrounding sea water without increasing the salt concentration (*74*: 393). As a result of this mechanism, the marine sharks and rays have no special need of conserving water. According to Black, "They rarely drink salt water and obtain free water in their food" (*12*: 187). Marine bony fishes, never having chanced on this device, prevent an accumulation of salt-ions

[25] Kendall and Crawford (*42*: 10, fig. 1A) pictured *Argentina* as having a complete spiral valve, but Cohen writes that while he has noted spiral thickenings in the intestine of various Argentinidae, including six specimens of *Argentina silus* (*16*: 121), in none of these last did he "observe a functional spiral valve as figured by Kendall and Crawford."

[26] According to Jacobshagen (*9*: 611), the structure that has been called by this name among the Isospondyli actually represents a series of simple circular ridge-like thickenings of the inner surface of the intestine. For further discussion, see Cohen (*16*: 96, 98).

[27] Estimated by Denton and Marshall (*21*: 754) from data assembled by Krogh (*44*: 130 FF).

in their body fluids by a complicated excretory process. Thus, via their gill membranes, they excrete most of the salt from the sea water that is consumed, and at the same time they reduce their excretion of water to the minimum that will provide the necessary amount of urine. In some groups this reduction is effected by atrophy or loss of the glomeruli,[28] but in other saltwater groups that still retain the glomeruli, including the living coelacanths (*31*: 2588, Millot and Anthony), this goal appears to be reached by constriction of the glomerular arterioles.[29]

We have yet to learn how bony fishes that spend part of their life in fresh water and part in salt water or that suffer no apparent harm from rapid changes in the salinity of the water manage to maintain themselves in osmotic balance with their surroundings. This applies equally to such of the cyclostomes as spawn and pass through their early stages in fresh water but make their growth in salt water. Those that pass their entire life in salt water are isotonic to their surroundings, or very nearly so (see especially McFarland and Munz, *48*: 348).

Subclasses. Students of phylogeny have disagreed widely concerning the relationships of the various groups that make up the ichthyological tree. In the first instance, a decision on the best arrangement of the various groups of the Class Osteichthyes into Subclasses depends on the relationship of the Dipnoi (lungfishes) to the other bony fishes. Johannes Müller (*53*), writing in 1844, rated the Dipnoi as a separate Subclass of the Class Pisces, and this scheme was later adopted by Smith Woodward (*91*: 234), by Goodrich (*45*: 230), by Bridge, and by Jordan (*39*). Berg's (*4*) later characterization of them as a class of the *Series* Pisces embodies this same point of view, as does Bertin and Arambourg's treatment of them as the Subclass Dipneusti of the Class Osteichthyes (*31*: 2522). It is likely, indeed, that this scheme would still be adopted generally were our knowledge of the Dipnoi limited to those of today, for these are set apart from all other living groups of bony fishes by the solid fusion of the palatopterygoid-quadrate elements of the upper jaw-complex with the lower surface of the skull, by the general morphology of their brains and hearts, and by their total lack of both premaxillary and maxillary bones (a significant difference); in addition, the living Dipnoi are set apart further from all other bony fishes except the coelacanths by the presence of a jointed axial skeleton in their paired fins (Fig. 2G). None of the other various features that have been cited as alternative between Dipnoi and other bony fishes is strictly so. Palaeontological evidence, furthermore, is to the effect that the oldest known fossil Dipnoi (Devonian) resemble in many characters the Rhipidistia (Middle Devonian), whose nearest relatives among present-day fishes are the coelacanths (*73*: 114).

Accordingly, the Dipnoi and the coelacanths among living fishes have been united by several recent writers (*55*: 376; *71* [1937]: 327; *73*: 589; *77*: 227; *47*:

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[28] Examples cited by Smith (*79*: 104) are *Lophius* (anglerfishes), *Opsanus* (toadfishes), *Hippocampus* (seahorses), and *Syngnathus* (pipefishes).

[29] For more extended discussions of this general subject, from which the foregoing summary has been drawn, see Prosser *et al.* (*64*: 48–52), Smith (*79*: 62–64, 102–105), Romer (*74*: 392–393), Denison (*20*: 429–430, 439–441), and Black (*12*: 182–199, refs. 199–206).

154) to form one of the Subclasses of the Class Osteichthyes, and this same course is followed here.

In 1861 Huxley proposed for this Subclass the name Crossopterygidae (subsequently changed to Crossopterygii) as a *Subordo* of his *Ordo* Ganoidei (*38*: 23, 25). Other names proposed later are: Amphiboidei by Hubbs in 1919 (*35*: 589); Choanichthyes by Romer in 1937 (*72*: 56), with Crossopterygii retained as an Order to include fossil as well as living Choanichthyes (*73*: 589); and Sarcopterygii by Romer in 1955 to replace his earlier name Choanichthyes (*75*: 126).

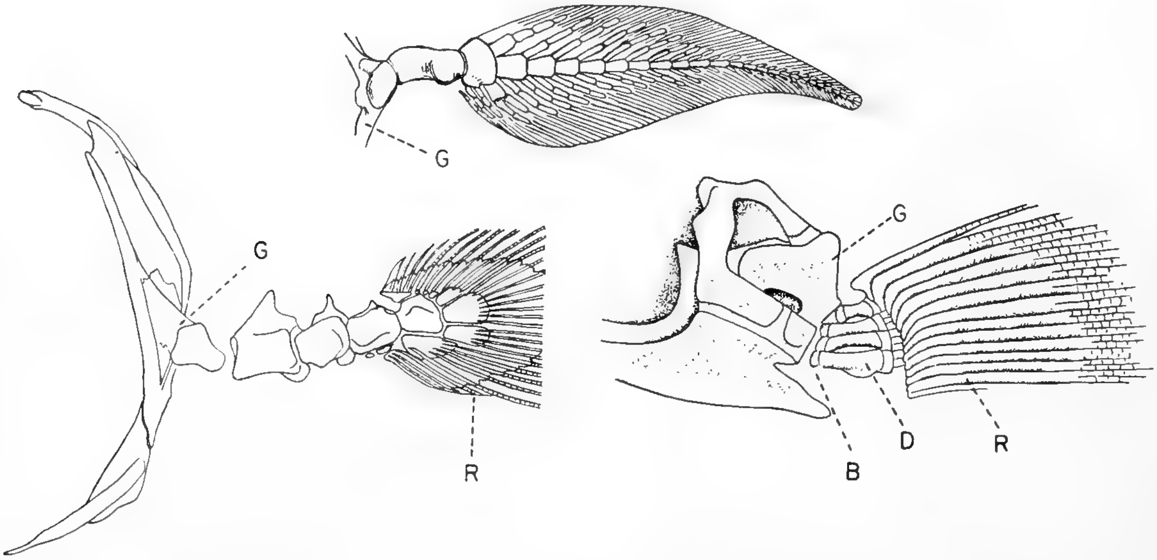

FIGURE 2. Skeleton and basal part of pectoral fin rays of: TOP, *Latimeria*, after Millot and Anthony, somewhat emended; LOWER LEFT, *Neoceratodus* (lungfish), after Günther, somewhat emended; LOWER RIGHT, *Salmo trutta* (European trout), after Parker and Haswell, somewhat emended. G pectoral girdle; B basal segment, and D distal segment of radialia; R fin rays.

None of these names seems wholly appropriate. While Crossopterygii, in a restricted sense, has been widely employed in scientific literature,[30] its continued use seems likely to lead to confusion because it has long been associated with the polypteroids, which were the basis for Huxley's name but which have been excluded from the Crossopterygii, Goodrich (*29*: 91) having shown that the affinities of the polypteroids lie with the actinopterygian fishes.

Amphiboidei does not seem a happy choice, for while the fishes concerned may be "related to amphibian ancestry," the living coelacanths are about "as unamphibian as a fish can be," as Romer has aptly expressed it (*75*: 125, 126).

Choanichthyes is a misnomer if the coelacanths are included, for internal nares neither were nor are present among fossil (*75*: 126) or living coelacanths, regardless of the situation in their hypothetical ancestors; and it is doubtful whether the internal

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[30] For a recent defense of this course, see Trewavas, *et al.* (*87*: 126–127).

nares of the Dipnoi are homologous with those of the tetrapod vertebrates. At any rate, they are not used in respiration.

Although objection may be raised to the use of Sarcopterygii when older names are available, this name does not carry with it any evolutionary implication that may not be warranted; and furthermore, it has never been employed in more than one sense, hence it is accepted here. This Subclass need not concern us further, for the Dipnoi are strictly confined to fresh water while living representatives of the coelacanths have been taken only off the southeastern coast of Africa and near Madagascar.

Actinopterygii has been chosen here as a Subclass name to represent the bony fishes that remain after subtracting the Sarcopterygii, a course which accords with the weight of contemporary opinion. An alternative scheme, proposed by Regan (*69*: 458; *71* [1937]: 312) and adopted by Norman (*55*: 376–377), would distribute them in two Subclasses: Palaeopterygii for acipenserids, polyodontids, and polypteroids; and Neopterygii for the remaining groups. But this seems an unnatural arrangement; although the polypteroids and acipenserids are similar in that the number of fin rays is greater than the number of their basal skeletal supports and because there is an unmistakable spiral valve in the intestine, the polypteroids differ widely from the acipenserids in the nature of both caudal fin[31] and dorsal fin, in the segmentally constricted notochord, and in the presence of a pair of bony gular plates between the branches of the lower jaw. Indeed, the polypteroids differ so widely from all other living bony fishes that Bertin and Arambourg's separate Subclass for them, Brachyopterygii (*31*: 1981, 2500), may represent a step forward in attempts to present more accurately the affinities of the various groups of bony fishes.

Subclass ACTINOPTERYGII[32]

Ray-finned Fishes

Characters of Living Members. The skull in its early stages is a primitive cartilaginous cranium that is replaced during development by bone in varying degrees in different groups; in most of the living bony fishes it is completely ossified in adults. Its outer surface is invested with a covering sheath in an intricate pattern of so-called dermal or membrane bones that develop as new structures "in the membranes of certain regions of the skull" and that appear to represent such modified scales; thus the entire skull is "so welded together to form a compact whole that in the adult fish it is often impossible to decide as to which category a particular element belongs" (*55*: 161).

Generally the upper jaw includes paired premaxillary and maxillary bones;[33] the premaxillaries, supplemented in many cases by the maxillaries, form the upper region

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[31] Symmetrical in the polypteroids, with the posterior part of the vertebral column continuing the axis of the body; strongly asymmetrical in the acipenserids and polyodontids, with the posterior part of the vertebral column bent upward (heterocercal).

[32] Including the polypteroids.

[33] Premaxillaries are lacking among acipenserids (sturgeons) and polyodontids (paddlefishes) (*32*: fig. 20); in *Bathysaurus* of the Iniomi and in *Gigantura* maxillaries are lacking; both premaxillaries and maxillaries are lacking

of the mouth; the premaxillaries, and often the maxillaries, are attached to the skull with varying degrees of firmness in different groups. The palatopterygoid-quadrate elements of the upper jaw-complex are articulated anteriorly with the ethmoid (nasal) region of the skull and are suspended posteriorly (usually via a symplectic bone) from the hyomandibular arch; but they are not fused solidly anywhere with the lower surface of the skull, except in one known case.[34] A bony gular plate is present in the chin region between the two branches of the lower jaw in the Amiidae and Elopidae, and there is a pair of such plates in the polypteroids. The cheek region of the skull is without squamosal bone.

In most of the bony fishes, the jaw teeth, if present, are separate from each other, and their substance is separate from that of the jaw except for those in which it is cemented basally "by bony substance which is resorbed when the tooth is shed" (*45*: 272 – Goodrich).

A persistent spiracular opening is present in only a few (polypteroids, some acipenserids, and polyodontids). The nasal cavities end blindly in the great majority; however, in *Astroscopus* (*22*: 993; *23*: 348–365; *1*: 371) and in *Uranoscopus* (original observation) of the Uranoscopidae they open both inwardly to the mouth and outwardly to the exterior, as they do in various members of the eel tribe as well (*1*: 371); this is suggestive of similar conditions among the Dipnoi (lungfishes), but the two are probably not homologous. Gill rakers, present in the great majority,[35] vary widely in number. Branchiostegal rays, though present in the great majority, are lacking in a few (sturgeon and paddlefish tribes, polypteroids, and Lyomeri).

The endoskeletal support of the pectoral fin consists typically of one or two series of short basal radialia, either in parallel or in more or less fan-like arrangement; these radialia articulate with the pectoral girdle directly in most Actinopterygii but indirectly in a few. The endoskeletal support of the pelvic fin is essentially similar, but here the radialia are greatly reduced. The dorsal and anal fins are supported basally by a single series of more or less rod-like radialia; in most, the rays of both dorsal and anal fins are equal in number to the basal radialia, but in both acipenserids (sturgeons) and polyodontids (paddlefishes) the rays of both fins are much more numerous than the radialia; among the polypteroids, while the dorsal rays more or less equal the number of radialia, the anal rays are much more numerous.

The outer surface of the scales (if any) consists of a simple calcified layer in most, but is enamel-like in appearance (ganoine) in a few.

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or are very small in some members of the Argentinoidea (*86*: 605–614, pl. 11; *62*: 30–31, figs. 9–11); and the Monognathidae (an aberrant family of lyomerids) have no upper jaw-complex at all (*5*: 533–540, figs. 1–4; *6*: 1, 5, figs. 2, 3).

[34] In the argentinoid genus *Macropinna*, according to Chapman (*15*: 273), the palatoquadrate complex is "immovably synchronized" with the occipital portion of the skull. Among the Ophiocephalidae and Symbranchii, the metapterygoid bone (part of upper jaw-complex but not forming part of gape) is in contact with the sphenotic bone, which is part of the posterior rim of the orbital capsule of the skull. For references, see Berg (*4*: 306, 471). For an explanation of the mode of suspension of the upper jaw that is typical of ray-finned fishes, see especially Parker and Haswell (*59*: 243, fig. 207; 244).

[35] Lacking in some members of the Cetomimidae (*61*: 20–32), in the Istiophoridae, and perhaps in some others.

Usually each of the genital, urinary, and intestinal tracts opens separately to the exterior, but among the syngnathids (*33*: xxvii, ftn. 1) and lophotids (information from Vladimir Walters) they empty into a common cloacal pouch. In many, a swim bladder is developed as a single outpocketing from the dorsoanterior part of the digestive tract, and an open pneumatic duct persists throughout life in some but not in others; in the polypteroids a functional paired lung is developed as a ventral outpocketing from the pharynx.[36]

The brain, consisting of a large cerebellum, large optic lobes, and a feebly developed cerebral region, is roofed (typically) in its anterior part with simple nonnervous epithelial tissue. The notochord is more or less constricted segmentally except in the acipenserids, polyodontids, and deep-sea halosaurids. The jugal sensory canal (forward extension of the lateral line) is represented in most by a horizontal line of sensory pits that cross the cheek region (*89*: 378). The pericardium is thick-walled posteriorly; the heart chambers show no indication of subdivision into arterial and venous channels.[37]

Nomenclature. The choice of a name for this Subclass lies between Actinopterygii and Teleostomi.

In 1839 Bonaparte proposed the name Teleostomi[38] as a *sectio* to include his Ganoidei and certain other groups of bony fishes, but excluding the acipenserids (sturgeons) and some others (*10*: 15). Many years later Owen expanded Bonaparte's Teleostomi to include the bony fishes as a whole, excepting the Dipnoi, which were unknown to Bonaparte (*57*: 7). Since 1868 Teleostomi has been used in this sense by numerous authors.

The Subclass name Actinopteri,[39] changed subsequently to Actinopterygia and Actinopterygii, was coined by Cope to include the acipenserids, lepisosteoids, amioids, and all higher groups of bony fishes, except the polypteroids (*17*: 449). The Subclass was employed in this same sense by Traquair (*85*: 505, 507), Goodrich (*45*), Jordan (*39*: 111), Lehman, Bertin, and Bertin and Arambourg (*31*: 2070–2500). In 1928 it was expanded by Goodrich to include the polypteroids (*29*: 91), and it has been employed with this modification by Stensiö,[40] Berg (*4*: 159, 392), Romer (*73*: 105, 579), and Schultz and Stern (*77*: 228).

Superorders. Several students have distributed the Orders of Actinopterygii among three Superorders, namely: Chondrostei (or Chondrosteoidea) for the acipenserids (sturgeons) and polyodontids (paddlefishes); Holostei for the Lepisosteoidea (gars) and Amioidea (bowfin); and Teleostei for the remaining bony fishes. It does not seem possible to draw a line of distinction between these Superorders if the fossil record be taken into account, hence they are not recognized here.[41]

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[36] For discussion of the relationship of swim bladder to lungs, see especially Romer (*74*: 343–350, figs. 225, 227).

[37] Among the living Dipnoi, the pericardium is thin-walled, and there is an "incipient division of the heart into a venous and an arterial channel" (*45*: 249 — Goodrich).

[38] From the Greek words *teleos* (meaning perfected) and *stoma* (meaning mouth).

[39] Based on the Greek words *aktis,* meaning a ray, and *pteron,* wing or fin. The spelling was later changed to Actinopterygia by Cope and to Actinopterygii by subsequent writers.

[40] In a series of papers (1932–1936).

[41] For a discussion of this matter, see especially Berg (*4*: 160–163, or 392–395).

The name Teleostei[42] has proved far too useful to be banished from nontechnical literature, whatever its fate may be in technical writings; we urge that it be transliterated henceforth to fit the language in which an author may be writing; for example, teleosts in English, téleostéens in French, Teleostier in German, etc.[43] However, the sooner "Ganoidea" and "ganoids" be relegated to oblivion the better, for the groups of living or extinct fishes[44] that were united under this name by Müller (*53*: 203) and that have been grouped similarly by subsequent authors do not represent a natural assemblage.

Orders of the Subclass Actinopterygii. The various classifications that have been proposed for the living ray-finned fishes since the appearance in 1844 of Müller's classic "system" (*53*: 201–204[45]) have been reviewed by Lönnberg (*11*: 2–62), by Berg (*4*), and more recently by Matsubara (*47*: 1–54). Hence it seems sufficient to remark here that the number of Orders that have been recognized within the Subclass Actinopterygii during the past 50 years or so has ranged from nine by Goodrich (*30*: x–xvii) and 12 by Romer (*73*: 579–585) to 24 by Matsubara (*47*), 32 by Regan (*67*: 76–82), 36 by Schultz and Stern (*77*: 220–247), 43 by Jordan (*39*), 44 by Berg (*4*), and 35 by Bertin and Arambourg (*31*: 1978–1981). This clearly illustrates the diversity of opinions and conclusions at which eminent students have arrived from consideration of essentially the same facts.

Part 3 of this series of volumes deals with the Acipenseroidei (sturgeons) of the western North Atlantic, with such of the Lepisostei (gars) as enter brackish or salt water, and with part of the Isospondyli, namely the Elopoidea (Elopidae, Albulidae), Clupeoidea (Engraulidae and Clupeidae, with only interim accounts of Alepocephalidae and Searsiidae), and Salmonoidea (Salmonidae, Coregonidae, and Osmeridae). Parts 4 and 5 deal with the remainder of the Isospondyli, the Iniomi, the Giganturoidei, and the Lyomeri.

Order of Presentation. Since it is not possible to represent the true interrelationships of different large groups of animals on the printed page, any sequence of presentation that may be adopted (other than an alphabetical one) must necessarily be artificial. This would be true even if the taxonomic units in question could be traced back through the ages to their earliest known fossil ancestors and even if we had a uniform yardstick by which we could measure the relative extent to which the different groups have diverged during their evolutionary histories. In any general account of a group as large and as varied as the bony fishes, the most one can hope for is that the sequence of treatment—Orders within Subclasses, and Families within Orders—shall be consistent with animal affinities "insofar as is practical" (*78*: 13). The sequence followed here represents a compromise between antiquity of ancestry, degree of specialization, and accepted precedent.

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[42] From the Greek *teleos* (meaning perfected or completed) and *osteon* (meaning bone).

[43] Ichthyostés, as used by Moreau (*51*: 2; *52*: 89), is an equivalent.

[44] Among living fishes—the sturgeon family, the paddlefish family, the polypteroids, and the gars. For a list (perhaps only partial) of the various extinct groups that have been joined together recently as "Ganoidei," see Jordan (*39*: 111–116).

[45] For other places of publication, see Dean (*19*: 174).

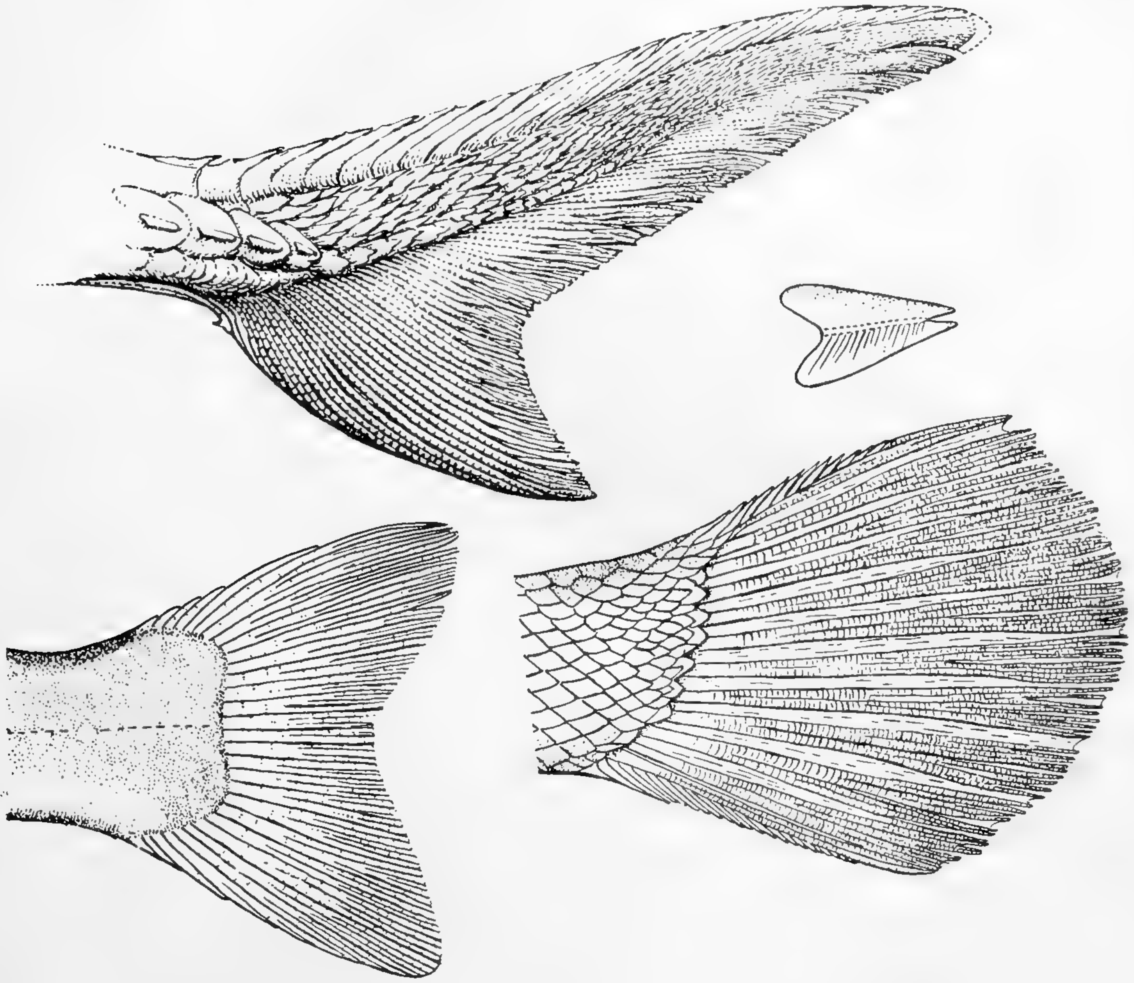

Figure 3. Caudal fin of: TOP, *Acipenser oxyrhynchus* (sturgeon), showing especially the extended scaly axis and fulcral scales, drawn by E. N. Fischer; LOWER LEFT, *Salvelinus alpinus* (Arctic charr), from eastern Greenland, drawn by Jessie H. Sawyer. LOWER RIGHT, *Lepisosteus* (longnose gar), after Kölliker, combined with drawing of *L. osseus* by Jessie H. Sawyer, with fulcral scale from upper margin, about × 2.

The sturgeons head the list, with the gars in second place, for while the known fossil record does not reach back beyond the upper Cretaceous for the living representatives of either of these groups,[46] fishes that seemingly were ancestral to both of them are known from as far back as the Upper Triassic. The Isospondyli and the Iniomi come next in recorded antiquity; the Elopidae (tarpon and ladyfishes), Clupeidae (herrings), and Chanidae (milkfishes) are known from the Lower Cretaceous, with the Albulidae (bonefishes) and even the Myctophidae (or some closely allied genera) and Aulopidae known from the Upper Cretaceous. There is no known fossil record

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[46] Wilimovsky (90: 1205–1208, pl. 132) has described and figured an undoubted sturgeon from the Upper Cretaceous of Montana.

for either the Bathylaconoidea or the Lyomeri, curiously modified groups that are included in Parts 4 and 5 because they appear to stem back either to isospondylic or to eel-like ancestry; for further details, see Romer (*73*: 579–584).

Identification. The sturgeons, the gars, the lyomerids, and the giganturoids are set apart by external features so obvious that no one at all acquainted with fishes would be likely to mistake any one of them for any other kind of fish that is known from the western North Atlantic. Although the Isospondyli, and probably the Iniomi as well, represent several phyletic lines of descent, with their members being correspondingly varied in appearance, they are easily separated as a group from the other Orders that are dealt with in Parts 3–5.

The following Key to the Orders described in these three volumes is offered solely as an aid to identification. The reader is referred to the sections dealing with the several Orders for information as to their internal features.

Key to External Characters of Orders Represented in the Western North Atlantic and Described in Parts 3–5

1 a. Separate rayed caudal fin clearly marked off from anal fin, from dorsal fin, or from both anal and dorsal.
  2 a. Caudal fin with conspicuous fleshy axis (marking rearward extension of vertebral column) bending sharply upward at base of caudal and continuing outward, close to upper margin of fin, nearly to its tip; upper margin of fin much longer than lower margin (Fig. 3). Acipenseroidei, Part 3, p. 24.
  2 b. Caudal fin without conspicuous fleshy axis; upper margin of fin little if any longer than lower margin.
    3 a. Trunk, rearward from gill openings, completely clothed below and above with thick rhomboid scales in mosaic pattern, interlocking but hardly overlapping, forming a flexible armor; rear boundary of fleshy base of caudal fin sloping obliquely rearward-upward (Fig. 3); anterior part of upper margin of caudal and nearly entire length of lower margin edged with a series of large "fulcral" scales, shaped as in Fig. 3. Lepisostei, Part 3, p. 61.
    3 b. Trunk, rearward from gill openings, not clothed in a continuous armor of interlocking scales; rear boundary of fleshy base of caudal either nearly vertical or symmetrically rounded; margins of caudal fin without fulcral scales.
      4 a. Point of origin of pectoral fins higher on sides than upper end of gill openings; fin rays not branched. Giganturoidei, Part 4.

4b. Point of origin of pectoral fins at least no higher than upper end of gill openings, and usually much lower; at least most of fin rays branched.

    5a. Upper edge of mouth formed by the maxillary bones as well as by the premaxillaries. Isospondyli, Part 3, p. 89, and Part 4.

    5b. Upper edge of mouth formed by the premaxillary bones alone. Iniomi, Part 5.

1b. No distinct rayed caudal fin; extreme tip of tail either like a whiplash or narrow band; its membrane, if any, without rays. Lyomeri, Part 5.

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Names of Bones

GILES W. MEAD[1]
Museum of Comparative Zoology, Harvard University
and
MARGARET G. BRADBURY
Hopkins Marine Station, Stanford University

The bones of the skull and pectoral girdle of the hickory shad, *Pomolobus mediocris* (Mitchill), are depicted in Figs. 1–3. These figures do not represent an attempt at a critical osteological study, and the names used were chosen with regard to those most frequently used in the descriptive accounts that follow, as well as to questions of homology. The species illustrated may serve as an adequate guide to the bones of the more common and conservative of the Isospondyli, but it will be of limited value in the study of grotesque forms such as the stomiatoids and the Lyomeri. Notes on the osteology of these, or references to such studies, are included in the accounts of the various species.

The fishes used were caught in Chesapeake Bay north of the town of Solomons, Maryland, in November 1958. All were between 280 and 310 mm SL. One dry skeleton was prepared and two were cleared in potassium hydroxide and stained with alizarine. These preparations and two additional whole specimens are now in the United States National Museum (USNM 186078, 186090, and 186091).

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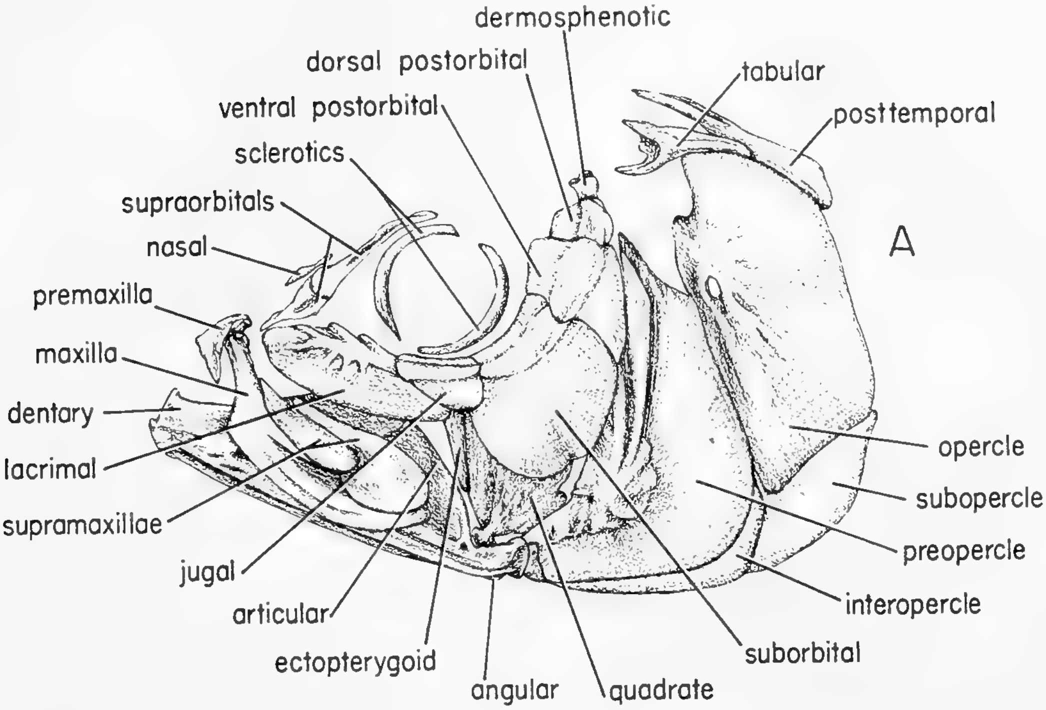
[1] This work was done while both authors were with the Ichthyological Laboratory, U.S. Fish and Wildlife Service.



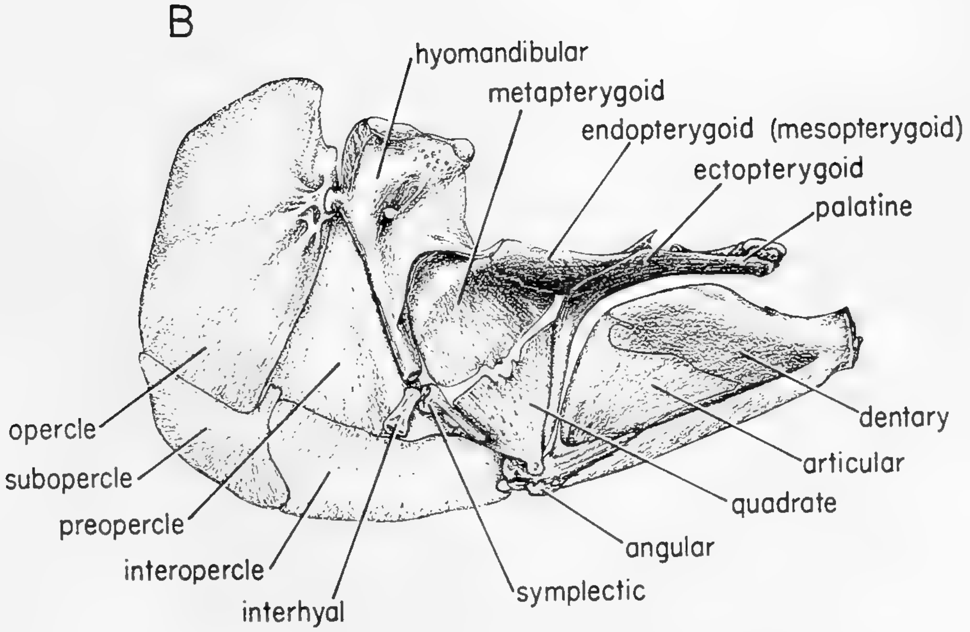


FIGURE 4. Superficial face bones and suspensorium of *Pomolobus mediocris*. A lateral view of left side of head; underlying bones of the neurocranium not shown. B inner view of left suspensorium, lower jaw, and opercular series. Drawn by Margaret G. Bradbury.

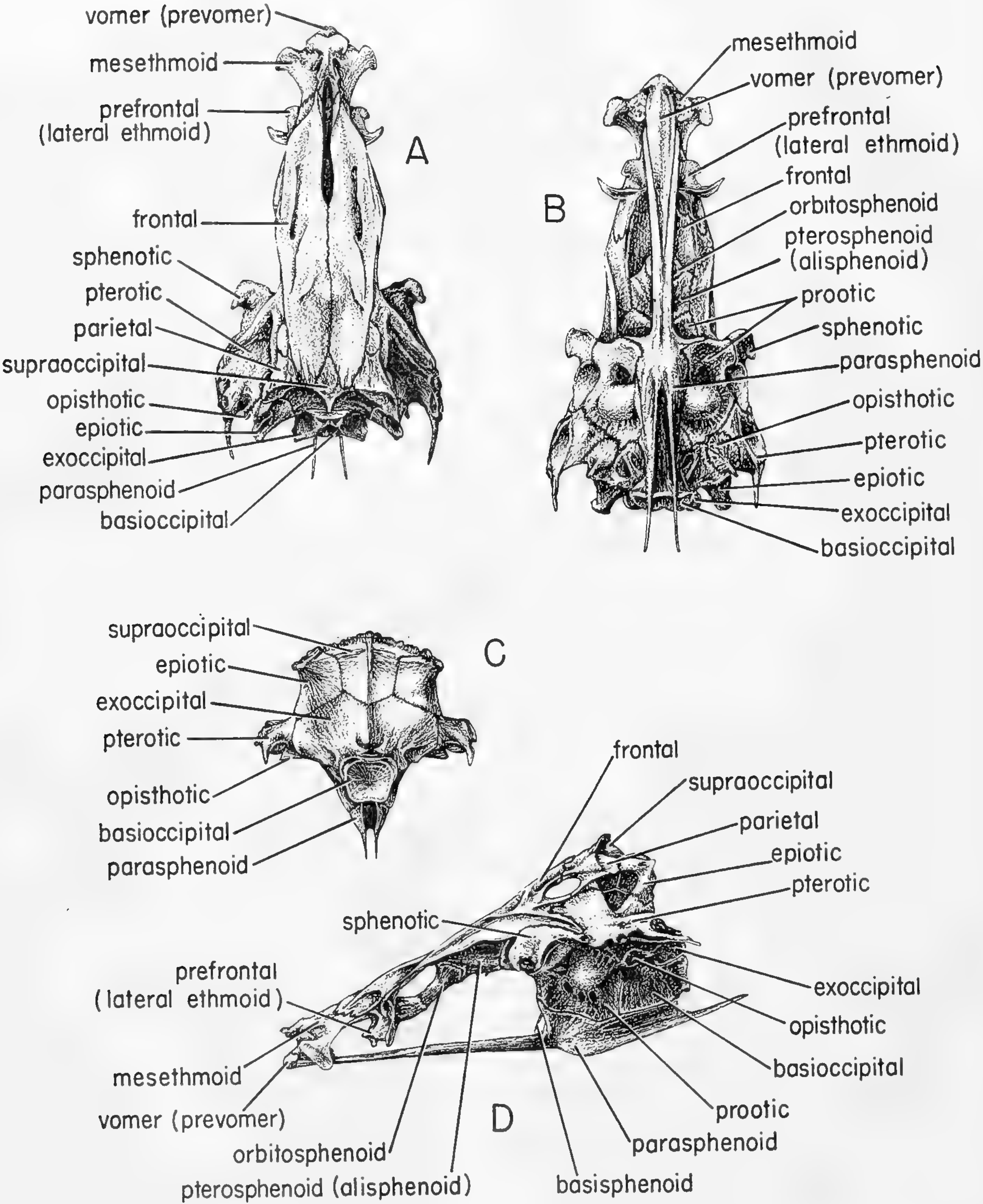


FIGURE 5. Neurocranium of *Pomolobus mediocris*. A dorsal view; B ventral view; C posterior view; D lateral view. Drawn by Margaret G. Bradbury.

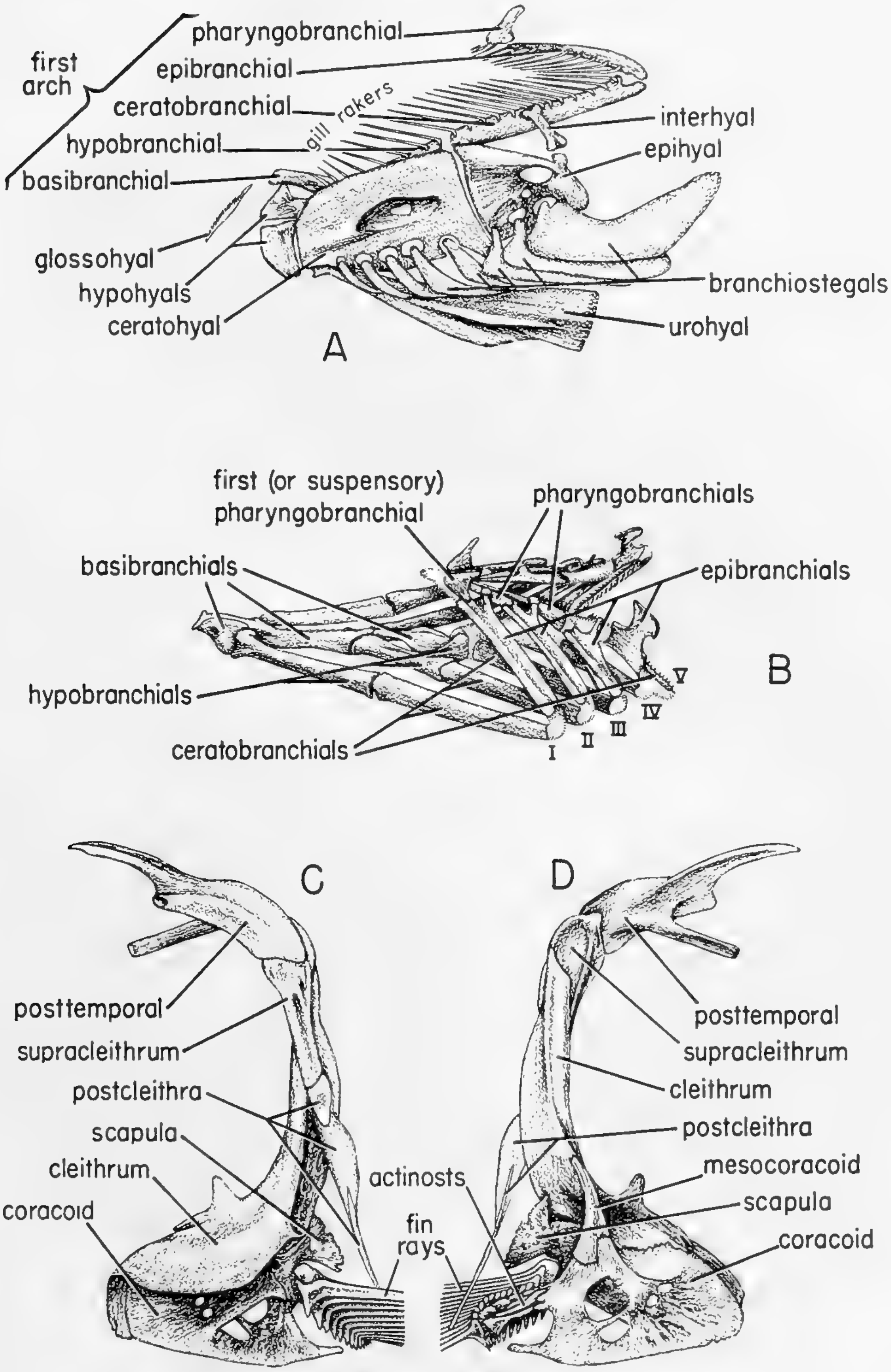


FIGURE 6. Hyoid arch, branchial basket, and pectoral girdle of *Pomolobus mediocris*. A lateral view of left hyoid arch with associated branchiostegal rays and first branchial arch; B three-quarter view of branchial arches; C outer view of left pectoral girdle; D inner view of left pectoral girdle. Drawn by Margaret G. Bradbury.

Order Acipenseroidei[1]

VADIM D. VLADYKOV[2]
and
JOHN R. GREELEY[3]

Acknowledgments. We are indebted to the late Léon Bertin and to Miss Rolande Estève for their help and for their permission to examine Duméril's types of Sturgeons in the Paris Muséum National d'Histoire Naturelle. We are also grateful to Henry W. Fowler and Leonard P. Schultz for making available for study the Sturgeon collections in the Academy of Natural Sciences at Philadelphia and of the United States National Museum; to Loren P. Woods for specimens from the Chicago Natural History Museum; to Carl E. Guthe and Ralph S. Palmer for their kind offer of a rich collection of Acipenser brevirostris *from the New York State Museum; to the late Alexander D. Bajkov, R. E. Dimick, Ivan J. Donaldson, and Charles E. Warren for collecting Sturgeons in Oregon; and to Henry B. Bigelow and William C. Schroeder for their careful editing of this manuscript and for making available their unpublished notes.*

The illustrations were drawn by Paul I. Voevodine, artist of the Department of Fisheries, Quebec.

Scope of Study. In the following text we give the characters of the Order Acipenseroidei and of the family Acipenseridae; also descriptions, life histories, and geographical distributions, as well as synonyms and references, for the following Sturgeons: *Acipenser brevirostris*, *A. fulvescens*, *A. oxyrhynchus oxyrhynchus*, and *A. oxyrhynchus*

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[1] Contribution No. 53, Department of Fisheries, Quebec, P. Q., Canada.

[2] Present address: Department of Biology, University of Ottawa, Ontario, Canada.

[3] Present adress: Division of Fish and Game, Conservation Department, Albany, New York, U.S.A.

desotoi; all of these occur in the western North Atlantic or Gulf of Mexico in fresh, brackish, or salt water. Since *A. sturio* of the eastern Atlantic and Mediterranean has sometimes been considered synonymous with *A. oxyrhynchus*, the relationship of these two is discussed on p. 57.

Most of the material for our study consisted of collections made in New York (*35*: 45–103) and Quebec (*83*: 143–204; *84*: 129–154). Supplementary data were obtained by examination of the material at the Paris Muséum National d'Histoire Naturelle, the United States National Museum, and the Academy of Natural Sciences of Philadelphia.

The *Descriptions* are based on the *Study Material* listed for each species. An explanation of terms, measurements, and counts is given on p. 33. The accounts of the habits and geographical distributions are based upon published records and personal observations.

Many of the earlier authors who dealt with the taxonomy of Sturgeons based their conclusions on differences associated with the age of the specimens, with the consequences that they recognized several nonexistent species. Hence, among the references, we use only those that we consider to be the most important from a taxonomic point of view, and particularly those dealing with the life histories of the species.

Characters. BODY subcylindrical. SNOUT greatly extended, blade-like and flexible in some, in others only slightly extended, if at all, and rigid. MOUTH on lower surface of head, protractile or not. CHIN BARBELS prominent in some but lacking in others. DORSAL fin situated far rearward; only one. CAUDAL fin more or less deeply forked, with fleshy axis (enclosing notochord) extending rearward to tip of upper lobe, bending upward beginning at base of fin; heterocercal, wider below than above the fleshy axis. VENTRAL fins well developed, abdominal in position. FIN RAYS much more numerous than their basal skeletal supports. PECTORALS with the first ray transformed in some into an ossified ray, the fins otherwise without spines. SKIN of trunk rearward from eyes seemingly naked in some but actually with minute scattered PLATELETS; others with five longitudinal rows of SCUTES (large bony shields), the skin roughened elsewhere with small scattered DERMAL OSSIFICATIONS.[4] A continuous series of rhombic to lanceolate PLATES, closely set, on axis of caudal; the upper margin of caudal with a dorsal fringe of large v-shaped FULCRA (spine-like scales), each representing the fusion of a pair of opposing plates. TEETH minute, if present. BRANCHIOSTEGAL RAYS absent.

SKELETON cartilaginous for the most part, the primitive cartilaginous cranium (chondrocranium) persisting and growing throughout life; ossification chiefly representing development of membrane bones (p. 4) in regions of skull, jaws, and pectoral girdle. Upper jaw not articulating with skull either in the ethmoid region or in the sphenoid. Premaxillary bone fused with maxillary. Pectoral girdle fused with clavicle.

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[4] There is no definite terminology for the plates or granules found in the skin between the regular rows of bony shields; they have been variously called: stellate plates, stellate roughnesses, stellate ossifications, minute rough spinules, small prickle-like plates (*43*: 104–106), dermal plates, and small spinous asperities (Ryder, *The Sturgeons*, with an account of experiments bearing upon Sturgeon culture, *65*: 231–328). In the present manuscript they are called "dermal ossifications."

Myodome absent. Interopercular bone absent. Radials in dorsal and anal fins cartilaginous. Vertebral centra absent, the notochord entirely unconstricted throughout its length. AIR BLADDER well developed, oval, with smooth inner surface, opening into oesophagus through a short, wide duct. INTESTINE with well-developed spiral valve (see Berg, *10*: 387).

Habitat. Fresh water, or, if marine, entering fresh water to breed.

Families. Of the two living families, the Acipenseridae with four genera is much more important throughout the northern hemisphere than Polyodontidae, which is represented now by only two freshwater genera, each with a single species; *Polyodon spathula* (Walbaum), with a nonprotractile mouth, is found in eastern North America,[5] whereas *Psephurus gladius* (Martens), with a protractile mouth, inhabits China; one family, Chondrosteidae, is extinct, being known only from fossils of the Lower Lias to Lower Cretaceous periods.

Key to Modern Families

1a. Snout in front of eyes little if at all longer than remainder of head, subconical, rigid, more or less flattened in some but not blade-like in shape; a transverse series of four fleshy and conspicuous barbels close in front of mouth; mouth on lower surface of head, protrusible; jaws toothless in adult; five longitudinal rows of large bony shields (scutes) on body, the lateral row extending onto base of caudal, the skin elsewhere between them rough with small dermal ossifications; bony plates separated by evident sutures covering head; anterior edge of pectoral fins with a stout ossified ray; upper lobe of caudal much longer than lower.
Acipenseridae, below.

1b. Snout in front of eyes much longer than remainder of head, blade-like in form and flexible in American species; no barbels in front of mouth; mouth lateral in position, protrusible (in *P. gladius*) or nonprotrusible (in *P. spathula*); jaws with minute teeth; no bony shields on body, the skin everywhere on trunk smooth to the touch; head not covered with bony plates; no ossified ray in pectoral fins; lower lobe of caudal at least as long as upper lobe in American species.
Polyodontidae. Paddlefishes.
Fresh water of eastern North America and China.

Family ACIPENSERIDAE

Sturgeons

Characters. BODY elongate and fusiform. SCUTES or bony shields in five rows: one dorsal, two lateral, and two ventral; all scutes very sharp and strongly developed

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[5] According to Dr. R. D. Suttkus (personal communication, July 9, 1957), a specimen of *P. spathula*, 481 mm FL and weighing 354 g, was taken in the brackish water of Vermilion Bay at Cypremont Point, Louisiana, on May 15, 1954, by Antoine Carrere while trawling for penaeid shrimp.

in young individuals, but becoming progressively blunter with age or even disappearing through absorption. SKIN between scutes with small ossifications. SNOUT protruding. MOUTH inferior, protractile. TEETH absent in adults. BARBELS 4, in a crossrow in front of mouth. GILLS 4, and an accessory opercular gill. BRANCHIOSTEGALS absent. GILL RAKERS fewer than 50. OPERCLE absent. HEAD covered by bony plates separated by sutures; particularly visible in younger specimens. DERMAL SKELETON without ganoine. CAUDAL fin with typical fulcra. DORSAL and ANAL fins behind ventrals. PECTORAL fin with first ray enlarged and ossified. TAIL heterocercal. AIR BLADDER large, simple. STOMACH with numerous pyloric appendages, forming a compact and rather large gland. RECTUM with spiral valve.

Anadromous and freshwater fishes of the northern hemisphere; Upper Cretaceous to Recent.

Remarks. The cartilaginous skull has an opening under the frontal and parietal plates, usually completely roofed over by these membrane bones. Hence there is a cavity, evident in sagittal section of the head, for which we propose the name *frontal sinus.*

In young specimens of *A. oxyrhynchus* of America and *A. sturio* of Europe, there is a membranous, elongated, nonossified area on the top of the head which Ryder[6] called the "fenestra" or "fontanelle." In specimens less than 40 inches long, this can usually be found by probing with a needle between the frontal and parietal plates; thus a probe can be passed downward into the *frontal sinus.* Adults, and in rare instances young, have the plates fully joined, closing the fontanelle.

The protractility of the mouth is made possible by movements of the jaws and palatoquadrate bone (*10*: 409).

The pseudobranchs are rudimentary in *Scaphirhynchus* (*31*: 26) and completely lacking in *Pseudoscaphirhynchus* (*11*: 104). The large element of the gill cover represents the subopercle, not the opercle (*70*: 48–50).

The appearance of the Sturgeon changes considerably with age; the snout becomes shorter and blunter and the shields smoother while the lower caudal lobe, not fully formed[7] in very small specimens, becomes longer. Apparently the shields may be partially or completely absorbed in connection with ripening of the gonads.

Genera. The family Acipenseridae is divided into two subfamilies. Acipenserini (true Sturgeons), with spiracles present, is represented by two genera: *Huso*, Lower Pliocene to Recent, with two species; and *Acipenser*, Upper Cretaceous to Recent, with about 16 species. Scaphirhynchini (Shovelnose Sturgeons), without spiracles, also includes two genera: *Scaphirhynchus*, with two species;[8] and *Pseudoscaphirhynchus*, with three species.

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[6] Ryder was probably the first American author to describe the presence of a fontanelle in *A. oxyrhynchus* (*65*: 233); for that in *A. sturio*, see Stannius (*68*: 26) and Antoniu (*4*: 113, 114).

[7] Grote, *et al.* (*36*: 215, fig. 158) and Roule (*62*: pl. 4, fig. 7) have presented drawings of young *A. sturio* in which the lower lobe is not well grown as yet.

[8] Although one of the American species has been described as a separate genus, *Parascaphirhynchus* (*31*: 37–44), recent studies fail to substantiate this (*8*: 174).

Key to Genera[9]

1a. Spiracles present; snout subconical; tail not depressed or completely mailed; gill rakers lanceolate.
  2a. Gill membranes joined to isthmus. *Acipenser* Linnaeus 1758, below.
  2b. Gill membranes free from isthmus and broadly connected between themselves. *Huso* Brandt 1869.
  Basins of the Adriatic, Black, and Caspian seas, and the Far East (Amur River).

1b. Spiracles absent; snout shovel-shaped, depressed above; tail depressed and mailed; gill rakers fan-shaped.
  3a. Caudal peduncle completely mailed, and long, with tip of anal fin remote from caudal base; barbels fringed. *Scaphirhynchus* Heckel 1835.
  Mississippi River Basin.[10]
  3b. Caudal peduncle incompletely mailed, and short, with tip of anal fin reaching almost to caudal base; barbels smooth. *Pseudoscaphirhynchus* Nikolski 1900.
  Turkistan (Basin of the Aral Sea).

Genus *Acipenser* Linnaeus 1758

Acipenser Linnaeus, Syst. Nat., ed. 10, 1758: 237; type species, *A. sturio* Linnaeus. Atlantic Ocean, along European coast.

Generic Synonyms:

Ichthocolla Geoffroy, Descr. de 719 Plantes, etc., 1767: 399 (presumably *A. huso* L.).
Sterleta Güldenstädt, Nov. Com. Acad. Petropol., *16*, 1772: 533 (*A. ruthenus* L.).
Sturio Rafinesque, Indice Ittiol. Sicil., 1810: 41 (*Sturio vulgaris* Rafinesque = *A. sturio* L.).
Sterletus Rafinesque, Ichthyol. Ohiensis, 1820: 80 (*A. serotinus* Rafinesque = *A. fulvescens* Rafinesque).
Helops Brandt and Ratzeburg, Medizinische Zool., *2*, 1833: 3, 349 (*A. stellatus* Pallas = *A. helops* Pallas).
Sterletus Brandt and Ratzeburg, Medizinische Zool., *2*, 1833: 349 (*A. ruthenus* L.).
Sturio Müller, Vergleich. Anat. Myxinoiden, 1835: 77 (*A. sturio* L.).
Antaceus Heckel and Fitzinger, Ann. Wien. Mus., *1*, 1836: 293 (*A. schypa* Eichwald).
Lioniscus Heckel and Fitzinger, Ann. Wien. Mus., *1*, 1836: 370 (*A. glabra* Fitzinger).
Sterletus Bonaparte, Cat. Metod., 1845: 21 (*A. vultharius* L.).
Ellops, Gistel, Naturg. Thierreichs, *9*, 1848 (*A. helops* Pallas).
Schipa Brandt, Bull. Acad. Sci. Petersb., *7*, 1850, 113 (*A. schypa* Eichwald).

Characters. Gill membranes joined to isthmus. Spiracles present. Snout subconical. Tail depressed and completely mailed. Gill rakers lanceolate. Characters otherwise those of the family.

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[9] Since Sturgeons change with age in such features as head proportions and characteristics of scutes, the preparation of keys applicable to both young and adult stages has involved selection of those characters that are most constant throughout life.

[10] According to Dr. R. D. Suttkus (personal communication, July 9, 1957), a specimen of *S. album*, 532 mm FL and weighing 553 g, was taken in the brackish water of Vermilion Bay at Cypremont Point, Louisiana, on May 10, 1954, by Lester Boudreaux while trawling for penaeid shrimp.

Subgenera. There have been several attempts to subdivide the genus *Acipenser* as defined by Linnaeus in 1758. The preferences of earlier authors may be judged from the Generic Synonyms. Among contemporary authors, Berg (*11*: 66), for instance, favors three subgenera: *Lioniscus* Heckel and Fitzinger for *A. nudiventris*, *Gladostomus* Holly for *A. stellatus*, and *Acipenser* s. str. for the rest. On the other hand, Antoniu (5: 317, 318) has grouped Black-Sea Sturgeon in two subgenera: *Euacipenser* Antoniu, comprising *A. ruthenus* and *A. nudiventris*, and *Acipenser* Linnaeus, embracing *A. sturio*, *A. güldenstädti*, and *A. stellatus*. We believe that in the future any subdivision of the genus *Acipenser* should be based on meristic and anatomical characters; this is not possible yet because the anatomy of the Pacific species is completely unknown and that of Atlantic species has not been sufficiently studied.

Size. Among *Acipenser* species, the range in size is wide. The largest species is *A. transmontanus*, with occasional individuals weighing up to 1,800 pounds (*21*: 74), as in the case of one taken about 60 years ago at Mission, British Columbia; the smallest is no doubt *A. brevirostris*, about nine pounds (p. 38). The species of *Huso* are much larger. Berg (*11*: 61) has mentioned the capture of a female *H. huso* in the Volga in 1924 that weighed 2,707 pounds (1,228 kg). A still larger specimen, weighing 6,614 pounds (3,000 kg), was taken in 1827. Females grow much larger than males.

Span of Life. The species of *Acipenser* and *Huso* may have a longer life span than most fishes. For instance, through study of cross sections of the pectoral bony ray, an *A. sturio* 230 cm long was found to be 25 years old (*20*: 61). The age of a *Huso dauricus*, 500 cm long and weighing 1,600 pounds (655 kg), was estimated to be between 50 and 55 years (*60*: 199). Further information is given in the accounts of the western North Atlantic species.

Age in Sturgeons has been studied by two methods, one employing cross sections of the pectoral ossified ray, the other otoliths.[11]

Breeding Habits and Sex. Sturgeons breed for the first time at a much more advanced age than most other fishes, and apparently the small species are more precocious than the large. For instance, the relatively small *A. ruthenus* from the Volga may mature at four years (*11*: 75) and *A. brevirostris* from the Hudson River at five years (*35*: 82–83). On the other hand, such a large species as *A. oxyrhynchus* reaches maturity in 10–12 years. According to Harkness,[11] *A. fulvescens* from Lake Nipissing, Ontario, spawns for the first time at 22 years of age.[12]

Apart from the period when they are sexually mature, there is practically no exterior distinction between the sexes. The cow Sturgeons, when full of ripe eggs, have a greatly swollen abdomen with rather thin walls, and the mature males have a more elongated appearance, with the walls of the abdominal cavity much thicker.

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[11] For schematic drawings of otoliths of *A. oxyrhynchus* and *brevirostris*, see Greeley (*35*: 81); and for *fulv-e scens*, see Harkness (*38*: 16–19). Harkness (*38*: 13–42) and Greeley (*35*) used otoliths for determination of age while Classen (*20*) and other European investigators based their findings on cross sections of the pectoral bony ray.

[12] For a review of the rate of growth and of the age at spawning of different species, see Classen (*20*).

Among the large species, accurate determination of the sex in specimens smaller than 30 inches is difficult and often requires the use of a magnifier.

All of the species are oviparous and spawn in fresh water, and there is no adaptation for the care of eggs or young. The eggs are large, at least 2.5 mm in diameter, demersal and adhesive (prior to water-hardening), and their number varies with the species and with the size of fish; in large specimens they exceed several million, as in the case of the 2,707-pound female reported by Berg (above), which yielded an estimated 7.7 million eggs weighing 542 pounds. More details are given in the accounts of the respective species.

In all Acipenseridae[13] the ripening gonads[14] have a characteristic appearance, being thick and elongate and extending along each side of the air bladder near the dorsal surface of the body cavity. The immature gonads in both sexes are covered on the underside by a large mass of yellow fat which apparently plays a role of energy storage for the ripening gonads; in those close to spawning it is almost entirely absorbed. The fully mature ovaries are very large and make up 10–20 % of the total weight of the fish. As the ripe eggs become dark,[15] the whole ovary darkens. Mature testes are pale yellow to whitish.

It is a common observation that, even in the spring during the spawning season, large individuals with immature ovaries are found among fully mature females. This may be explained by the fact that the fish, after the first spawning, may spawn only at intervals of two or even three years.

Studies of gonad maturation in *A. nudiventris* from the Aral Sea found that there are two distinct "waves" in the ripening process (*73*: 581–584). Fish ascend the Syr Darya River for spawning around the end of July, when they have rather well developed gonads. Soon the advanced sex cells are absorbed. After about two weeks, during the second "wave," the maturation of gonads starts again and is nearly complete by mid-October. During the winter the maturing fish hibernate in the river and spawn the following April or May. However, the material at Trusov's disposal was rather limited (160 gonads) and was collected during four different years (1941, 1946–1948).

Habits and Food. Sturgeons are sluggish but strong. During the summer they often leap from four to six feet above the water. There are many known cases of Sturgeons jumping into a passing boat. About 70 years ago Ryder mentioned such a case for *A. oxyrhynchus* near Delaware City, and on August 14, 1951, the Quebec newspaper *Le Soleil* (p. 20) reported that a 35-pound *A. fulvescens* jumped into a small rowboat on the Ottawa River, near Pembroke, Ontario.

The small protractile mouth preceded by four sensitive barbels in the middle of the lower surface of the head may be considered an adaptation for bottom feeding.

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[13] The same phenomenon has been reported for *Polyodon* as well (*46*: 116–124).

[14] For further details on the ripening of eastern American Sturgeons, see Ryder (*65*: 268–273).

[15] Nikitin (*56*: 76) gives practical suggestions for the recognition of eggs from different species of Sturgeon made into caviar. The eggs may be distinguished by size, color, and particularly by the tint of their germinal disc ("eye" of the egg).

However, it has been observed that Sturgeon may rise to the surface to seize swimming objects (*65*: 265).

The main Sturgeon food consists of bottom organisms such as oligochaete worms, insects, mollusks, and crustaceans; occasionally plant material is found in their stomachs as well. Sturgeons may feed on their own eggs, at least in the case of *A. fulvescens* from Lake St. Peter, Quebec (unpublished data from Messrs. L. Philippe and J.-P. Cuerrier), and on different species of fish and birds. The gigantic *Huso huso* of the Caspian Sea may even feed on newborn seals (*57*: 435).

Habitat. While the majority lives in both fresh and salt water and makes most of the growth in the sea, at least two, *fulvescens* and *ruthenus*, are found typically in fresh water, although the former has been reported as occurring in brackish water.

Range. The species of *Acipenser* are spread throughout the whole northern hemisphere, being particularly numerous in the Caspian and Black Sea basins.

Commercial Importance. The fisheries for Sturgeon in North America have declined greatly in the last hundred years, and their maintenance on a sustained-yield basis constitutes a challenge to conservationists. Toward the end of the 19th century, catches for certain years were over 5,000,000 pounds for all species combined, but in 1956 only 392,000 pounds were taken in Canada and 719,000 pounds in the United States (combined value about $386,000).[16] The Lake Sturgeon (*A. fulvescens*) in Canada and the White Sturgeon (*A. transmontanus*) in the western United States yield the greater part of the commercial catch.

Most of the catch is consumed in the form of smoked Sturgeon and as caviar made by curing the eggs with salt. Over the years, production of caviar has dropped[17] so that in 1951 only 2,000 pounds, made from eggs of *A. fulvescens*, were produced in Canada, worth about $10,000 to the fishermen.

In Europe, particularly in Russia, Sturgeon fisheries are extensive. The fish are valuable not only for the flesh and eggs but for several other products; the commercial product from the spinal cord is called "vyaziga," and the inner lining of the swim bladder is used for the preparation of gelatine and glue of the best quality.[18] The head of a Sturgeon, rich in gelatinous substances, is a valuable food product; in Russia it is sold separately from the flesh under the name "golovizna." In the Province of Quebec, older people use oil made from Sturgeon liver as an ointment against rheumatism.

Although angling for Sturgeon by hook-and-line is not common, it is practiced in some places, as around Montreal, Canada; there also is an important spear fishery for sport for *A. fulvescens* in several northern waters of the United States.[19] The

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16. A comprehensive summary of former catches of Sturgeon in North America is given by Rostlund (*61*: 10–12). The most recent available data for the whole continent are in "Fishery Statistics of the United States, 1956" (*74*) and in "Fisheries Statistics of Canada, 1956" (*26*).
17. According to Ryder, in 1888 fishermen from the Delaware River produced for the German market about 50 tons of caviar from eggs of *A. oxyrhynchus* (*65*: 278).
18. For the preparation of isinglass, see Ryder (*65*: 278) and Classen (*19*: 426–428).
19. Some information on Sturgeon spearing, for instance in Lake Winnebago, has been reported (*86*: 29).

occurrence of Sturgeon scutes in materials excavated from prehistoric American Indian villages indicates that these large fish were utilized in aboriginal times (*61*: 10–12).

Hybridization. Hybrids are found in nature quite frequently, not only between different species of *Acipenser* but between *Acipenser* and *Huso.* Antipa described at least eight different types of Sturgeon hybrids (*3*: 270–273), and recently Antoniu added two new findings among Roumanian Sturgeon (*6*: 308–313). In some areas, for instance the estuary of the Lena River, Siberia, the hybrid *A. baeri* × *A. ruthenus* is much more common than either of the parent species (*14*: 141).

Species. At present at least 16 species are recognized, five of which are found in North America. In eastern North America there are three: *A. oxyrhynchus* Mitchill 1814, *A. brevirostris* LeSueur 1818, and *A. fulvescens* Rafinesque 1817. The two found in the Pacific coastal waters of America are *A. medirostris* Ayres 1854 and *A. transmontanus* Richardson 1836 (p. 36).

In Europe there are five species of *Acipenser*: *A. ruthenus* Linnaeus 1758, a freshwater species inhabiting the rivers of the Black Sea and Caspian regions and the Arctic basin from the Ob to the Kolyma; *A. nudiventris* Lavetsky 1828, of the Black, Caspian, and Aral seas and their tributaries; *A. güldenstädti* Brandt 1833 and *A. stellatus* Pallas 1771, found principally in the Caspian and Black sea regions, but occasionally entering the Mediterranean; and *A. sturio* Linnaeus 1758, inhabiting both the Atlantic and Mediterranean areas. Furthermore, in his list of *Acipenser* species, Magnin recognized *A. nacarii* Bonaparte from the Adriatic Sea as a distinct species (*48*: 280). Chalikov has described a new species from the Caspian Sea under the name of *A. primigenius* (*17*: 47–50), but Berg considered it a hybrid *A. ruthenus* × *A. güldenstädti* (*11*: 77).

According to Professor Tamezo Mori (personal communication, December 20, 1954), seven species of *Acipenser* are represented in the waters of eastern Asia: *A. schrencki* Brandt 1869 is limited to the Amur River and Okhotsk Sea; *A. kikuchii* Jordan and Snyder 1901 and *A. multiscutatus* Tanaka 1908 are restricted to Japan; *A. dabryanus* Duméril 1868 has been reported from only the Yellow Sea basin in China and western Korea; and *A. sinensis* Gray 1834 is known from China, Korea, and Japan; the sixth, *A. medirostris* Ayres, which is found on our Pacific coast, also frequents the western Pacific coast; the seventh Asiatic species, *A. baeri* Brandt 1869, inhabits the Arctic Ocean basin along the coast of Siberia, from the River Ob to Kolyma. Some information on the taxonomic characters and distribution of Asiatic species has been given (*53*: 6–10; *54*: 1–228; *18*: 69–71; *55*: 15–17; *71*: 65–68).

Relationship between Species. The total number of gill rakers increases in American species in the following order: *medirostris* (18–20), *oxyrhynchus* (17–27), *brevirostris* (22–29), *fulvescens* (25–40), and *transmontanus* (34–36). The American species may be classified in order of increasing development of their bony shields in all the rows (using specimens of corresponding sizes) as follows: *brevirostris*, *fulvescens*, *transmontanus*, *oxyrhynchus*, and *medirostris.* Several small plates, with or without a weak crest, are present immediately behind the dorsal fin and in front of the anal; these plates are typically paired in the case of *oxyrhynchus* but are single in the case of the two other western North Atlantic species. In American species, the development of the modified predorsal shield increases in the following order: *transmontanus* (not only rudimentary, but sometimes absent), *brevirostris*, *fulvescens*, *oxyrhynchus*, and *medirostris*. In the case of the enlarged fulcrum along the lower lobe of the caudal and of the dermal ossifications, the order is *brevirostris*, *fulvescens*, *transmontanus*, *oxyrhynchus*, and *medirostris*.

Explanation of Terms, Measurements, and Counts. In order to facilitate the use of the Key and *Descriptions*, a brief explanation of certain terms and methods used in measuring and counting follows.

REGULAR ROWS OF BONY SHIELDS: The dorsal row and the lateral row on each side are the most important from a taxonomic standpoint. The first shield in the dorsal row corresponds to the occipital plate or nuchale, and the last is just in front of the modified shield (see below) at the beginning of the dorsal fin. The first shield of the lateral row, called the supracleithrum, borders the posterior margin of the branchial cavity; although its size may vary, it is typically larger than the next posterior shield; its spine is usually less developed than the spines on the shields posterior to it. The last shield of the lateral row (a small one) is situated at the posterior extremity of the caudal peduncle, just anterior to the shields that continue on from the lateral row along the upper lobe of the caudal.

The elongated fulcrum at the base of the lower caudal lobe (difficult to see on large fish) is of considerable taxonomic importance when compared to the length of the anal fin base.

There are also modified shields at the beginning of both dorsal and anal fins; these, because of their respective positions, can be called predorsal and preanal. The one in front of the dorsal fin is more important from the taxonomic point of view; this modified shield is oval in shape, has no median crest or spine, and its posterior end is somewhat bent upwards to embrace the first dorsal ray; the anterior end is not forked but does have a slight indentation. There are two or more preanal shields; the nearest one to the fin is very similar in shape and structure to the predorsal shield; those farther in front, according to the species, are present in pairs or in a single file; the disposition of these preanal shields is the same as that for postdorsal shields (see below).

DERMAL OSSIFICATIONS: These small bony structures (ftn. 4), which vary in size and shape with species and with age of fish, lie in the skin between the regular rows of bony shields; they are best developed on the sides between the dorsal and lateral rows. The degree of development, according to species, corresponds closely to that of the regular bony shields.

TOTAL LENGTH (TL) is taken along the median line from the tip of the snout to the posterior of the upper lobe of the tail when the fish is lying in a natural position. FORK LENGTH (FL) is measured from the tip of the snout to the posterior end of the median caudal rays—that is, to the fork of the tail. [In specimens less than five inches (125 mm) FL, the lower caudal rays are still not fully developed and are therefore short. The absence of the lower caudal lobe is not only typical of young *oxyrhynchus* but of other Sturgeons as well. We observed this in *fulvescens*; and Grote, *et al.* (36:

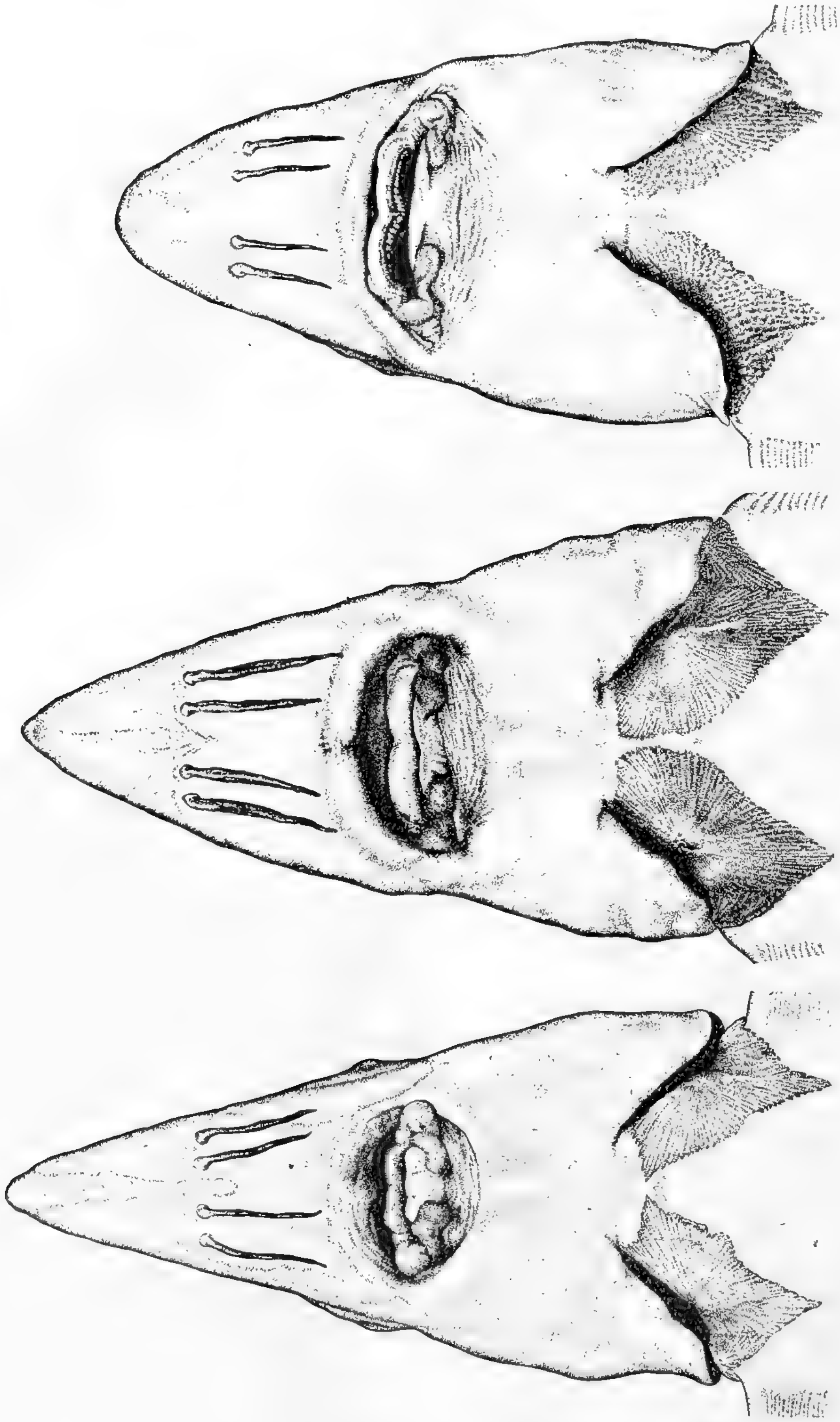

FIGURE 7. Ventral views of heads, left to right: *A. oxyrhynchus*, shown in Fig. 10; *A. fulvescens*, shown in Fig. 9; *A. brevirostris*, shown in Fig. 8.

215, fig. 158) and Roule (*62*: pl. 4, fig. 7) have presented drawings of young *A. sturio* in which the lower lobe is not well grown.]

Head length is the distance from the anterior tip of the snout to the rearmost point of the opercle, opercular membrane excluded. Snout length is from the anterior tip of the snout to the anterior margin of the orbit, the membranous rim included. Mouth width is the greatest transverse distance across the mouth slit, with the thick lips excluded and the mouth closed. Postorbital distance is that from the posterior edge of the orbit, membranous rim included, to the rearmost point of the opercle, membrane excluded. Interorbital width is the minimum distance across the top of the head between the bony edges of the orbits. Gill rakers are counted on the outer surface of the first branchial arch, including the rudimentary ones; they are usually counted on the left side of the fish; in specimens smaller than eight inches (20 cm), some rakers on the upper limb are not yet developed; therefore the counts for young individuals are not given (see also *84*: 149–154).

Base of anal fin is the length from the structural base of the first ray to the point where the membrane behind the last ray contacts the body. Fin ray counts for the dorsal and anal are sometimes given, but it is difficult to count these accurately, even after staining with alizarin and clearing in glycerin (*83*: 3–9); the fin membrane is very thick, and the rays are numerous, close together, and show little bifurcation; and in young individuals several rays are detached from the basal elements (radials). Since the counting of rays is not only tedious but uncertain, we omit the number of fin rays from the taxonomic characters.

Remarks on Identification. Within the same species, various characters change considerably with growth; young have much longer snouts than adults, and their scutes (shields) are sharper and closer together. Because of these natural changes it is difficult to prepare a universal key for the specific identification of young specimens as well as adults. There are, it is true, several fairly constant interspecific differences in anatomical features, such as the intestinal tract, gill arches, grinding ridges within buccal cavity, and otoliths, to mention a few. But to present these in abbreviated form seems likely to prove confusing rather than helpful, hence they are not included in the following Key to Species.

Key to American Atlantic and Pacific Species of *Acipenser*

1a. Species of the Atlantic Seaboard.
  2a. Mouth width less than 55% of interorbital; average difference between TL and FL 14% of FL; gill rakers 17–27 (av. 21.6); postdorsal and preanal shields in pairs; viscera pale, unpigmented.
    3a. In young specimens 50–70 cm long, head length 26–28% of FL; bony shields of dorsal row oval in shape, their longitudinal length being greater than their transverse width; carina on dorsal shields low, without a pronounced hook; dermal ossifications between dorsal and lateral rows

of shields only weakly developed; spleen short, not reaching farther back than middle loop of small intestine.

oxyrhynchus oxyrhynchus Mitchill 1814, p. 46.

3b. In young specimens 50–70 cm long, head length 30–34% of FL; bony shields of dorsal rows rather square in shape, their longitudinal length much shorter than their transverse width; carina on dorsal shields high, typically with two strong hooks; dermal ossifications between dorsal and lateral rows of shields strongly developed; spleen long, reaching much farther back than middle loop of small intestine.

oxyrhynchus desotoi Vladykov 1955, p. 56.

2b. Mouth width over 62% of interorbital; average difference between TL and FL less than 12% of FL; gill rakers 22–40; postdorsal and preanal shields in a single row; viscera blackish, heavily pigmented.

4a. Gill rakers 22–29 (av. 25.4); interorbital width 34–40% (av. 37%) of hl; dorsal shields 8–13 (av. 10); lateral shields 25–32 (av. 28.3); dorsal and lateral shields pale, contrasting with dark background; length, so far as known, not over 100 cm.

brevirostris LeSueur 1818, below.

4b. Gill rakers 25–40 (av. 33.1); interorbital width 29–35% (av. 32%) of hl; dorsal shields 9–17 (av. 13.4); lateral shields 29–42 (av. 35.4); dorsal and lateral shields brownish, of same color as background; length commonly over 100 cm. *fulvescens* Rafinesque 1817, p. 41.

1b. Species of the Pacific Seaboard.

5a. Caudal peduncle short; tip of anal fin reaching or even extending beyond base of lower lobe of caudal; modified shield at beginning of dorsal fin rudimentary or absent; 11–14 dorsal shields; 38–48 lateral shields; gill rakers 34–36; viscera blackish, heavily pigmented. *transmontanus* Richardson 1836.

Southern Alaska to California; enters salt water.

5b. Caudal peduncle long; tip of anal fin not reaching base of lower lobe of caudal; a large modified shield at beginning of dorsal; 8–11 dorsal shields; 23–31 lateral shields; gill rakers 18–20; viscera pale, practically without pigment.

medirostris Ayres 1854.

Southern Alaska to California; enters salt water.

Acipenser brevirostris LeSueur 1818

Shortnose Sturgeon

Figures 7, 8

Study Material. A total of 109 specimens: 95, 450–900 mm TL, from the Hudson River, New York;[20] 1, presumably LeSueur's type, ANSP 16953;[21] 1, from Dela-

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[20] For age and localities of these specimens, see Greeley (*35*: 89, 90).

[21] This specimen, originally No. 84, was described by Ryder (*65*: 236) and later by Fowler (*33*: 604, pl. 38, fig. 1). On June 23, 1949, the specimen (stuffed) measured 746 mm FL.

ware River at Bay-at-Green Creek, Cape May County, New Jersey, in salt water, May 5, 1907, ANSP 25471; 4, from Delaware River at Torresdale, Philadelphia County, Pennsylvania, in fresh water, November 1911, ANSP 44298–44301; 3, 470–580 mm FL, from Delaware River, March 29–31, 1913, USNM 125816–125818;[22] 1 young, 185 mm FL, Salmon Creek, North Carolina, USNM 64330; 1 of head, fins, and dried strips of skin with plates, from Potomac River, USNM 26273; 3 stuffed specimens in Paris Museum.[23]

Distinctive Characters. A. brevirostris is distinguished from *A. oxyrhynchus* by blackish viscera, a wider mouth (see Key), the absence of a fontanelle, almost complete absence of the postdorsal shields, and by preanal shields arranged in a single row. Also, individuals of *A. brevirostris* assume adult proportions when they are only about two feet TL; *A. oxyrhynchus* retains juvenile characteristics even up to four feet. The most conspicuous difference between *brevirostris* and *fulvescens* is in the lateral scutes, which are much paler than the background in the former but of the same shade as the background in the latter.

Description. SCUTES in all five main rows not closely set and rather weakly developed in adults in comparison with other eastern American species, but sharp and set close together in a young specimen 7.75 inches FL (USNM 64330); in 12 specimens, 8–13 (av. 10) dorsal shields, 25–32 (av. 28) lateral shields, and 7–11 (av. 8) ventral shields; shields behind dorsal fin either in a single row or paired; elongated fulcrum at base of lower caudal lobe shorter than base of anal fin.

HEAD averaging 22% of FL in adult, 28% in a young specimen 7.75 inches FL. FONTANELLE ab-

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[22] According to the tag, these specimens were submitted as "young Sturgeon" (presumably as *A. oxyrhynchus*) for identification.

[23] Details on these specimens are given by Bertin (*12*: 252). Two of these fish were sent to the Paris Museum by LeSueur, apparently as paratypes.

FIGURE 8. *Acipenser brevirostris.* Lateral view of spawning female, 580 mm long, from the Hudson River near Kingston, New York.

sent on top of head. Snout in 22 grown specimens (390–700 mm FL), much shorter than postorbital distance (av. 70% of the latter), but in a young specimen, longer than postorbital distance (183%). Postorbital distance in adults 51–61% (av. 55%) of hl, but 33% in a young specimen. Interorbital width 34–40% (av. 37%) of hl, and Mouth width (excluding lips) 69–81% (av. 74%) of interorbital width, these two characters not differing with age.

Gill rakers rather long, triangular, in 13 specimens 22–29 (av. 25.5) on first branchial arch; in number of gill rakers, *A. brevirostris* occupies an intermediate position between *A. oxyrhynchus* with 17–27 (av. 21.5) and *A. fulvescens* with 25–40 (av. 33).

Caudal fin with short upper but rather long lower lobe; average difference between TL and FL, 11% of FL; no notch at tip of upper caudal lobe.

Color. In preserved specimens, general color similar to that of *A. oxyrhynchus* (p. 46). Top of head and back dark, becoming paler on sides; entire lower surface white. Central part of dorsal shields whitish, contrasting with darkly pigmented back and black skin between shields. Lateral shields pale, clearly distinguished from surrounding skin. Ventral shields of the same whitish color as lower surface of fish. Intestinal tract, air bladder, and fat surrounding gonads darkly pigmented, nearly black; the peritoneum only slightly pigmented.

In an excellent photograph of a live *brevirostris*, the similarity in color to *oxyrhynchus* is particularly striking (*44*: 14, 15): in addition to the details observed on preserved specimens, the white edging on the paired fins is similar; but the anal fin in *brevirostris* is pigmented while that in *A. oxyrhynchus* remains whitish. Small live specimens from the Hudson River show black pigment blotches similar to those of young *A. fulvescens.*

Size: This is the smallest species of all the Sturgeons. Apparently it never grows to more than about three feet; the largest specimen recorded thus far is a female 39.5 inches TL (899 mm FL), from the Connecticut River. The measurements submitted by Professor Andrews and two specimens sent to us (p. 40) confirm his determinations. The largest sizes encountered during the present studies were: a female 34.8 inches TL, weighing eight pounds 15 ounces, in its 13th year as determined by its otoliths; and a male 25.5 inches, weighing four pounds five ounces; both were taken from the Hudson River (*35*: 68–70).

Development and Growth. The early life history is unknown. Few small specimens have been recorded; probably the smallest fish is one of 7.3 inches (about 185 mm), from North Carolina (USNM 64330). The smallest specimens taken in the Hudson River were two females; one was 17 inches (about 433 mm) and weighed only 15 ounces; the other was a little less than 18 inches (about 600 mm) and weighed 19 ounces. The sizes of five specimens from the Delaware River observed by Ryder ranged between 18–23 inches. Age determinations, based on otolith readings (*35*: 68–70), have shown that *A. brevirostris* is a very slow-growing species. Specimens of *brevirostris* from the Hudson River that measured 17–35 inches (about 430–890 mm) TL were 4–15 years old; on the other hand, *A. oxyrhynchus* 74–100 long were 11–13 years of age. The growth rate of the two species, however, is very similar in early life, which suggests that the subsequent divergence is due to more rapid growth by *oxyrhynchus* while at sea.

Spawning. Males may mature when they are only about 20 inches TL, and most of them do so by the time they pass 21 inches; most of the females mature at about 24 inches. The ripe eggs are dark brown. Their number is not known. Spawning takes place in rivers early in the spring. For Hudson River fish, Greeley (*35*: 90) stated that:

> The spawning season evidently included late April during 1936. Several fish approaching spawning condition were examined from Rhinecliff during early April. A female, weighing five pounds, from Highland April 21 contained eggs which appeared ripe, while a three pound male taken at the same time was spent. Roe fish from Highland, May 1, were spent (2 pounds, 13½ ounces; 5 pounds, 8 ounces). Several others, also taken during early May had spawned.

General Habits. On account of its small size, *A. brevirostris* has attracted little attention except when taken in nets in fresh, brackish, or salt water. It is found most often in tidal rivers. But the place of capture of Gulf of Maine specimens shows that some certainly go out into the open sea and wander for some distance from the parent stream.

Food. Studies of stomach contents from Hudson River specimens showed that *A. brevirostris* feeds upon the bottom, eating small animals and plants intermingled with mud (*72*: 141–144, table 4). The organisms consumed were sludgeworms, chironomid larvae, small crustaceans, etc., such as are found in the stomachs of young Atlantic Sturgeon (p. 52).

Abundance and Relation to Man. Because of its scarcity and small size, *A. brevirostris* is of slight interest to commercial fishermen, hence there is little information about its abundance.

Ryder (*65*: 232), writing of the fishery for *oxyrhynchus* in the Delaware River, stated, "It was my good fortune to secure no less than five specimens of the *A. brevirostris* of LeSueur, which has, so far as I can learn, not been certainly recognized since that Naturalist's time," and our own *Study Material* (p. 36) marks it as at least not uncommon in the Hudson today. But while LeSueur in 1811 stated that the Shortnose Sturgeon is "more sought after and commands a higher price than the large common species" in the Delaware River (*75*: 383–394), it is of virtually no economic importance at present due to its small size and apparent scarcity. Its flesh, however, is of good quality, and its eggs are suitable for caviar, but they are not very numerous. A few fishermen prior to 1937 set gill nets for *brevirostris* in the Hudson River just before the yearly run of American shad (*Alosa sapidissima*). Some have also been taken in the Hudson River with hook-and-line by anglers.

Range. Atlantic seaboard of North America, from New Brunswick, Canada (*47*: 504, and later comments), to Florida, mostly in rivers, including the Connecticut, Hudson, Delaware, and Potomac. This range is based upon records for a period of years, and the species may now occupy a more restricted area.

Until recently the southernmost definite record was for Charleston, South Carolina

(*43*: 106). Smith stated, "while it doubtless ascends all suitable streams in North Carolina, actual records of its occurrence are rare" (*67*: 58). However, thanks to Dr. Daniel M. Cohen, we had an opportunity to examine a female *A. brevirostris* (UF 5714) 735 mm TL taken on May 11, 1949, in Big Lake George of the St. Johns River drainage, Putnam County, Florida. This is a proven record of the occurrence of the Shortnose Sturgeon in Florida. Thus the geographic range of *A. brevirostris* is almost as extensive as that of *A. oxyrhynchus*.

It has been reported as being taken as far north as the St. Lawrence River (*32*: 70; *59*: 226; *37*: 44), but these records seem to be based chiefly on *A. fulvescens*, in part on *A. oxyrhynchus*. The most northerly proven record of its occurrence is for the St. John River, New Brunswick (*47*: 504). We also obtained some specimens from this same area, thanks to the kindness of the late Dr. Leim. Collections taken at Gagetown include three heads of adults caught in 1959 (collected by J. C. Medcof, Biological Station, St. Andrews, New Brunswick); also, seven adult females (700–870 mm TL) and three adult males (740–800 mm TL) were taken in May and early June 1960 (obtained by Fishery Officer J. O. Jenkins). One female and one male of the latter sample were almost ready to spawn. In the Connecticut River, near Hadley, Massachusetts, four adults were caught in October 1951 and September 1952 (obtained by Professor T. J. Andrews, University of Massachusetts).

The breeding range of *A. brevirostris* is not clearly defined, but it is known to include the Hudson River, where the spawning areas appear to be very restricted. The Delaware River may still maintain a small local population, and it seems likely that the St. John River, N. B., has a spawning population, judging by the near-spawning condition of the above-noted male and female taken at Gagetown. If, through increased pollution or habitat changes, the population is no longer able to persist in these northern rivers, the species may become dangerously reduced.

The Shortnose Sturgeon has no close relative in Europe.

Synonyms and References:[24]

Acipenser brevirostris LeSueur, Trans. Amer. philos. Soc., *1*, 1818: 390 (descr., Delaware R.); DeKay, Zool. N.Y., 4, 1842: 345 (descr., ident. from Virginia not certain); Ryder, Bull. U.S. Fish Comm. (1888), *8*, 1890: 231 (descr., Delaware R.); Jordan and Evermann,* Bull. U.S. nat. Mus., 47 (1), 1896: 106 (descr., synon., Cape Cod to Florida, specimen from Charleston, S. Carolina); Smith,* N.C. geol. econ. Surv., *2*, 1907: 57 (genl. acct., doubtless occur. N. Carolina); Kendall,* Occ. Pap. Boston Soc. nat. Hist., 7 (8), 1908: 17 (New England); Fowler, Proc. Acad. nat. Sci. Philad., 1910: 604; Halkett,* Check List Fish. Canad., 1913: 44 (genl. range of distr.); Nichols and Breder,* Zoologica, N.Y., *9*, 1927: 31 (genl. acct.); Hildebrand and Schroeder,* Bull. U.S. Bur. Fish., *43*, 1928: 76 (Provincetown, Massachusetts); Breder,* Field Bk. Mar. Fish. Atl. Cst., 1929: 43 (genl. acct.); Truitt, Bean, and Fowler, Bull. Md. Conserv. Dep., 3, 1929: 33 (genl. acct.); Jordan,* Manual Vert. Anim. NE U.S., 1929: 33 (distr., key, and brief characteristics); Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish. (1928), 2, 1930: 34 (in checklist); Jordan and Evermann, Amer. Food Game Fish., 1937: 12 (genl. acct., key); Greeley, N.Y. Biol. Surv. Lower Hudson Watershed (1936), 11, 1937: 90 (size ranges, age determ., Hudson R.); Schrenkeisen, Field Bk. Freshw. Fish. N. Amer., 1938: 14 (genl. acct.); Vladykov and Beaulieu, Nat.

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[24] We follow the lead of Jordan, *et al.* (*45*: 34) in calling this species *brevirostris*. The authors who used the spelling *brevirostrum* are marked by an asterisk (*) following their names.

Canad., *73*, 1946: 43 (detail. acct. of shields and gill rakers, size); Nat. Canad., *78*, 1951: 199 (detail. acct. of gill rakers for three w. Atlantic species).

Acipenser (*Huso*) *lesueurii* Valenciennes (Ms.) Duméril, Hist. Nat. Poiss. *2*, 1870: 166 (descr., New York).[25]

Acipenser (*Huso*) *rostellum* Duméril, Hist. Nat. Poiss., *2*, 1870: 173 (descr., New York?).[25]

Acipenser (*Huso*) *sinus* Valenciennes (MS.) Duméril, Hist. Nat. Poiss., *2*, 1870: 175 (descr., New York?).[25]

Acipenser fulvescens Rafinesque 1817

Lake Sturgeon,[26] Smoothback

Figures 7, 9

Study Material. Over 800 specimens, 6–229 cm or 2.5–90 inches TL (5.7–211 cm or 2.3–83 in. FL), from different sections of the St. Lawrence River, Quebec; also odd specimens from Lake Ontario on both the Canadian and New York sides. Specimens from a large number of interior waters not included. For details, see Vladykov and Beaulieu (*83*: 18).

Distinctive Characters. A. fulvescens, like *A. brevirostris*, is distinguishable from *A. oxyrhynchus* by: the arrangement of its preanal shields in a single row, a mouth not less than 66% as wide as the interorbital width, the absence of a soft area (fontanelle, p. 27) on the top of the head, and black viscera. From *brevirostris* it differs in that its lateral shields are of the same color as the background.

Description. SCUTES in young specimens (up to 12 in. FL), in all rows, developed even more strongly than in *A. oxyrhynchus* of corresponding sizes; progressively absorbed with age, beginning with the ventral rows, until they may be completely so, near spawning time, especially in the ventral rows (hence the commercial name Smoothback); in 516 Quebec specimens, 9–17 (av. 13.4) dorsal shields, and in 242 specimens, 29–42 (av. 35.4) lateral shields; shields behind dorsal fin in a single row; elongated fulcrum at base of lower caudal lobe never longer than base of anal fin. DERMAL OSSIFICATIONS minute, but the skin much tougher than in *A. oxyrhynchus.*

HEAD longer in young than in larger individuals, on the average 24% of FL in specimens 40–70 cm FL. SNOUT in specimens less than 50 cm FL longer than postorbital distance, but shorter in older individuals. INTERORBITAL width rather large, varying; in 79 young specimens 8–36 cm FL, 21.6–31.8% (av. 28%) of hl; in 143 older specimens 40–211 cm FL, 29–40% (av. 34%). MOUTH large, its width (excluding lips) 66–93% (av. 77%) of interorbital width.

GILL RAKERS rather short and blunt, but numerous; 350 Quebec specimens above 8 inches FL with 25–40 (av. 33.1) rakers.

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[25] The Duméril holotypes of these three species are kept mounted in good condition at the Paris Muséum National d'Histoire Naturelle. They were examined in 1950 and identified as *A. brevirostris* by Vladykov. A similar identification was made by Bertin (*12*: 252). Jordan, *et al.* (*45*: 34) quoted two more names given by Duméril (*28*: 164–168), based on locality only: *microrhynchus* (New York) and *dekayi* (New York).

[26] In Quebec, the French-speaking fishermen call the adults Esturgeon jaune or Camus, that is, short and flat snout; the latter name was already in use at the end of the last century (*52*: 188). The young specimens are usually named Escargot, or in certain sections (Nicolet) Charbonnier, on account of the black blotches (83: 32). On the New York market, this species is often called the Smoothback.

CAUDAL fin with rather short upper but long lower lobe; the average difference between TL and FL 9% of FL; no notch at tip of upper lobe.

Color. There is a pronounced difference between the young and the adult. In young below 300 mm (12 in.) FL, two pairs of large black blotches present on anterior half of upper surface of snout and on back between dorsal and lateral rows of shields, the anterior blotch the larger and immediately behind the base of pectoral fin, the smaller posterior one below the dorsal fin;[27] in addition, several small, irregular, black spots on top of head, on back and sides, and on lower surface of caudal peduncle. Intestinal tract darkly pigmented, nearly black. Air bladder and fat surrounding gonads, dark gray. Peritoneum pale or only slightly pigmented. In general, the dark pigmentation of the intestinal tract is similar to that of *A. brevirostris* but very distinct from that of *A. oxyrhynchus*. In half-grown specimens up to about 24 inches or 610 mm FL, the large blotches have disappeared, but black spots may persist. Older individuals above 40 inches FL are uniformly dark brownish or grayish on top of head and on back and sides. In fish of all ages, dorsal and lateral shields of the same color as background; shields of ventral rows sometimes pigmented on upper part but always whitish on lower part. Lower surface of young and adults uniformly whitish. In young below 24 inches FL or about 610 mm, preserved in 4–5% formalin, lower surface and sides of head and body clear green. At all ages, fins dark brown or gray, typically without white edging.

Size and Growth. Among western North Atlantic species, *A. fulvescens* reaches a size exceeded only by *A. oxyrhynchus*. The largest recorded is a female Lake Sturgeon, of approximately 275 pounds, taken in Lake Winnipeg, Manitoba, in the summer of 1941 (*40*: 17). The largest male, caught in Lake Erie in 1948, weighed 220 pounds (*66*: 7). The specimens from Quebec listed in *Study Material*, 2.5–90 inches TL, weighed 0.032 ounces–212 pounds (0.9 g–96

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[27] For a good illustration of these black blotches in young *A. fulvescens*, see Forbes and Richardson (*31*: 36); for color illustrations of an adult, see Vladykov (*82*: 6).

FIGURE 9. *Acipenser fulvescens.* Lateral view of immature female, 655 mm long, from the St. Lawrence River near Neuville, Quebec, P. Q., Canada.

kilo).[28] Data for the smallest 11 specimens from the St. Lawrence River, taken from August to November in pêches located near Quebec City, are tabulated in Table 1. Judging by their long snouts, dorsal scutes in a continuous row without separation, general coloration, and small size, we consider all of these specimens to be less than one year old. During the first year, juveniles of *A. fulvescens* (Table 1) and of *A. oxyrhynchus* grow at about the same rate.

Table I. Growth Rate of *A. fulvescens*.

Date	Total Length		Fork Length		Weight		Place
	(mm)	(inches)	(mm)	(inches)	(g)	(oz.)	
Sept. 19, 1952...	63	2.48	57	2.24	0.9	0.032	St. Nicolas
Oct. 19, 1953...	84	3.31	82	3.23	2.0	0.071	St. Nicolas
Aug. 8, 1947...	87	3.43	79	3.11	2.5	0.088	Neuville
Nov. 19, 1947...	99	3.90	90	3.54	3.2	0.113	Neuville
Oct. 31, 1952...	106	4.17	98	3.86	4.4	0.155	Neuville
Sept. 12, 1944...	109	4.29	96	3.78	4.3	0.152	Neuville
Aug. 20, 1952...	117	4.61	107	4.21	4.8	0.169	Neuville
Sept. 30, 1947...	121	4.76	109	4.29	4.7	0.166	Neuville
Aug. 29, 1947...	121	4.76	111	4.37	7.7	0.271	St. Vallier
Aug. 25, 1952...	123	4.84	112	4.41	6.5	0.229	Neuville
Sept. 30, 1947...	123	4.84	112	4.41	6.2	0.219	Neuville
AVERAGE........	104.8	4.13	95.8	3.77	4.29	0.151	

Although the ages of Lake Sturgeon in our material from the St. Lawrence River have not as yet been determined, probably their range is up to 30 years, or even more. According to Cuerrier and Roussow, who studied the growth of *fulvescens* from the upper St. Lawrence River (Lake St. Francis), fish 3–22 years old averaged 16.5–37.5 inches FL (*24*: 8–14). The oldest fish in their material, a female 23 years of age, was 50.5 inches FL and weighed 42 pounds.

Spawning and Reproduction.[29] The principal spawning season for *A. fulvescens* in Quebec extends from about the beginning of May to the end of June. The smallest male ready to breed, taken at St. Vallier on May 5, 1944, was 38 inches TL (35 in. FL) and weighed 11 pounds 4 ounces. The smallest mature female, taken at the same place on June 13, 1949, was 45 inches TL (41 in. FL) and weighed 17 pounds. The Lake Sturgeon from Lake Nipigon, Ontario, does not become sexually mature until it is about 22 years of age, when it is approximately three feet TL (*38*: 15–25).

Roussow, in studying cross sections of the first pectoral ray of *A. fulvescens*, found variations in the broad and narrow zones on this bone (*64*: 553–572). He concluded that "the growth retardations caused by the ripening of the gonads and the

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[28] For the length-weight relationship of St. Lawrence specimens from Quebec, see Vladykov (*78*: 57). Roussow has given some information on the rate of growth and movements of *A. fulvescens* from the St. Lawrence and Ottawa rivers (*63*: 1–124). Results of extensive tagging at Quebec of 1,507 *A. fulvescens* and 2,995 *A. oxyrhynchus* have been summarized by Magnin and Beaulieu (*50*: 237–252).

[29] Additional information on spawning habits and experimental hatching of Lake Sturgeon has been given by Stone (*69*: 118–123) and Carter (*16*: 60–63).

losses at the consecutive spawnings are visible in the ray sections in the form of 'belts' of 2 to 7 narrower zones (or annuli). These indicate that the interval between spawning periods can vary from 4 to 7 years and more." It is highly desirable to corroborate these findings by observing the frequency of spawning by tagged specimens.

The principal spawning rivers in Quebec are the St. Francis for Lake St. Peter, and the Batiscan and Chaudière for the respective sections of the St. Lawrence from Three Rivers to Montmagny.

The diameter of mature but unfertilized eggs preserved in 4–5% formalin varied between 2.7–3.1 mm. Thus the ripe eggs of *A. fulvescens* are somewhat larger than those of *A. oxyrhynchus*. Table II gives data on ovaries and eggs from mature females of *A. fulvescens* from the St. Lawrence River near Quebec.

Table II. Data on Ovaries and Eggs of *A. fulvescens*.

		Length			Weight		Wgt. of Ovaries		Diam. of Eggs
		TL	FL	FL					
Locality	Date	(cm)	(cm)	(in.)	(kg)	(lb.)	(kg)	(lb.)	(mm)
St. Vallier	June 5, 1944	136	127	50.0	17.1	37.6	3.1	6.9	2.7
St. Vallier	May 15, 1950	144	136	53.5	26.3	58	4.7	10.4	2.8
St. Vallier	May 15, 1950	142	133	52.4	19.1	42	2.9	6.4	2.9
St. Vallier	June 17, 1946	145	135	53.1	22.2	49	—	—	3.0
St. Vallier	May 19, 1946	175	170	66.9	50.3*	100*	—	—	3.0
St. Nicolas	May 8, 1949	170	163	64.2	37.0	81	11.2	24.6	3.1

* Approximate.

Food. In the St. Lawrence, *A. fulvescens* subsists on about the same type of food as *A. oxyrhynchus* (p. 52). In 29 stomachs of *fulvescens* we found that larvae of the burrowing May fly (*Hexagenia*) were present in 76% of the samples, amphipods in 73%, gastropod mollusks in 48%, bivalve mollusks in 35%, and fish in 24%. Indeed, *A. fulvescens* of different sizes are easily taken by hook-and-line, and the best bait is young shad, or, as second choice, banded killifish (*Fundulus diaphanus*). Harkness[30] found that *A. fulvescens* in Lake Nipigon, Ontario, fed principally on May fly and chironomid larvae and on mollusks.

Abundance and Commercial Importance. According to official statistics for 1951, the catches of Lake Sturgeon were (in pounds): 9,000 for Saskatchewan, 164,000 for Ontario, 194,000 for Quebec, and 13,000 for the U.S. Great Lakes; total, 380,000 pounds, with a combined monetary value of $ 300,000. Late nineteenth-century yields were several times greater. From Lake Michigan alone, in 1880, the catch was 3,839,600 pounds (*31*: 26). Lake of the Woods (Minnesota and Canada) was formerly called "the greatest sturgeon pond in the world"; the catch there in 1893 was 1.6 million pounds (*29*: 121–136).

In the St. Lawrence River, from the Ontario border to Cap St. Ignace at Quebec,

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[30] Harkness (*38*: 28, 29) has given references to other authors who studied food requirements of *A. fulvescens* from various localities.

there is a regular fishery for this species; at Quebec, although present catches are less abundant than formerly, *A. fulvescens* is still taken in fair quantity; and it is reported as being still very plentiful in the Hudson Bay area. Large *A. fulvescens* are taken early in the spring or late in the fall. During the summer months, in the vicinity of Quebec City from St. Nicolas to Montmagny, *A. oxyrhynchus* is more plentiful than *fulvescens*; however, both species are taken together quite often at the beginning and end of the fishing season. The fish are caught with either gill nets (8–10 in. stretched mesh) or weirs, and a few are taken on set lines baited with fish, or in New York on unbaited set lines ("trap lines").

Relation to Man. Considering its entire range, the Lake Sturgeon is at present of much greater commercial value than both the American Atlantic Sturgeon and the Shortnose Sturgeon combined. The principal product is the meat for "smoked Sturgeon." In 1951, in Canada, 2,000 pounds of caviar were made from the eggs of this species.

Range and Occurrence in the Western North Atlantic. Larger rivers and lakes, from Hudson Bay to the Mississippi Valley; according to Hubbs and Lagler (*41*: 30), "from the Red River of the North, the Saskatchewan River in Alberta, and the Hudson Bay, St. Lawrence and Lake Champlain drainages of Canada (and possibly from Labrador), southward, west of the Appalachian Mountains, to the Tennessee River of Alabama, to Missouri and to eastern Nebraska." On several occasions it has been reported as being taken on the shores of Hudson Bay (*75*: 30 [42]).[31] In the St. Lawrence River, where a general line of demarcation between fresh and brackish water can be drawn from Cap Brulé on the north shore to St. Jean-Port-Joli on the south shore, it is taken in commercial quantities from Lauzon to Cap St. Ignace, together with *oxyrhynchus*. Occasionally Lake Sturgeon venture even farther into brackish water. For instance, on October 10, 1954, an *A. fulvescens* weighing five pounds was taken in a pêche at St. Roch-des-Aulnaies; information from Mr. Alfred Pelletier, proprietor. For further details see Vladykov (*79*: 54–57). It should be emphasized, however, that a sea-resident stage, characterized by a rapid growth rate, has not been demonstrated for this species.

Synonyms and References:

Acipenser fulvescens Rafinesque, Amer. Mon. Mag., *1*, August, 1817: 288 (descr., Great Lakes); Hubbs, Copeia, 1917: 48 (synon.); Hubbs, Misc. Publ. Mus. Zool. Univ. Mich., *15*, 1926: 8 (in checklist); Dymond, Univ. Toronto Stud. Biol., *27*, 1926: 33 (descr., Lake Nipigon, Ontario); Dymond, Hart, and Pritchard, Univ. Toronto Stud. Biol., *33*, 1929: 13 (statist. of catches); Jordan, Manual Vert. Anim. NE U.S., 1929: 33 (distr., key, and brief characteristics); Jordan, Evermann, and Clark, Rept. U.S. Comm. Fish. (1928), *2*, 1930: 35 (in checklist); Greeley, N.Y. Biol. Surv. Champlain Watershed (1929), 4, 1930: 73 (Lake Champlain); Bajkov, Trans. Amer. Fish. Soc. (1930), 60, 1931: 11 (statist. of catches, Manitoba); Greeley, N.Y. Biol. Surv. St. Lawrence Watershed (1930), 5, 1931: 81 (St. Lawrence R., New York); Bajkov, Trans. Amer. Fish. Soc. (1930), 60, 1931: 11 (Manitoba, statist. of catches); Gowanloch, Bull. La. Conserv. Dep., 23, 1933: 412 (genl. acct.); Vladykov, Contr. Canad. Biol., *8* (29), 1933: 30 (42) (Hudson Bay region); Schrenkeisen, Field Bk. Freshw. Fish. N. Amer., 1938: 13 (genl. acct.); Kuhne, Guide Fish. Tennessee, 1939: 17 (genl. acct.); Dymond, Contr. R.

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[31] A young specimen of *A. fulvescens* about 107 mm FL (USNM 27784) was taken by Walton Hayden at Moose Factory, James Bay (a southern extension of Hudson Bay), no doubt in brackish water.

Ontario Mus. Zool., *15*, 1939: 8 (statist. of catches, Ottawa R.); Hinks, Fish. Manitoba, 1943: 15 (Manitoba); Eddy and Surber, North. Fish. Upper Mississippi Valley, 1943: 57 (size, artif. propag., Mississippi R.); Vladykov and Beaulieu, Nat. Canad., *73*, 1946: 27 (detail acct. of shields and gill rakers, size, Quebec); Hubbs and Lagler, Bull. Cranbrook Inst. Sci., 26, 1947: 30 (distr.); Dymond, Misc. Publ. R. Ontario Mus. Zool., *1*, 1947: 4 (genl. distr., range); Vladykov and Beaulieu, Nat. Canad., *78*, 1951: 129 (detail. acct. of gill rakers for three w. Atlantic species); Scott, Freshw. Fish. East. Canada, 1954: 7.

Acipenser rubicundus LeSueur, Trans. Amer. philos. Soc., *1*, 1818: 38 (descr., Lakes Ontario, Erie and all upper lakes); DeKay, Zool. N.Y., 4, 1842: 344 (descr.); Jordan and Evermann, Bull. U.S. nat. Mus., 47 (1), 1896: 106 (descr., synon., distr.); Carter, Trans. Amer. Fish. Soc., 34, 1904: 60 (artif. propag. Vermont); Evermann and Goldsborough, Proc. biol. Soc. Wash., *20*, 1907 (Canada); Kendall, Occ. Pap. Boston Soc. nat. Hist., *7* (8), 1908: 16 (Lake Champlain, Vermont); Nash, Vertebr. Ontario, 1908: 14 (genl. acct.); Kendall, Proc. Portland Soc. nat. Hist., 2, 1909: 219 (checklist, Labrador); Halkett, Check List Fish. Canad., 1913: 44 (Canada); Forbes and Richardson, Fish. Illinois, 1920: 24 (descr., statist. of catches); Harkness, Univ. Toronto Stud. Biol., *24*, 1923: 13 (age, food); Kendall, Contr. Canad. Biol. (1923), 23, 1924: 21 (439) (between Lake Winnipeg and Hudson Bay); Breder, Field Bk. Mar. Fish. Atl. Cst., 1929: 43 (genl. acct.); Jordan and Evermann, Amer. Food Game Fish., 1937: 10 (genl. acct., key).

Acipenser maculosus LeSueur, Trans Amer. philos. Soc., *1*, 1818: 393 (descr., young from Ohio R.).

Acipenser serotinus Rafinesque, Ichthyol. Ohiensis, 1820: 80 (Ohio R.).

Acipenser ohiensis Rafinesque, Ichthyol. Ohiensis, 1820: 81 (Ohio R.).

Acipenser macrostomus Rafinesque, Ichthyol. Ohiensis, 1820: 81 (Ohio R.).

Dinectus truncatus Rafinesque, Ichthyol. Ohiensis, 1820: 82 (erroneous, based on drawing by Audubon).

Acipenser rupertianus Richardson, Fauna Boreal. Amer., 1836: 311 (specimen from Albany R., Rupert Land).

Acipenser laevis Agassiz, Lake Superior, 1850: 267 (Lake Superior).

Acipenser carbonarius Agassiz, Lake Superior, 1850: 271 (Lake Superior).

Acipenser rhynchaeus Agassiz, Lake Superior, 1850: 276 (Lake Superior).

Acipenser liopeltis Günther, Cat. Fish. Brit. Mus., *8*, 1870: 341 (Mississippi).

Nominal specific names, given by Duméril (*31*: 105, 220) to specimens of *A. fulvescens*, according to locality only: *copei* (supposedly upper Missouri), *rauchi* (Osage R., Missouri), *richardsoni* (upper Mississippi), *anasimos* (Missouri R.), *paranasimos* (Huntsville, Alabama), *anthracinus* (Lake Erie), *megalaspis* (Lake Champlain), *lamarii* (supposedly Lake Erie), *atelaspis* (Saskatchewan R.), *rafinesquii* (Ohio R.), *rosarium* (supposedly Lake Erie), *platyrhinus* (supposedly upper Mississippi), *kirtlandi* (Lake Erie), *nertinianus* (Michigan), *cincinnati* (Ohio R.), and *buffalo* (Lake Erie).

Acipenser oxyrhynchus oxyrhynchus Mitchill 1814

Atlantic Sturgeon, Sea Sturgeon, Common Sturgeon[32]

Figures 3, 7, 10

Study Material. Over 3,000 specimens: 1, *ca.* 485 mm (19 in.) FL, New Britain, Florida, Jan. 6, 1900, CNHM 35376 (received through kindness of Loren P. Woods); 42, 200–2,490 mm TL, Hudson River, New York[33]; the remainder, 65–

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[32] According to the List of Common and Scientific Names (*1*: 7), *oxyrhynchus* should be called the Atlantic Sturgeon, but the name Sea Sturgeon is more generally used. In the Hudson River adults are known as the Big Sturgeon and small ones as Sharpnose Sturgeon or Pelican (*35*: 89). In Quebec, French-speaking fishermen commonly call the larger ones Esturgeon noir, or Esturgeon d'eau salée, while the young are known as Escargots or Ecailles (*83*: 43).

[33] For age and size of these specimens, see Greeley (*35*: 68, 139).

2,670 mm TL (60–2,500 mm FL), St. Lawrence River, Quebec, between Three Rivers and Rivière-aux-Outardes.[34]

Distinctive Characters. A. oxyrhynchus oxyrhynchus is readily distinguishable from both *brevirostris* (Shortnose Sturgeon) and *fulvescens* (Lake Sturgeon) by the arrangement of its preanal shields in a double row, by its pale unpigmented viscera, by a mouth less than 55% as wide as the space between the orbits, and by the presence of a soft area (fontanelle) on the top of its head. It differs from *A. oxyrhynchus desotoi* (p. 56) in that its bony shields are oval and longer than broad, and that the carina on its dorsal shields do not have a conspicuous hook. Among western Atlantic species, furthermore, *A. oxyrhynchus* has much the longest upper caudal lobe but a rather short lower one. In *A. oxyrhynchus* the average difference between TL and FL is 14% of FL, in *A. brevirostris* 11%, and in *A. fulvescens* 9%. For a discussion of the differences between *oxyrhynchus* and *sturio* of the eastern Atlantic, see p. 57.

Description.[35] SCUTES strongly developed in all longitudinal rows; in 1,814 Quebec specimens, 7–13 (av. 9.8) dorsal shields, and in 692 specimens, 24–35 (av. 28.7) lateral shields; shields behind dorsal fin in pairs; elongated fulcrum at base of lower caudal lobe decidedly longer than base of anal fin. DERMAL OSSIFICATIONS also well developed on skin between dorsal and lateral rows.

HEAD elongate. A membranous FONTANELLE between frontal and parietal plates in young individuals, and a sinus at all ages. SNOUT longer than postorbital distance in individuals up to 95 cm, but in older specimens shorter than postorbital distance. INTERORBITAL width rather narrow, varying; in 239 young specimens (6–49 cm), 22.4–28.4% (av. 26%) of hl, in 439 older specimens (50–231 cm), 25–35.6% (av. 29%). MOUTH narrow, its width (excluding lips) less than 55% of interorbital width.

GILL RAKERS among specimens from the St. Lawrence River, Quebec (studied by Vladykov and Beaulieu, *83*: 43–

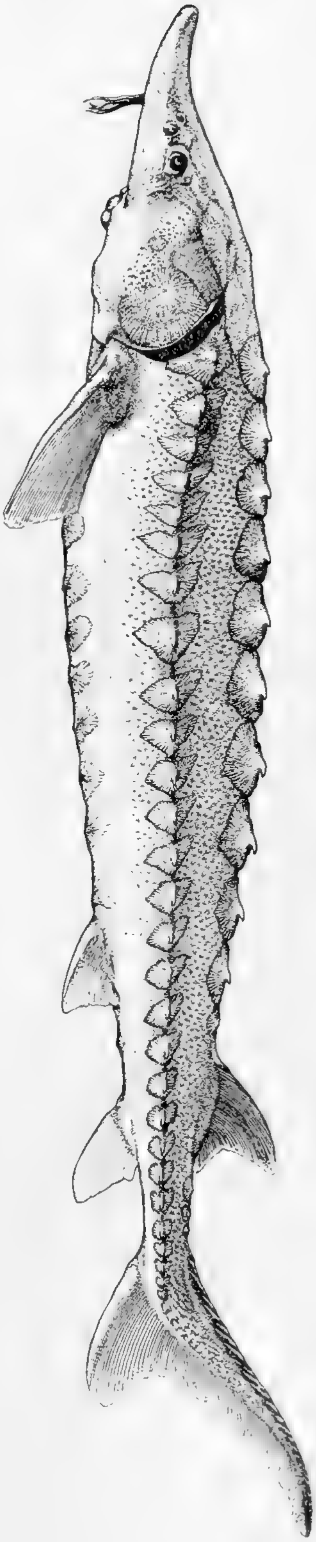

FIGURE 10. *Acipenser oxyrhynchus.* Lateral view of immature male, 581 mm long, from the St. Lawrence River near St. Vallier, Quebec, P. Q., Canada.

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[34] For origin, size, and method of fishing, see Vladykov and Beaulieu (*83*: 43–47).

[35] In part from Vladykov and Beaulieu (*83*: 43–47), but mainly from an unpublished manuscript by the same authors on the morphometric studies on Quebec Sturgeons.

47): total number on first branchial arch in 70 young below eight inches, 15–24 (av. 20.4); in 800 large individuals 8–91 inches, 16–27 (av. 21.5). This difference was due to the fact that in young specimens not all rakers were developed as yet on the upper limb. Therefore, for purposes of comparison of gill raker counts, only individuals above eight inches FL should be used. In 70 large specimens of *A. oxyrhynchus*, 9–14 (av. 11.5) rakers on lower limb and 7–13 (av. 9.8) on upper limb.

Caudal fin with average difference between TL and FL, 14% of FL; a notch at tip of upper caudal lobe in undamaged specimens.

Color. There is no significant difference in coloration between young specimens and adults.[36] Back and top of the head bluish-black, becoming progressively paler down the sides; entire lower surface whitish. Median carina and spine on dorsal shields (in dorsal row) whitish, contrasting strongly with darkly pigmented back, particularly with the jet-black skin covering the extremities of each shield, the dorsal row thus appearing as a series of whitish spots on a dark background. Upper half of lateral shields of same color as background, but central and lower part of these shields whitish, contrasting well with pigmented sides of fish, but not as sharply as in the case of the dorsal shields. Sides of head and body, including ventral row of shields, white. Iris pale golden. Anterior edge of pectorals, ventrals, and lower caudal lobe white, clearly defined against remaining dark grey part of these fins; anal fin entirely white; dorsal fin and upper caudal lobe dark grey or blue-black in the central portion, their broad posterior margins whitish. Intestinal tract and peritoneum nearly white, never darkly pigmented.

The coloration of the three species that occur on the Atlantic coast of America, when preserved in 4–5% formalin, is characteristic. In *A. oxyrhynchus*, the ventral surface and sides of the fish, even after a long period in perservative, are whitish or faintly pinkish. The skin of the two other species (*brevirostris* and *fulvescens*), however, soon acquires and permanently retains a green color that is particularly pronounced on the unpigmented parts of the body, such as the ventral surface, sides of the head, etc.

Size. Ryder found that females averaged about 8 feet TL, and sometimes reached 10 feet, whereas males ranged between 6–7 feet (*65*: 268). Weights and total lengths of two specimens taken in the Hudson River in 1936 and recorded by the New York State Conservation Department were as follows: unspent male 7 feet 4 inches, 176 pounds; a spent male 8 feet 4 inches, 199 pounds 15 ounces. For the Gulf of Maine, Bigelow and Schroeder (*13*: 82) stated that "about 12 feet is perhaps the greatest length to be expected today. But 18 feet, reported for New England many years ago, may not have been an exaggeration.... The heaviest Gulf of Maine Sturgeon reliably reported (to our knowledge), was one of 600 pounds, landed in Portland by the steam trawler *Fabia* from Georges Bank, December 21, 1932." A 14-foot female, weighing 811 pounds, was caught at Middle Island Maguerville, about 64 miles off the estuary of the St. John River, New Brunswick, in July 1924.[37]

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[36] For color illustrations of an adult Atlantic Sturgeon, see Vladykov (*82*: 7).

[37] Caught by Mr. John Neilson of Moncton. This information was kindly furnished by Mr. J. Raymond Tippett, Moncton, New Brunswick, a Sturgeon fisherman himself.

The St. Lawrence River specimens noted in the *Study Material*, 65–2,670 mm TL, weighed 0.0015–352 pounds (0.7–160 kg). Every year in the St. Lawrence River, Quebec, some Atlantic Sturgeons weighing between 200 and 300 pounds are taken by local fishermen. The two largest specimens at our disposal were taken in the brackish section of the St. Lawrence River at Ile-aux-Patins in a fascine weir.[38] A spent female[39] 8 feet 3 inches TL (7 ft. 7 in. FL) and weighing 203 pounds was taken July 5, 1946. Another female, almost ready to spawn, 8 feet 9 inches TL (8 ft. 2.5 in. FL) and weighing 352 pounds, was caught June 23, 1954.

Development and Growth. Eggs hatch in about one week at a temperature of 17.8° C (64° F). In one of the New York hatcheries where some fry were kept until they were about an inch long, the yolksac apparently lasted for about six days.[40] Unfortunately, the temperatures were not recorded. The newly hatched fry are about 11 mm (0.4 in.) long. The later growth of young *oxyrhynchus* has not been followed, but in Europe *A. sturio* reach a length of 4–5.5 inches in two months.

Little is known about the early stages of *oxyrhynchus* in nature, but it appears that yearlings grow rather rapidly, for in freshwater sections of the St. Lawrence River in Quebec we collected some young specimens ranging between 60–96 mm FL that we consider to be less than one year of age (see Table III). The smallest of these was tangled in one corner of a net with 8-inch stretched mesh, set in 60 feet of water. The others were taken in pêches, that is, weirs made from chicken wire or fascines. Berthier-en-Bas and St. Vallier are on the freshwater section of the St. Lawrence River. Rivière Ouelle is situated at the estuary of the river of the same name, which empties into the brackish section of the St. Lawrence. Additional information about the growth of young fish that we consider to be yearlings is given in Table IV.

Table III. Data for the Five Smallest Specimens from Fresh Water, St. Lawrence River.

Date	Place	TL (mm)	FL (mm)	Weight (g)
Aug. 8, 1945	Berthier-en-Bas, fresh water	65	60	0.7
Aug. 24, 1950	St. Vallier, fresh water	96	87	3.4
Sept. 26, 1944	Berthier-en-Bas, fresh water	103	89	4.3
Sept. 26, 1944	Berthier-en-Bas, fresh water	102	91	4.0
Sept. 22, 1944	Rivière Ouelle	110	96	4.2

Determinations of the apparent growth rates of *A. oxyrhynchus* tagged in the St. Lawrence are made difficult because of damage to their tails.[41] However, instances

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[38] Taken by Mr. Maurice Ouellet, Kamouraska, Quebec, a Sturgeon fisherman.

[39] The ovaries of this fish weighed 30 pounds.

[40] Eighth Annu. Rep. Comm. Fish., New York (1875), 1876: 12–14.

[41] In Quebec, fishermen who catch Sturgeon in a pêche built in salt water at St. André de Kamouraska carry them alive in a horse-drawn cart ("tombereau" locally) for about 30 minutes and dump them in a freshwater brook. But if one of them is a tagged fish, it is measured and weighed and returned to the sea by horse-cart after a sojourn of a few hours to one or two days in the brook. On a hot summer day, fish in the cart thrash so

Table IV. Sizes and Weights of Young Taken during 1944 in a Pêche at Ste. Famille Ile d'Orléans, near Quebec City.

Date	No. of Specimens	Fork Length (mm)		Weight (g)	
		Range	Average	Range	Average
August 31	25	130–144	122.8	6.8–17.4	10.7
Sept. 6–28	43	100–205	150.6	5.6–35.1	21.1
Oct. 11–26	40	125–201	168.5	9.9–47.7	28.0

of good growth are afforded in four specimens, 27.8–33.3 inches FL and weighing 4.8–8.8 pounds; the indicated annual increases were 6.3–14.4% in length, corresponding to 28.8–47.0% in weight (for further details, see Vladykov, *78*).

Sturgeon 11–34 inches long from the Hudson River were 2–8 winters old, as indicated by their otoliths (*35*: 68, tab. 10). Otolith studies, though based on few specimens, also indicate a greatly accelerated growth following the seaward migration of the immature Sturgeon, if estimated ages of 11 years for a 75-inch fish and of 12 years for two others of 88 and 100 inches are approximately correct. The maximum age, as indicated by the winter marks on the otoliths, is at least 18 winters in the case of a female 8 feet 8.5 inches and weighing about 225 pounds, taken from the Hudson River, Malden, N.Y., April 30, 1937.[42] Vladykov (*78*) has given a graph for the length-weight relationship for a series of 1,592 Atlantic Sturgeon from the lower St. Lawrence River, Quebec.

Spawning and Migrations. The Atlantic Sturgeon is an anadromous species, invariably spawning in fresh water but making its growth in salt water. Adults migrate from the sea to fresh water in advance of the spawning season. The spawning migration begins during February in the St. Marys River, Georgia, typically during April in Chesapeake Bay (*39*: 73–76), at the end of April and in May in the Hudson River, and during May and June in the Gulf of Maine (*13*: 82). The exact movements of mature Sturgeon in the St. Lawrence River have not been reported, but they probably begin to ascend the current in May (fishing during this month is prohibited) and continue to run upstream through June and sometimes in early July.

In the Delaware River in 1925, the spawning migration started on April 23; a few fish were taken during the last of April and the first part of May, with the largest catches between May 12 and 22 inclusive (*15*: 184). During the last week of May and the first ten days of June the catch was scarcely one fish per day, and on June 10 the Sturgeon fishing ceased. The gill nets (13-in. stretched mesh) were set in a narrow arm of the river between Pea-Patch Island and the New Jersey shore opposite Delaware City, where the channel is about 2.5 miles long, 6–7 fms. deep, and the current strong. The Sturgeon gathered for spawning in the upper part of the river near the eastern shore, where the bottom is hard clay. Spawning took place

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hard with their tails that the posterior ends of the caudal rays are broken, and only by slow regeneration do they regain their original length. Thus some fish, after repeated recaptures within the same season, seem to have grown somewhat shorter.

[42] Age determination by Greeley, not previously published.

at water temperatures ranging between 56°–64°F. Among 63 adult females, three were "pasters"; i. e. with the roe in the form of a slimy, grayish white paste consisting of squeezed eggs, white yolks, and ruptured membranes. Between the 10th and 22nd of May, seven females with running roe and three males with ripe milt were taken during the act of spawning.

Little is known about the breeding grounds or spawning behavior along the rest of the Atlantic coast. Apparently the sexually mature individuals ascend the St. Lawrence River through deep channels that are kept free of nets because of navigation, and it is probable that spawning takes place in pools below waterfalls of certain St. Lawrence tributaries, for instance the Batiscan River along the southern shore. Moreover, there are several rivers along the northern shore (Rivière-aux-Outardes, for instance) where *A. oxyrhynchus* spawn. It is probable that the spent fish return gradually to salt water.

The eggs when laid are light to dark brown. The outside membrane of ripe eggs readily imbibes water and becomes glutinous and sticky. Being demersal and adhesive, they become attached to weeds, stones, and so forth, and it is believed that the eggs are scattered over a wide area. There is no evidence of prenatal care, such as preparation of a nest area (*65*: 267–268; *39*: 73).

The diameter of ripe eggs is 2.5 or 2.6 mm; using this size as a basis for estimates, there would then be 168,000 eggs per gallon (U.S.) and 800,000–2,400,000 eggs per fish (*65*: 268; *15*: 186).

The largest ripe female examined by us, caught on June 23, 1954, in the St. Lawrence River at Ile-aux-Patins, Quebec, was 8 feet 9 inches TL (8 ft. 2.5 in. FL), weighed 352 pounds, and would have spawned in about a week; its ovary weighed 91 pounds and contained an estimated total of 3,755,745 eggs. No female *A. oxyrhynchus* have been reported as being ready to spawn before reaching at least 150 pounds and an age of about 10 years. The testes of the smallest ripe male encountered during this study, a fish of 69 inches TL (60 in. FL) and 70 pounds, taken in the St. Lawrence River at St. André de Kamouraska on June 2, 1949, weighed 3 pounds 13 ounces.

General Habits. Sturgeon are bottom fish and are seldom seen except when taken in nets or when jumping. It is of interest that this relatively sluggish species is capable of making powerful jumps (p. 30). In the opinion of fishermen, at least in Quebec, Sturgeon jump to rid themselves of attached lampreys.

Very little appears to be known about the behavior of the Sturgeon in salt water. It is astonishing how easily these fish can adapt to a sudden change from salt to fresh water, or vice versa. Some tagged specimens were forced to abruptly change habitats at least twice during the same season, apparently without harmful results, because they were recaptured again alive.

Thus far the actual movements of *A. oxyrhynchus* have been studied by means of tagging in Quebec only.[43] During five years, 1945–1949, a total of 1,948 was liberated

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[43] For details, including a photograph of a tagged Sturgeon, see Vladykov (*80*: 65–69; *76*: 47). Recently in Oregon several White Sturgeon (*A. transmontanus*) were marked with Peterson modified tags (*58*: 4–5).

at different localities in the St. Lawrence River, in both fresh and salt water. Up to December 31, 1952, a total of 47 fish was recovered. Several of them were recaptured as many as four and five times each and were subsequently reliberated. The majority of the recaptures showed definite mass movements toward fresh water in spring (May–June) and back to salt water in the fall (Sept.–Nov.). There were four recaptures of tagged Atlantic Sturgeon of unusual interest: three liberated at Kamouraska and one at Ile aux Coudres, Quebec. After periods varying between 307–705 days, three of them were recaptured not far from Halifax, Nova Scotia, having traveled a minimum of 900 miles. The fourth fish was retaken near the Strait of Canso. The weights of these fish when recaptured, according to the fishermen, ranged between 6–24 pounds.

Food and Feeding. The large Sturgeon feeds on mollusks and other bottom organisms. The fish roots in the sand or mud with its snout, like a pig (the barbels serving as organs of touch), as it noses up the worms and mollusks on which it feeds and which it sucks into its toothless mouth with considerable amounts of mud (*65*: 265). The Sturgeon also eats small fishes, particularly launce (*Ammodytes*) (*13*: 83). The mature Sturgeon, like the salmon, eats little or nothing while it travels up the river to spawn.

The digestive tracts of 26 young *oxyrhynchus* weighing 1–7 pounds, from the Hudson River, contained bottom mud along with plant and animal matter, including sludgeworms (*Limnodrilus*), chironomid larvae, isopods, amphipods, and small bivalve mollusks (*Pisidium*) (*72*: 141–144, tab. 5). The food of *A. oxyrhynchus* varies with the type of habitat, as in the St. Lawrence River, Quebec. In 27 half-grown Sturgeon taken in salt water, polychaete worms (*Nereis virens*) were found—265 on the average; the maximum number in a single stomach was 1,221. In addition, the Sturgeon fed on marine gastropods, shrimps (*Crago*), amphipods, and isopods, in that order. In fresh water, the bulk of the food consisted of aquatic insects, amphipods, and oligochaete worms; in 88% of 178 Sturgeon examined, larvae of the burrowing May fly (*Hexagenia*) were present.[44]

Abundance and Commercial Importance. The present Sturgeon fishery along the western Atlantic coast is very small. In 1956, according to statistics (in pounds), the following catches of *A. oxyrhynchus* were made: Quebec 57,000, New Brunswick 800, Nova Scotia 1,000, New England 9,000, Middle Atlantic, U.S., 15,000, Chesapeake Bay 23,000, South Atlantic, U.S., 129,000, and Gulf of Mexico 15,000; the total was 249,800 pounds.

Former catches were manyfold greater: the catch in North Carolina in 1880 was 437,000 pounds (*67*: 56), in Chesapeake Bay in 1890 over 900,000 pounds (*39*: 75), and in the Delaware River that year, 5,000,000 pounds (*22*: 372). Seven years later, however, the Delaware catch was only 2,428,616 pounds, about half as large as in 1880. By 1920 the catch had declined to 22,886 pounds in Chesapeake Bay, by 1950 to about 1,200 pounds in and at the mouth of Delaware Bay, and to 18,900 pounds in Chesapeake Bay (see also *Details of Occurrence*, p. 54).[45]

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[44] For further details on the food of *A. oxyrhynchus* in Quebec, see Vladykov (*77*: 53–55).

[45] For the abundance of Sturgeon in New England waters in Colonial days, see Bigelow and Schroeder (*13*: 83).

At the turn of the century, when Sturgeon were caught in very large numbers and when mature individuals were the mainstay, fishing was so intensive that very few fish were able to reach the upper waters to spawn. This was probably one of the reasons for their great decrease in subsequent years. Also, the building of dams in many important rivers (e. g. the Susquehanna, Maryland) deprived Atlantic Sturgeon of their favorite spawning areas, and pollution by wastes of all kinds from the factories and by municipal sewage from the towns and cities along the Atlantic shore aided in reducing still further the local populations.

Laws prohibiting the capture of Atlantic Sturgeon below a minimum size or during certain periods of fishing (*39*: 76) were helpful in protecting and maintaining the species. However, even at its lowest ebb the Atlantic Sturgeon in North America never was close to complete extermination, as some authors[46] were inclined to believe (in 1950). There are indications, along the Atlantic seaboard, that this Sturgeon is coming back. The small number of large fish taken during recent years is partially due to a reduction in the quantity of appropriate fishing gear. In New York, for instance, the 10-inch mesh nets, legally specified for taking this species, are not used in the Hudson River because fishermen do not consider it likely that enough fish could be taken to justify the expense of gear and license (*35*: 139).

In Quebec, the Atlantic Sturgeon is perhaps as plentiful now as it used to be in bygone years. For instance, at our request a fisherman of St. Vallier counted all the young *A. oxyrhynchus* that he liberated alive from his pêche; during the night of October 2, 1944, he freed 1,000 young 6–15 inches long.

The principal Quebec catches are made with weirs situated along the southern shore of the St. Lawrence River, from Rivière Ouelle to St. Nicolas. Some fish are also taken regularly with gill nets in the same area. Along the northern shore of the St. Lawrence, some large fish are caught in either weirs or in salmon nets, particularly in the estuaries of Rivière-aux-Outardes and Rivière Manicouagan, and occasionally large fish are taken at Sept Iles.

Relation to Man. The Atlantic Sturgeon is a good quality foodfish, but less so than the Lake Sturgeon (*fulvescens*), which reaches maturity at around 20 pounds and is more generally appreciated for "smoking" purposes. The flesh of the young or half-grown Atlantic Sturgeon, which make up the great bulk of the catch of this species, is coarse, contains many ligaments, and has only a small amount of fat; it is only the large adult that furnishes a tender and rich flesh. Some years ago the price paid to Quebec fishermen for a fish weighing 30 pounds when dressed was 35 cents a pound for an Atlantic Sturgeon as compared with 80 cents or even one dollar per pound for a Lake Sturgeon of the same dressed weight; the male fish brings a better price than the female. Moreover, the Atlantic Sturgeon carries heavier scutes, thus there is a greater loss of weight during preparation of the meat. Dressing for the United States market consists

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[46] Darlet and Prioux (*25*: 6), in their review of the Atlantic Sturgeon supply in different countries, said that there were no more left in America ("aux Ameriques il n'y en a plus").

of removing the head, collar bone (cleithrum), tail, all fins, and the viscera.[47] Thus the weight of prepared meat, which varies with size of fish, sex, stage of maturity, and condition of fatness, is only about 50% or even 40% of the entire Sturgeon. The roe from Atlantic Sturgeon is as good for making caviar as that from Lake Sturgeon, and being mature at a larger size, the Atlantic Sturgeon furnishes a larger quantity of eggs. In early Colonial days, around 1709 in North Carolina, the rough Atlantic Sturgeon scutes were considered "good nutmeg graters" (*67*: 56).

The value of the Atlantic Sturgeon for angling purposes is negligible. Nevertheless, occasional captures of large ones with hook-and-line stir public interest. It is worthwhile to mention the capture of a 6-foot Sturgeon, foul-hooked, by a skilled woman angler at Wasque Point, Martha's Vineyard, Nantucket Sound (*13*: 84).

General Range. The regular range of *A. oxyrhynchus* is limited to the Atlantic coast of North America and the Gulf of Mexico. The northern subspecies, *A. oxyrhynchus oxyrhynchus*, occurs from Hamilton Inlet on the Atlantic coast of Labrador (*7*: 290) and the Gulf of St. Lawrence to eastern Florida. In the Gulf of Mexico is found the southern subspecies *A. oxyrhynchus desotoi* (p. 56) (*34*: 408, 409, 411). Occasional captures of Atlantic Sturgeon have been reported for Bermuda[48] and even for French Guiana,[49] but these southern stragglers probably are of the subspecies *desotoi*. And a large Sturgeon, taken near the mouth of the Mississippi River, the photograph of which has been published (*34*), can be identified as *desotoi* by its broad and strongly developed scutes.

There are early reports of the presence of *A. sturio* (equals *A. oxyrhynchus*) in Hudson Bay, but from the descriptions it is evident that the specimens in question were *A. fulvescens* (see also *75*: 30 [42]).

Details of Occurrence. Hamilton Inlet on the Atlantic coast of Labrador is the most northerly point where *A. oxyrhynchus* has been reported (*7*: 290). Blanc Sablon, on the Quebec side of the Strait of Belle Isle, is the next most northerly point (some specimens from this locality are in our collections). Atlantic Sturgeon are found regularly throughout the Gulf of St. Lawrence and in the St. Lawrence River up to Three Rivers, and odd specimens are taken even in Lake St. Peter, near Sorel, Quebec (*23*: 19). They are found also in small numbers on the Newfoundland side of the Gulf of St. Lawrence, are well known in Nova Scotian waters, especially near estuaries (*85*: 58), and are caught regularly in the St. John River, New Brunswick, as well as at the head of the Bay of Fundy (*42*: [10] 58).

To the south, Atlantic Sturgeon are (or were) well known in the Penobscot, Kennebec, and Merrimack rivers; indeed, they entered nearly every stream of any size

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47. Ryder (*65*: 276) and Hildebrand and Schroeder (*39*: 75) have given details on the methods of preparing Sturgeon for the market.

48. According to Beebe and Tee-Van, two records of *A. oxyrhynchus* were mentioned in early Bermuda lists, one for 1876 and the other for 1887 (*9*: 32).

49. In 1867 Duméril (*27*: 161) described a new Sturgeon, as *A. cayennensis*, from French Guiana "de la riviere Oyapock dite la Cayenne." Bertin (*12*: 248–249), after examining the holotype (No. 3493, 740 mm, stuffed, in good condition) in the Paris Museum, considered it as a possible hybrid *A. sturio* × *A. brevirostris*, but Vladykov, who re-examined it in 1950, identified it as *A. oxyrhynchus*.

that empties into the Gulf of Maine. There are also definite records of Sturgeon taken off the open coast from the Bay of Fundy southward to Cape Cod (*13*: 83), and along the coasts of southern New York. Along the Middle and South Atlantic seaboard of the United States there are several rivers that formerly maintained important fisheries: the Hudson, Delaware, Susquehanna, Potomac, York, James, St. Marys (Georgia), and St. Johns (Florida).[50]

At Quebec, it seems that young *A. oxyrhynchus* pass their entire growth in the fresh and brackish water of the St. Lawrence River, for Sturgeons of all sizes are taken there—from a few inches long up to nine feet or longer (*78*: 53–56). Why it was that some half-grown tagged fish were recaptured several hundred miles from the place of release is not known (pp. 51, 52). But the small number of these stragglers does not appreciably change the impression that the majority of the Atlantic Sturgeon produced in the St. Lawrence River does not venture far from the estuary, for they are taken there in some numbers throughout the entire fishing season.

In the Hudson River, where gill nets used for shad and other species accidently capture Sturgeon 11–34 inches long and 2–8 winters old (age determinations based on otoliths), there is abundant evidence from both winter and summer catches that these immature Sturgeon inhabit the freshwater areas of the river throughout the year. But there is a wide gap in the Hudson River collections between these and the adults; since immature Sturgeon are frequently encountered in salt water in the general vicinity, it seems likely that all of them go to sea sooner or later to complete their growth. This rule seems to apply also to the rivers of the Gulf of Maine. However, some of the Delaware River Sturgeon seeking salt water may remain within the lower reaches of Delaware Bay while others go to sea, as proven by catch records of fish taken in the pound nets near Ocean City, Maryland. In Chesapeake Bay, fish of all sizes are taken in both the upper and lower parts of the Bay throughout that portion of the year when the pound nets are in operation (*39*: 73). But it is not known how many Sturgeon stray beyond the outer headlands, from Chesapeake Bay, the sounds of North Carolina, or the rivers farther southward.

Published reports of Sturgeon taken at sea are mostly for waters close to shore, but landings of 3,700 pounds in 1950 and 3,900 pounds in 1952 in New York and New Jersey by otter trawlers show that some wander out on the Continental Shelf; and to the east, some even stray to the offshore fishing banks. Thirty Sturgeon, for example, were landed in Boston and Portland from Brown Bank, Georges Bank, the South Channel, and Nantucket Shoals by otter trawlers during the years 1927–1934; and landings of 5,300 pounds in 1940 and 6,600 pounds in 1947 in New England ports from these offshore grounds correspond to about 50 and 70 fish, respectively, if an average weight no greater than 100 pounds is assumed.[51]

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[50] We believe that the specimens from South Carolina and Florida, referred to as *A. brevirostris* by Jordan and Evermann (*43*: 106) and by several subsequent authors, were *oxyrhynchus*.

[51] From data collected by the late Walter H. Rich, U.S. Bureau of Fisheries, and from notices in the daily press.

Synonyms and American References:[52]

Acipenser oxyrhynchus Mitchill, Trans. Lit. philos. Soc. N.Y., *1*, 1814: 462 (descr., New York); DeKay, Zool. N.Y., 4, 1842: 346 (descr.); Provancher, Nat. Canad., *8*, 1876: 226 (genl. acct.); Smith, N.C. geol. econ. Surv., 2, 1907: 57 (Albemarle Sd.); Hildebrand and Schroeder, Bull. U.S. Bur. Fish., *43*, 1928: 72 (Chesapeake Bay); Breder, Field Bk. Mar. Fish. Atl. Cst., 1929: 42 (genl. acct.); Jordan, Manual Vert. Anim. NE U.S., 1929: 32 (distr., key, brief descr.); Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish. (1928), 2, 1930: 34 (in checklist); Gowanloch, Fish. Fishing Louisiana, Bull. La. Conserv. Dept., 23, 1933: 411 (mouth of Mississippi R.); Schrenkeisen, Field Bk. Freshw. Fish. N. Amer., 1938: 12 (genl. acct.); Vladykov and Beaulieu, Nat. Canad., *73*, 1946: 43 (detail. acct. of shields and gill rakers, size, Quebec); Vladykov and Beaulieu, Nat. Canad., *78*, 1951: 129 (detail. acct. of gill rakers for three w. Atlantic species); Rostlund, Univ. Calif. Publ. Geogr., 9, 1952: 248 (import. to native Indians).

Acipenser sturio Linnaeus,[53] Syst. Nat., ed. 10, 1758, 237 (descr., European seas); Ryder, Bull. U.S. Fish Comm. (1888), *8*, 1890: 232 (descr., Atlant. cst.); Jordan and Evermann, Bull. U.S. nat. Mus., 47 (1), 1896: 105 (descr., Atlant. cst.); Kendall, Occ. Pap. Boston Soc. nat. Hist., 7 (8), 1908: 16 (New England); Kendall, Proc. Portland Soc. nat. Hist., *3* (1), 1914: 13 (Maine); Huntsman, Contr. Canad. Biol. (1921), *3*, 1922: 10 (58) (St. John R., head of Bay of Fundy); Bigelow and Welsh, Bull. U.S. Bur. Fish., 40 (1), 1925: 74 (descr., habits, Gulf of Maine); Borodin, Trans. Amer. Fish. Soc., 55, 1925: 184 (biol. observ.); Nichols and Breder, Zoologica, N.Y., *9*, 1927: 30 (size, distr. New England, New York); Truitt, Bean, and Fowler, Bull. Md. Conserv. Dep., 3, 1929: 33 (Chesapeake Bay); Beebe and Tee-Van, Field Bk. Shore Fish. Bermuda, 1933: 32 (2 recs. for Bermuda cited); Vladykov and McKenzie, Proc. N.S. Inst. Sci., *19* (1), 1935: 53 (genl. acct.); Jordan and Evermann, Amer. Food Game Fish., 1937: 8 (genl. acct., key); Bigelow and Schroeder, Fish. Bull. (74) U.S. Fish Wildl. Serv., 53, 1953: 81 (descr., habits, Gulf of Maine).

Acipenser sturio oxyrhynchus, Smith, Bull. U.S. Fish Comm. (1891), 1893: 190 (N. Carolina rivers: Pasquotank, Edenton, and Roanoke); Halkett, Check List Fish. Canad., 1913: 44 (distr.); Greeley, N.Y. Biol. Surv. Lower Hudson Watershed (1936), 11, 1937: 89 (age determ., size ranges, Hudson R.); Bailey, Biol. Surv. Merrimack Watershed, New Hampshire Fish Game Dept., 1938: 155 (former abund. Merrimack R.).

Acipenser cayennensis, Duméril, Nouv. Arch. Mus. Hist. nat. Paris, *3*, 1867: 161 (descr., River Oyapock known as Cayenne, French Guiana; see ftn. 49).

To the above Synonyms should be added several nominal specific names, which were given by Duméril (*27*: 161–177; *28*: 116–228) to specimens of *A. oxyrhynchus* according to locality only: *mitchilli* (New York), *kennicotti* (James R.), *girardi* (Maryland), *macrohinus* (New York), *milberti* (New York), *bairdi* (Maryland), *storeri* (Boston), *holbrooki* (Charleston), and *lecontei* (New York).

Acipenser oxyrhynchus desotoi Vladykov 1955

Gulf of Mexico Sturgeon, Common Sturgeon

Figure 3

Study Material. Two specimens, 50 and 60 cm FL, obtained by T. Dawson between Twin and Rabbit islands at the mouth of Singing River, off Gautier, Mississippi, November 30, 1953, CNHM 59803, 59804);[54] 3 specimens (seen by V.D.V.), from western coast of Florida (two from Cedar Keys, the other from Suwannee River), UF collections.

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[52] Among the references, we have omitted some early authors whose incomplete or erroneous descriptions of the species are of little scientific value.

[53] European authors in general, such as d'Ancona (*2*), Berg (*11*: 94), and others, consider the American form identical to the European *A. sturio*.

[54] Kindness of Loren P. Woods. These specimens served as the basis for the original description (*81*: 2, pls. 1, 3, 5, 7).

Distinctive Characters and Description. The subspecies *desotoi* is distinguishable from typical *oxyrhynchus* of comparable size by the following differences, the most striking and characteristic difference being the length of the spleen. Head, pectoral, and spleen given in per cent of fork length. For other details, see Vladykov (*81*).

Character	*desotoi*	*oxyrhynchus*
Scutes – dorsal row ...	squarish, with length much shorter than width; carina (keel) typically with two strong hooks	oval, with length greater than width;* carina (keel) low, without a pronounced hook
Head	30.9–33.6%	26.5–27.6%
Pectoral fins	15.5–16.3%	11.5–15.1%
Spleen length	16–19%	3–9%

* Specimens from eastern Florida and Quebec. † Two specimens.

Habits. The subspecies *desotoi* is anadromous, as is the northern subspecies *oxyrhynchus*. Further than this there is no detailed information on its habits, except that Louisiana fishermen occasionally capture large Sturgeon around the mouth of the Mississippi River and in the Sound, where they have been reported as "Common Sturgeon" (*34*: 411–412). Adults probably visit several rivers on the northern and eastern shore of the Gulf of Mexico for spawning purposes.

Range. Apparently its occurrence is limited to the Gulf of Mexico, the northern coast of South America, and Bermuda (p. 54).

Synonyms and References:

Acipenser oxyrhynchus de sotoi Vladykov, J. Fish. Res. Bd. Canada, *12* (5), 1955: 2 (orig. descr.).
Acipenser oxyrhynchus Gowanloch, Bull. La. Conserv. Dep., 1933: 411 (mouth of Mississippi R.).
Acipenser sturio Rivas, Bull. U.S. Fish Wildl. Serv., 55 (89), 1954: 504 (n. and e. shore, Gulf of Mexico).
Acipenser (*oxyrhynchus*) *de sotoi* Springer and Bullis, Spec. Sci. Rep., U.S. Bur. Comm. Fish., *196*, 1956: 46 (Mississippi Sd.).

Relationship of *A. oxyrhynchus* to *A. sturio*

Some authors (see Synonyms and References, p. 56), following Ryder (*65*: 234–238), have considered the Atlantic Sturgeon of America to be the same species as the Common Sturgeon of Europe, *A. sturio* Linnaeus; the two species resemble each other very closely in certain features, as is shown in Table v.

Table V. Comparative Counts of *A. sturio* and *A. oxyrhynchus*.

Species	*A. sturio*	*A. oxyrhynchus*
Authority	Berg (*11* : 93–95)	Vladykov and Beaulieu (*83* : 44–57)
Dorsal shields ...	9–13	7–13
Lateral shields ..	24–35	24–35
Gill rakers	18–25	17–27

D'Ancona, in a summary of the characters of *A. sturio*, presumably from the Mediterranean Sea, has quoted somewhat higher figures than those given in Table v for the shields: 10–14 in the dorsal row (excluding the nuchale) and 25–36 in the lateral row (*2*). Antoniu, for *A. sturio* from the Black Sea, mentioned the presence of pairs of postdorsal shields and of a frontal sinus in the cartilaginous skull; both of these characters are found in *A. oxyrhynchus* (*4*: 109–116).

Of two specimens obtained by Cope nearly a century ago in Adige (Verona), Italy, and labeled *A. sturio*, one is probably *A. güldenstädti* (ANSP 646) and the other is definitely an *A. sturio* (ANSP 645), 15 inches long (380 mm) FL. The latter has a fontanelle, 10 shields (including nuchale) in the dorsal row, and 30 shields (including supracleithrum) in the lateral rows. On the first branchial arch we counted 20 gill rakers. The body proportions are also very similar to those of *A. oxyrhynchus* of corresponding size, and its color, or what remains of it, corresponds very closely to that of American specimens.

In a drawing of *A. sturio* by d'Ancona, the coloration is also very similar to that of the western Atlantic Sturgeon (*2*: fig. 1); on the other hand, the mouth of d'Ancona's *A. sturio* is larger than that of *A. oxyrhynchus* (*2*: fig. 2), the shape of its lower lip is very different, and there are other differences as well. According to Berg, the adult of *A. sturio* has several (up to 10–12) dense, oblique series of rhombic plates (dermal ossifications) between the dorsal and lateral rows of shields (*11*: 97); in western Atlantic specimens these ossifications are much less developed and are rather irregular in shape. Moreover, Classen (*20*: 88–102) has mentioned several ripe females of *sturio* from the Gulf of Cadiz, Spain, 63 inches TL (145 cm FL) and weighing as little as 62 pounds (28 kg); *oxyrhynchus* apparently attains sexual maturity at a larger size than *sturio*, the males of *oxyrhynchus* being approximately six feet TL and 70 pounds in weight, the females not less than 150 pounds (p. 51).

In Europe, probably because of a general scarcity of *A. sturio* (*25*: 5–13), little work has been done to elucidate the problem of local races. Nevertheless, there are observations by Marti that *A. sturio* from the Black Sea are similar to those from the Mediterranean region but differ from those of the Baltic (*51*: 435–442, Russ.); the Black Sea specimens have on the average higher numbers of dorsal and lateral scutes and dorsal rays. Magnin, by studying cross sections of the pectoral ray, found that the rate of growth of the European Sturgeon varies according to geographical region (*49*: 152–159). The growth observed was fastest in Italy (Tiber and Po rivers), intermediate in Spain (Guadalquivir River), and slowest in France (Gironde River).

In conclusion, until an adequate comparison of anatomical and meristic characters of these two species is made, it is preferable to retain separate specific rank for *A. sturio* and *oxyrhynchus*.

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Order Lepisostei

ROYAL D. SUTTKUS

Tulane University

Acknowledgments. My thanks are due the following persons for the loan of specimens or for help in making specimens available for study: Leonard P. Schultz, Ernest A. Lachner, William Ralph Taylor, Robert Kanazawa, and James Tyler of the United States National Museum; James E. Böhlke of the Academy of Natural Sciences at Philadelphia; Henry B. Bigelow and Mrs. Myvanwy Dick of the Museum of Comparative Zoology at Harvard University; Reeve M. Bailey, Robert R. Miller, and Carter Gilbert of the Museum of Zoology, University of Michigan; Clark Hubbs of the University of Texas; Charles M. Breder and Vladimir Walters of the American Museum of Natural History; Luis Rivas of the University of Miami; William M. Clay and Louis A. Krumholz of the University of Louisville; Loren P. Woods, Robert F. Inger, and Pearl Sonoda of the Chicago Natural History Museum, and Shelby D. Gerking of the University of Indiana. Thanks are also due Edward C. Raney and Henry B. Bigelow for reading the manuscript and for making helpful suggestions for improvement; to Bill Komodore for delineation of Figs. 11, 14, 15, 16; to Rudolph J. Miller for Figs. 12, 13, 18; and to Miss Patricia Hale for Fig. 17. Preparation of the illustrations and examination of many specimens at various museums and institutions were made possible by financial aid from the Sears Foundation through a grant-in-aid from the National Science Foundation (N. S. F. No. G 7123), and from a National Science Foundation grant to the author (N. S. F. No. G 9026).

Scope of Study. This account gives detailed descriptions of the Order Lepisostei and family Lepisosteidae, of the genus *Lepisosteus*, and of four species—*oculatus*, *osseus*, *platyrhincus*, and *spatula*. The "Key to Species of the Western North Atlantic" encompasses subgenera as well as species and gives the alternate characters that are readily recognizable. The *Study Material* is listed for each species; in most cases this includes specimens from the many institutions listed. For easy and quick identification, the *Distinctive Characters*, as in the Key, compare the easily recognizable features of one species with the others. Many specimens were examined in preparing the taxonomic accounts, and the methods of measuring and counting the characters are detailed on p. 68.

The *Descriptions* are broken down into three major categories: (1) Proportional measurements in per cent of length, (2) Proportional measurements in per cent of head length, and (3) Meristic counts. Thus measurements for most of the head characters (snout, lower jaw, etc.) are given in per cent of head length as well as in per cent of length of fish. Following submission of this account for publication, a small specimen of *spatula*, 49.5 mm (57.3 mm TL), came to hand; the measurements for this individual have been incorporated in the *Description* with figures enclosed in brackets.

What is known of the life history of Gars in general and of the species in particular has been culled from the literature and gained by direct observation and personal communication with field workers. The Synonyms and References at the end of each species account include references to only those taken in salt water; these are not numerous, because Gars for the most part frequent fresh water, and less commonly brackish or salt water.

Characters. Lepisostei are slender ray-finned fishes with well-ossified skeletons, as in the teleosteans, but with ganoid scales (see below), an archaic character shared by the polypteroids alone among living fishes. The arterial cone of the heart has eight transverse rows of 4–8 valves each,[1] a number of rows greater than in any other living ray-finned fish; this character also puts the Gars apart from the polypteroids. The caudal fin has no prolonged fleshy axis, but all of the hypural bones that bear the fin rays are supported by the upturned end of the vertebral column (caudal "abbreviate heterocercal," Fig. 11), and the rear boundary of the fleshy caudal peduncle slopes obliquely dorsoposteriorly, the latter character shared by *Amia* alone among living fishes.

The vertebrae are completely ossified and opisthocoelus, i.e. posterior face concave and anterior face convex, a conformation unique among living fishes though paralleled in some tailed Amphibia and in the thoracic region of penguins, gulls, and plovers among birds. In the adult the pleural ribs extend from the vertebrae to the skin (Balfour and Parker, *7*: 387, pl. 28 fig. 72; Emelianov, *20*: 176–180, figs. 8–10).

The elongated snout, with nasal openings and olfactory sacs at its end, is the result of a lengthening of the ethmoid region, and olfactory nerves course through long canals in the ethmoid cartilage (Regan, *58*: 447, fig. 3). The preorbital (lacrimal or maxillary of some authors) is subdivided into a row of 6–8 bones that bear small, medium, and large teeth (Holmgren and Stensiö, *10*: 474, fig. 363; Hammarberg, *29*: figs. 41, 43; Berg, *8*: 211, 414); the larger teeth are radially grooved at the base. The infraorbital sensory canal is a prominent surface feature of the preorbitals in the early

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[1] For an excellent illustration and for a table giving the numbers of valves in various other fishes, see Bertin (*25*: 1402, fig. 1005B, 1404).

developmental stages (Collinge, *15*: 265, pl. 4, fig. 2; *14*: 511, 512; Landacre and Conger, *42*: 593, 594; Hammarberg, *29*: 309, figs. 39–43). A small sliver-shaped bone is present, at least in the young, at the angle of the mouth; this bone is continuous with the preorbitals in its dentition but is not traversed by the infraorbital canal; thus it is considered to represent the maxillary. The vomer is paired. There is no opisthotic (Mayhew, *47*: 327), supraoccipital, gular plate, or myodone in the Garfishes. The lower jaw, a complex of six dermal bones—dentary, articular, angular, preangular, prearticular, and coronoid (Arambourg and Bertin, *25*: 2185, fig. 1546)—articulates in front of the eye. The sacculus and lagena form a common sac, the largest otolith being in the former. Three pairs of branchiostegals support the gill membrane. The opercular gills are especially well developed in the Garfishes, an upper horizontal "arm" and a bisegmented lower one being noticeable (Wright, *76*: 483).

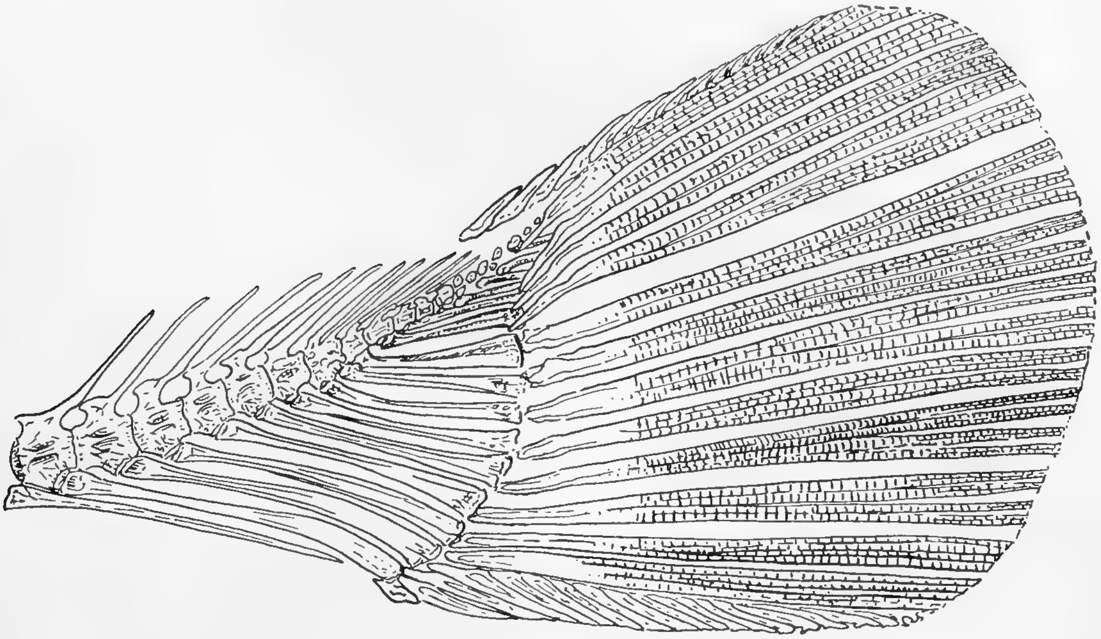

FIGURE 11. *Lepisosteus spatula.* Caudal fin skeleton; original drawing (natural size) of a specimen from Lake Pontchartrain, Louisiana.

The dorsal fin is situated posteriorly, above the anal fin. The fins are without spines, and the rays of the dorsal and anal fins are equal in number to the supporting radialia. There is no adipose fin.

The body of the adult is completely encased in an armor of rhombic ganoid scales, which may be denticulated and sculptured on the exposed surface.[2] Most of the scales

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[2] The degree of sculpturing is of some taxonomic value when specimens of comparable size are used.

are hinged by a peg- and groove-type articulation. Although the bony scales form nearly an impenetrable covering, the articulations, the fibrous connections, and the arrangement in diagonal rows allow some flexibility of the body. The lepisosteid ganoid scale is composed of two layers, ganoine above and isopedine below, both of which are irregularly penetrated by vascular canals.[3] In addition, both layers, especially the latter, are perforated by a system of small tubes; these tubules penetrate the scale from all sides and are dendritic at their inner terminations. A similar layer of ganoine is present on the dermal bones about the head. Both margins of the caudal fin as well as the leading margins of the other median and paired fins are fortified with a biserial row of fulcra. The cheeks are covered by numerous irregular plates.

The swim bladder,[4] cellular and highly vascularized, is connected to the pharynx by the enlarged pneumatic duct (Wiedersheim, *70*: 1–16, pls. 1–3). The gonads are staggered (Müller, *49*: pl. 6, fig. 2), i.e. the right one is mostly anterior to the pelvic fins and the left one mostly posterior to them. The ovaries are closed, and the right and left oviducts join the respective urinary ducts. A short distance posterior to their junction, a common chamber is formed by the union of right and left parts; thus the products from both systems exit from the body through a single urinogenital sinus. No vestigial Müllerian ducts exist in the male (Pfeiffer, *52*: 465). The conus arteriosus is a contractile vessel with several rows of valves (*49*: pl. 5, fig. 2). Remnants of the spiral valve occur in the posterior part of the gut. There is no luminescent organ.

Taxonomic Rank. In 1844, Johannes Müller combined his family Lepidosteini (evidently to include the amiids) with his family Polypterini to constitute his Order Holostei (*49*: 201–204), and they have been similarly ranked as one of the constituent divisions of a more widely inclusive Order by some subsequent authors. Thus they were associated: with the Amiidae and Polypteridae by Günther (*28*: 328) and with the Amiidae (among living fishes) by Bridge (*12*: 495, 502) as the Order Holostei; with the Amiidae (among living fishes) by Arambourg and Bertin (*25*: 2181–2194) in 1958 as the Order Amiiformes.

They have been regarded, however, as the sole living representatives of a separate Order by the majority of recent authors: Ginglymodi by Cope (*16*: 452, 453), Rhomboganoidea by Jordan and Evermann (*37*: 108), Lepidosteoidei by Goodrich (*23*: 340), Holostei by Jordan (*36*: 115), Ginglymodi by Regan (*59*: 313), Holostei by Jordan *et al.* (*38*: 36), Lepidosteiformes by Berg (*8*: 211, 414), Semionotoidea by Romer (*62*: 580), Lepisosteida by Matsubara (*46*: 170), and Ginglymodi by Norman (*51*: 61). Here also they are regarded as representing a separate Order.

Name of the Order. The choice here lies between Ginglymodi and some derivative

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3. For accounts of the scales, see especially L. Agassiz (*2*: 74, 75, 77, tab. G, figs. 8–10), Williamson (*73*: 435–447, 470, pl. 40, figs. 1, 2; *74*: 651, 658, 687, 699), Reissner (*61*: 254–268, pl. 5, figs. 1–6), Nickerson (*50*: 115–139, 4 pls., 31 figs.), Scupin (*63*: 166, 167, pl. 10, fig. 1), Goodrich (*23*, 758, 759, fig. 199; *43*: 218, 219, fig. 192), Kerr (*40*: 63–66, figs. 3, 4).
4. Apparently the swim bladder functions as a breathing organ (Potter, *54*: 63) in addition to the gills. When removed from water, the Garfishes regularly breathe air into and out of the swim bladder.

of *Lepisosteus*.[5] Lepisostei is chosen here because of the connotation carried by this name.

Relationships. It is customary in general works on living fishes to place the Lepisostei next to the amiids, with which they agree: in the abbreviate-heterocercal nature of their caudal fin skeleton (made evident externally by the dorsoposterior slope of the rear boundary of the fleshy caudal peduncle); in their flattened, overlapping pelvic bones; in their chambered swim bladder that serves as an accessory respiratory organ; and in the presence of a rudimentary spiral valve in their intestine. However, they differ widely from the amiids in many respects. The body scales, for example, which are thick and interlocking but not overlapping in the lepisosteids, are thin and widely overlapping in the amiids, but the fulcral scales that arm the margins of the fins in the former are rudimentary in the latter. The long snout, the segmented "maxillary" bones, a lower jaw articulating anterior to the eye, and the three rod-like branchiostegals of the lepisosteids are replaced in the amiids by a short snout, unsegmented maxillaries, a lower jaw articulating posterior to the eyes, and by 10–12 broad plate-like branchiostegals; and the free margin of the branchiostegal membrane, which crosses the isthmus in a continuous arc of long radius in the lepisosteids, is deeply incised there in *Amia*, one side overlapping the other. In lepisosteids the preopercular bone does not extend as far forward as that in the amiids, the cheek region is covered by irregular plates in lepisosteids but not in amiids, there is no bony gular plate in the chin region between the branches of the lower jaw as in *Amia*, and the dorsal is much shorter in lepisosteids than in amiids. The following internal differences deserve mention: the vertebral centra, which are concave posteriorly but convex anteriorly in the lepisosteids, are concave anteriorly as well as posteriorly in *Amia*; the vertebral column in the tail region is diplospondylous; and the arterial cone of the heart, which has eight transverse rows of valves in the lepisosteids, has only two rows in the amiids.

Among fossil groups, lepisosteids are usually associated with the Semionotidae, some of which are known from as far back as the Jurassic.

Spawning and Development. Spawning takes place entirely in fresh water during a rather brief period beginning about mid-May and lasting until mid-June, in the latitude of New York (*1* [1879]: 65, 67). When Garfish move into shallows to spawn, each female is accompanied by one to four males and there is a great amount of thrashing during the breeding activities. Fertilization is external. The large numbers of individuals that concentrate in the shoal areas suitable for spawning disperse rather suddenly to other areas afterwards.

The eggs are adhesive and adhere to the substratum. No parental care is given to the eggs or young. On the ventral surface at the end of the snout the larvae have peculiar adhesive suckers that are used for attachment to objects on or above the bottom. The larvae are relatively inactive until the yolk mass is absorbed, but then they become very active predators.

A characteristic caudal filament that develops at the termination of the upturned

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[5] Many authors have preferred the spelling *Lepidosteus*.

vertebral column is generally kept in constant rapid motion, as are the fringed, fleshy pectoral fins. The caudal filament atrophies at different times in the various species. Fin rays develop much sooner in the pelvic than in the pectoral fins; hence the pelvics are actually well-defined fins while the pectorals are still delicately fringed, fleshy stumps.[6]

The lateral-line sensory system appears early in life, before any scales are formed. The lateral-line scales develop in a posterior-to-anterior direction, as do the other body scales. Usually by the time the anterior lateral-line scales are developed, lateral scales have formed on the caudal peduncle; on the lateral areas, scales develop ahead of those on the mid-dorsal and midventral regions. Moreover, those of the mid-dorsal area develop ahead of the ones on the midventral section, so the breast is the last to become scaled. The most posterior fringe of scales that is superimposed on the bases of the caudal rays does not appear until after the scales on the whole anterior part of the lateral line and on the body up to the region of the pelvic fins have developed. This terminal fringe of scales usually contributes one to three scales to the lateral-line count. Fulcral scales appear after the fins are otherwise well developed. The caudal fin is somewhat of an exception in that one to three rays form in the superior region following the caudal filament. The last of these upper rays may not be fully developed until the early juvenile stage is reached.

Differential growth of structures is pronounced in the Garfishes; although it becomes less marked with age, it does not terminate with maturity. The diameter of the orbit continually changes in proportion to other parts of the body—particularly to snout length, interorbital distance, and postorbital distance. Primarily because workers have failed to consider such changes properly, the systematics of these fishes has been in a chaotic condition for many years.[7] Males not only mature at a smaller size but grow to a smaller size than females, and sexual dimorphism exists in some structures, e. g. length of snout in the Spotted Gars.

Habits and Food. The Garfishes are sluggish creatures most of the time. During the summer they frequent the surface waters and appear more or less motionless for minutes at a time. In streams below barriers, such as dams or falls, frequently large numbers of Longnose Gar can be seen near the surface on bright sunny days. In this quiet state, the caudal fin is usually undulated slowly while they are at rest or moving slowly forward or backward. But they are capable of swimming rapidly for short distances by rapid undulations of the body. When disturbed, they immediately "sound." In the winter they are found in the deeper waters; the shrimp trawlers frequently catch Alligator and Longnose Gars in their trawl nets from the deep holes of estuaries and bayous in the salt marshes of Louisiana.

During the summer months the periodic surfacing of Garfishes is a common sight, and there is some debate about their successfulness in gulping air during these surface

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[6] A young specimen of *L. osseus* without scales and with the peculiar fleshy pectoral fins induced Rafinesque to describe the form as a new genus, *Sarchirus* (*56*: 418).

[7] L. Agassiz (*4*: 360) recognized the remarkable changes that take place in the ontogeny of Garfishes, and possibly this was the reason he never followed through with the description of 22 supposed new species, most of which were discovered during a journey in the eastern United States (L. Agassiz, *3*: 136).

excursions. However, considering their anatomy, results of experimentation, observations on individuals in their natural habitat, and the regular breathing actions of individuals removed from water, there is little doubt that the swim bladder and associated structures leading to it serve as a supplementary respiratory mechanism.

Gars feed primarily on other fishes, most of which are forage species (Bonham, *11*: 358–360). There are very few published accounts of cannibalism, but Gars with portions of their tails missing are frequently captured, indicating that they have been snapped at by other individuals; this has been observed in streams and canals of peninsular Florida, where the Florida Gar (*L. platyrhincus*) is very abundant. In estuarine waters of Louisiana, Alligator Gar frequently consume the blue crab, *Callinectes sapidus*, as well as garbage (Weed, *69*: 9, 10; Gudger, *26*: 120, 121) where refuse is regularly thrown into the water.

Relation to Man. Although Alligator Gar, *L. spatula*, attain a large size, no authenticated records of an attack on man are available (*69*: 9, 10; *26*: 120, 121). The usual response by Gar when disturbed by a bather or fisherman is a dash for deeper water. While Gars are considered to be a nuisance and are detrimental to game fishes, sport fishing for Alligator Gars has become popular in recent years in Louisiana, Arkansas, Mississippi, and other states in the Mississippi Valley.

Alligator Gar are sold in the French Market in New Orleans at the present time, and small numbers are consumed elsewhere in the United States. Dr. Robert R. Miller contributes the information that *L. tropicus* is of considerable importance as a food item on the Pacific side of southern México and Guatemala. And personal conversation with Nicaraguans reveals that *L. tropicus* is used for food in the Lago de Nicaragua area and lower Rio San Juan. The North and Central American Indians used the ganoid scales and bones for arrow points, ritual instruments, and ornaments. The late Mr. Percy Viosca, Jr., of New Orleans, at one time made an array of ornaments and jewelry from their scales.

Habitat and Range. Their range extends from Quebec in the northeast, west to the upper Mississippi Valley and Great Lakes region, and south to Costa Rica in Central America and southwestern Cuba, including the Isle of Pines. Although they are primarily inhabitants of freshwater streams and lakes, several species enter brackish and marine waters. *L. spatula* is a common inhabitant of brackish water in Louisiana, and several specimens have been captured from the Gulf of Mexico, on the Gulf side of Breton Island and Grand Isle, Louisiana, and at Destin, Florida. The Longnose Gar, *L. osseus*, is somewhat less tolerant of marine waters and is seldom captured outside of the brackish estuarine areas. The Spotted Gar, *L. oculatus*, is a common summer inhabitant of the fresher parts of the estuaries in Louisiana.

One species, *L. sinensis* (Bleeker, *9*: 148, 154), supposedly occurs in China (Wagner, *68*: 738–741). Most standard references fail to mention an extant Asiatic form.

Geological History. Garfishes are known from the Upper Cretaceous to Lower Miocene time; in the Eocene of India and in North America from the Middle Eocene to Recent period (Berg, *8*: 214, 415; Romer, *62*: 548).

Measurements and Counts.

LENGTH: measurement from tip of snout to posterior margin of last lateral-line scale at base of caudal fin. Unless stated otherwise, LENGTH is used.

STANDARD LENGTH (SL): nearly equivalent to length.

TOTAL LENGTH (TL): measurement from tip of snout to longest rays of caudal fin.

CAUDAL BASE: defined as a point at end of lateral-line row of scales, located approximately at center of caudal fin in a vertical direction; this point is used in: LENGTH; CAUDAL PEDUNCLE: length; and CAUDAL FIN: length.

CAUDAL PEDUNCLE: length—measurement from caudal base to posterior tip.

HEAD: mid-dorsal length—measurement from tip of snout to occiput.

HEAD: length—distance from tip of snout to posterior margin of bony opercle.

HEAD: depth—measurement at occiput.

HEAD: width—measurement at occiput.

SNOUT: length—measurement from tip of snout to anterior rim of bony orbit.

SNOUT: least width—measurement immediately behind perforations usually formed by the large anterior teeth of lower jaw; these tooth perforations are immediately posterior to the nares and should not be confused.

SNOUT: width—measurement at posteriormost teeth.

LOWER JAWS: width—measurement at articulation with skull.

LOWER JAWS: least width—measurement immediately posterior to symphysis of dentaries.

POSTORBITAL DISTANCE TO: bony margin—measurement from posterior bony rim of orbit to posterior margin of bony opercle.

POSTORBITAL DISTANCE TO: fleshy margin—distance from posterior rim of orbit to posterior margin of fleshy opercular valve.

POSTSNOUT: distance—measurement from anterior rim of orbit to free margin of bony opercle.

FRONTAL BONES: least width—measurement at central constriction.

SCALES: lateral line—includes the small scales at base of caudal fin, whether pores are discernible or not, so long as they are within the lateral-line scale row.

SCALES: predorsal—includes all median dorsal scales anterior to the paired structures (fulcra) on the anterior margin and at the origin of dorsal fin.

SCALES: transverse rows—includes all those in an anteriorly slanted diagonal row from the single median anal plate to the mid-dorsal scale, including the anal plate and mid-dorsal scale.

GILL RAKERS: total—number on left outer arch.

Family LEPISOSTEIDAE

Garfishes

Characters. Those of the Order.

Genera and Subgenera. All modern Garfishes fall within a single genus, *Lepisosteus.* Rafinesque (55: 69, 71, 76) placed the Gar or Gar-like fishes in three genera: *Sarchirus*, *Lepisosteus*, and *Litholepis*, the first being based on a young individual of *L. osseus* and the last on inaccurate information communicated personally by J. J. Audubon. The sketch and description (long dorsal and anal, bilobed tail) of the fish in Rafinesque's field notes and the description in "Ichthyologia Ohiensis" clearly indicate a fictitious fish that should not be recognized with a valid name. Rafinesque subdivided the genus *Lepisosteus* into two subgenera, *Cylindrosteus* and *Atractosteus*.

Fowler recognized two genera, *Lepisosteus* and *Cylindrosteus* (*22*: 604, 605). Holly divided the genus *Lepisosteus* into three subgenera: *Litholepis*, *Lepisosteus*, and *Cylindrosteus* (*65*: 49). More recently, Moore (*67*: 54) and Eddy (*19*: 39–41) have recognized a single genus, *Lepisosteus*. When Fowler split the Gars into two genera on the basis of presence or absence of enlarged teeth on the palatine (*22*: 604), he did not find a second row of enlarged teeth on the palatine surface in the smallest specimens of *L. osseus*; however, small examples of the same form in the Tulane University collection reveal an inner row of enlarged teeth on the upper jaw.

Two subgenera, *Lepisosteus* and *Atractosteus*, are recognized here. The nomenclature of fossil Gar material has been confused because of chaotic conditions that have existed for many years with regard to the recent forms. Perhaps additional subgenera will have to be recognized for some of the fossil forms.

Genus *Lepisosteus* Lacépède 1803

Lepisosteus Lacépède, Hist. Nat. Poiss., *5*, 1803: 331; type species, *Lepisosteus gavialis* Lacépède 1803 equals *Esox osseus* Linnaeus.

Generic Synonyms:

Esox Linnaeus (in part), Syst. Nat., 10th ed., 1758: 313; type species, *Esox osseus* Linnaeus 1758.

Litholepis Rafinesque, Amer. Mon. Mag., *3*, 1818: 447; type species, *Litholepis adamantinus* Rafinesque 1818; based on a fictitious description personally communicated by J. J. Audubon.

Sarchirus Rafinesque, J. Acad. nat. Sci. Philad., *1* (2), 1818: 418; type species, *Sarchirus vittatus* Rafinesque 1818; young of *Lepisosteus osseus*.

Cylindrosteus Rafinesque, Ichthyol. Ohiensis, 1820: 72; type species, *Lepisosteus platostomus* Rafinesque 1820.

Atractosteus Rafinesque, Ichthyol. Ohiensis, 1820: 75; type species, *Lepisosteus ferox* Rafinesque 1820.

Lepidosteus Koenig, Icon. Foss., 1825: t. 12, emended spelling for *Lepisosteus* Lacépède 1803; *Lepidosteus* Agassiz, Rech. Poiss. Foss., *2* (2), 1843: *1*, emended spelling for *Lepisosteus* Lacépède.

Doubtful Synonym:

Psallisostomus Walbaum, P. Artedi Genera Pisc., Emend. Ichthyol., 1792, 581; *Psallisostomus* Fowler (after Walbaum), Fish. New Jersey *in* Rep. N. J. Mus., Pt. 2, 1905: 89; Suppl. Acct. Fish. N. J., Pt. 3, 1906: 263, 387, pl. 83 (after Agassiz, Rech. Poiss. Foss., 1843).

Characters. TEETH numerous, of various sizes on both jaws and on most bones lining roof of oral and pharyngeal cavities; one row of enlarged teeth with radially grooved base on lower jaws, and two rows on upper jaws, at least during younger stages; outer margin of both upper and lower jaws fortified with a closely set row of needle-shaped teeth; a pair of large teeth at anterior end of lower jaws fitting into depressions in upper jaws and, in many individuals, perforating anteriormost preorbital (maxillary auctorum). A peculiar wedge-shaped BLIND POCKET in skin of gular region. TONGUE bifurcate-spatulate. Three MODIFIED SCALES bordering anus; median scale, anterior to anus, a large shield-shaped plate; lateral plates elongate and slightly curved. Other characters those of the Order.

Species. Currently seven species are recognized in North American waters, but detailed studies that are in progress may show that two of these forms are only subspecifically distinct. There is some indication of hybridization, but verification of this must await further study. *L. oculatus*, *osseus*, *platyrhincus*, and *spatula* are treated in the following account.

Key to Species of the Western North Atlantic

1a. Total gill raker count on left outside arch, 59–81 (70 specimens); palatines of adult with a series of enlarged teeth. Subgenus *Atractosteus* Rafinesque 1820.

  2a. Lateral-line scales, 58–62 (25 specimens); diagonal rows between insertion of pelvic and origin of dorsal fin, 34–38; predorsal scales, 48–54.

    3a. Total gill rakers on left outside arch, 59–66 (20 specimens); females maturing at a larger size, probably not less than 600 mm; anterior body scales of 400-mm specimens finely serrated on posterior border. *spatula* Lacépède 1803, p. 83.

    3b. Total gill rakers, 67–81 (5 specimens); females maturing at a smaller size, 470 mm; anterior body scales of 400-mm specimens strongly serrated on posterior border. *tristoechus* (Bloch and Schneider) 1801.
    Fresh waters of southwestern Cuba and Isle of Pines; not yet recorded for salt water but likely to be found there.

  2b. Lateral-line scales, 51–56 (60 specimens); diagonal rows between insertion of pelvic and origin of dorsal fin, 28–32; predorsal scales, 43–48 (usually 44–47). *tropicus* (Gill) 1863.
  Rio Usumacinta of Guatemala and México and tributaries of Lake Nicaragua and Rio San Juan in Costa Rica on the Atlantic slope, and from Pacific drainage of Chiapas, México (Miller, *48*: 230, 231).[8] *Atractosteus bocourti* Duméril 1870; mouth of (Rio) Nagualate, 14°N.

1b. Total gill rakers, 14–33 (148 specimens); palatines of adult without enlarged teeth. Subgenus *Lepisosteus* Lacépède 1803.

  4a. Snout's least width 13–25.5 times in its length (specimens more than 50 mm long). *osseus* (Linnaeus) 1758, p. 75.

  4b. Snout's least width 4.5–11 times in its length (specimens more than 50 mm long).

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[8] There are no records from salt water on the Atlantic side but *L. tropicus* is common in the tidal zones of the Pacific drainages.

5a. Lateral-line scales, 59–65, usually 60–63 (47 specimens); predorsal scales 50–55, usually 52 or 53; anterior part of body and head without dark spots. *platostomus* Rafinesque 1820. Larger rivers of the Mississippi River drainage.

5b. Lateral-line scales, 53–59, usually 54–58 (249 specimens); predorsal scales 45–54, usually 47–50, rarely more than 51; anterior part of body and head with dark spots and blotches.

- 6a. Adults with bony plates on ventral surface of isthmus, under gill membrane (177 specimens); snout and lower jaw longer and narrower. *oculatus* Winchell 1864, below.
- 6b. Adults without bony plates on ventral surface of isthmus (76 specimens); snout and lower jaw shorter and broader. *platyrhincus* DeKay 1842, p. 81.

Lepisosteus oculatus Winchell 1864

Spotted Gar

Figures 12, 14

Study Material.[9] A total of 177 specimens, 32–819 mm TL, including the type of *L. oculatus* Winchell 1864 (dry mount with fins broken; length 700 mm, estimated caudal length 119 mm, total length 819 mm, UMMZ 55062), from Michigan, Indiana, and Ohio south to the Gulf of Mexico, and from western Florida to central Texas along the Gulf coast, in TU, UMMZ, ANSP, USNM, AMNH, and UT collections.

Distinctive Characters. L. oculatus is readily distinguished from *L. osseus* and *L. spatula* by the profusion of dark spots on the body, head, and fins, and from *L. platyrhincus* by the plates on the ventral surface of the isthmus. The Spotted Gar has a head of medium width, approximately intermediate between the narrow head of *L. osseus* and the very broad head of *L. spatula.*

Description. Proportional dimensions in per cent of length, based on 32 specimens: from Lake Pontchartrain near New Orleans, Louisiana (5), Sabine R., Texas (3), Mermentau R., Louisiana (4), Biloxi R., Mississippi (1), Pearl R., Louisiana and Mississippi (19); specimens 180–512 mm length.

Body: depth 9.2–12.8; width 8.6–12.6.
Caudal peduncle: length 10.8–13.4; least depth 5.0–7.3.
Head: mid-dorsal length 24.5–33.9; length 27.1–36.2; depth 6.6–8.3; width 7.6–10.0.
Snout: length 15.9–23.3; least width 2.3–3.2; width 3.8–5.3.

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[9] All of the types listed under *Study Material* were examined by me.

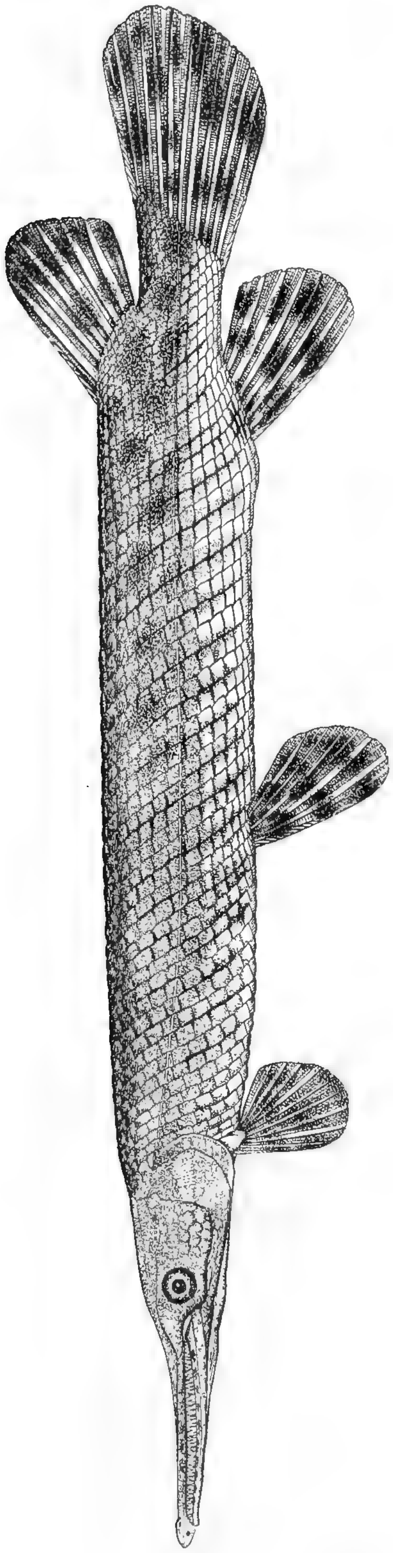


FIGURE 12. TOP. *Lepisosteus oculatus*, 534 mm TL, from Lake Pontchartrain at Goose Point, St. Tammany Parish, Louisiana, TU 6454.

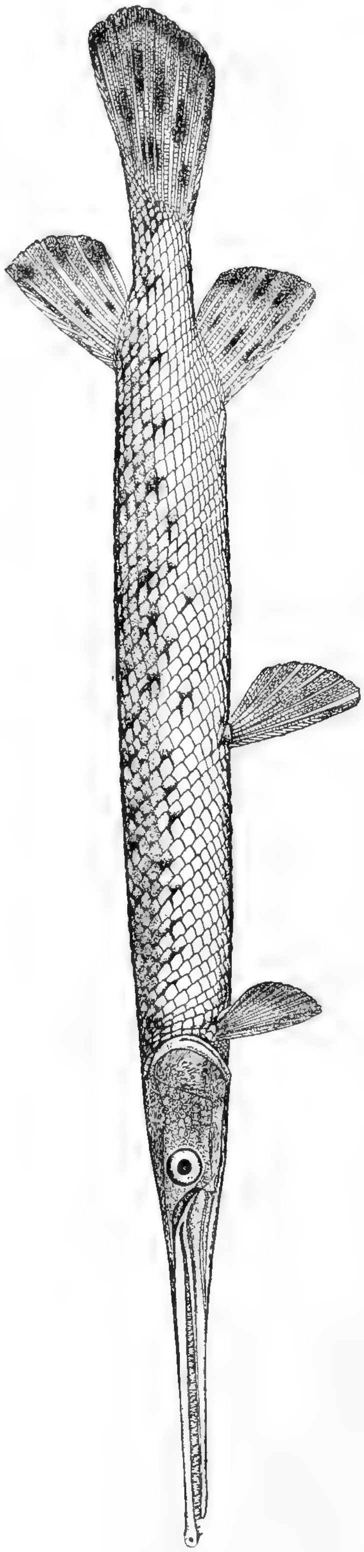


FIGURE 13. BOTTOM. *Lepisosteus osseus*, 554 mm TL, from Pearl River, Washington Parish, Louisiana, six miles east of Varnado, TU 1119.

Orbit: length 2.3–3.3.
Interorbital: least bony distance 4.8–5.9.
Postorbital distance to: bony margin 7.8–9.8; fleshy margin 8.9–11.0.
Frontal bones: least width 2.0–3.1.
Lower jaws: least width 1.7–3.0.
Mandible: length 13.6–20.8; posterior width 4.8–6.9.
Dorsal fin: depressed length 13.7–17.6.
Anal fin: depressed length 12.0–18.7.
Caudal fin: length 13.5–24.3.
Pectoral fin: length 8.2–12.8.
Pelvic fin: length 10.2–15.0.
Distance from tip of snout to: dorsal origin 83.2–87.6; pelvic insertion 53.4–61.2.
Distance from pelvic insertion to: anal origin 23.8–29.9; pectoral insertion 23.5–29.3; lateral line 4.6–6.8.
Distance from dorsal origin to: occiput 52.4–60.2; caudal base 14.0–17.2; lateral line 5.2–7.6.
Distance from anal origin to: caudal base 16.8–20.6.

Proportional dimensions in per cent of head length for 31 specimens, 180–700 mm length, with head lengths 65.1–196.0 mm.

Snout: length 57.0–65.0; least width 6.5–10.6.
Orbit: length 8.2–11.0.
Interorbital: least bony distance 15.4–21.5.
Postorbital distance to: bony margin 26.4–32.2.
Lower jaws: least width 5.0–10.8.
Mandible: length 50.0–57.5.

Proportional dimensions in per cent of snout length (sl) and mandible length (ml).

Snout: least width 5.1–9.9 times in sl.
Lower jaw: least width 4.8–11.6 times in ml.

Statistics of meristic characters: first number—number of specimens; second and third numbers—extremes in range of variation; fourth number—mean figure.

Scales: transverse rows between pelvic and dorsal origins 172, 27–32, 30.3; transverse rows 170, 18–24, 20.6; predorsal 173, 45–54, 48.2; lateral line 177, 53–59, 56.1.
Gill rakers: total 32, 15–24, 19.3.
Fin rays: dorsal 33, 6–9, 7.4; anal 33, 7–9, 7.8; caudal 32, 12 and 13, 12.5; pectoral on left 32, 9–13, 10.6, and on right 32, 9–13, 10.7; pelvic on left 33, all with 6 rays, and on right 33, all with 6 rays except 1 with 5.

Sexual Dimorphism. It is apparent in this species (Hubbs and Lagler, *33*: 76, 77) and occurs in at least one proportion. The female proportionally has a longer snout than the male, but this difference is not easily demonstrated because the snout-length/head-length ratio changes with size of individual.

Color. General coloration darker than in *L. osseus*; intervening spaces between numerous dark spots also dark in some specimens, making such individuals appear black; contrast between dark spots and background coloration usually greater in specimens living in clear water. Seemingly the intensity of pigmentation and the area of body pigmented are somewhat correlated with the color of the water, i.e. how darkly stained; streams and bayous that course through pinelands and cypress swamps have light brown to nearly black water and their fish inhabitants tend to be darkened also, even to the extent of a darkened ventral surface.

The young are brightly colored as in *L. osseus* (p. 78), but a few differences in color and pattern are apparent. Median dorsal stripe very broad and dark brown in contrast to narrow reddish or cinnamon stripe in *L. osseus*. Dark lateral band nearly straight on its upper margin, and narrow reddish-brown stripe above usually separated from lateral band. Ventral surface usually a chocolate color as in *L. osseus*. Mid-dorsal stripe and lateral band each breaking up into a single row of spots. Mid-dorsal spots developing first and forming in a posterior-to-anterior direction. These spots begin to form when the fish is between 100 and 150 mm length. The lateral spots appear in the same sequence but do not start to form until the individuals have reached an approximate length of 170 mm.

Size. The 26 *oculatus* collected from the brackish waters of Lake Pontchartrain from July 1953 to February 1955 were 297–690 mm TL. On March 25, 1959, four *oculatus* were seined in one haul from a borrow pit in the Bonne Carre Spillway, near Norco, Louisiana. The total length for the largest individual, a female, was 757 mm; for the three males, 522, 524, and 575 mm. This was probably a spawning group, but no spawning activity was observed prior to capture. The female was greatly distended at the time of capture because of the enlarged ovaries, but no ova were present in the oviducts.

Development. The scales develop in a posterior-to-anterior manner as described in *Development* (p. 66), but the Spotted Gar develops scales and other structures at a small size. Specimens 100 mm long have a fully developed lateral line as well as lateral body scales forward to the region of the pelvic fins at the same time as the pectoral fin rays are just starting to develop. Specimens of 130 mm have scales on the body except for the anterior belly and breast, and the pectoral fins may have half to all of their rays formed. The body scalation is complete in specimens 140–150 mm. Plates begin to form on the ventral surface of the isthmus in individuals of about 200 mm. The enlarged teeth in the row on the palatines remain as prominent structures until about 200 mm, and some retain them until they reach 300 mm; however, most individuals have only relatively small teeth at that size. The caudal appendage may be atrophied in individuals as small as 160 mm but may not be completely atrophied until a length of 225 mm.

Habits. The feeding habits of this species are similar to those described for *L. osseus* (p. 78). In the Lake Pontchartrain area, the diet of the Spotted Gar is composed of fishes and crustacea, the crustacean most often eaten being the blue crab, *Callinectes sapidus*.

Relation to Man. The Spotted Gar is usually considered an obnoxious fish.

Range. *Lepisosteus oculatus* ranges from the Great Lakes south in the Mississippi

Valley to the Gulf of Mexico, and from western Florida to central Texas along the Gulf coast. It does not invade brackish or marine waters as much as either the Longnose or Alligator Gars. In the Lake Pontchartrain area, *L. oculatus* is found most often along the marshy shore, and seldom very far out in the lake.

Specimens in the Tulane University collection were obtained from the tidewater section of Deer River on the west side of Mobile Bay, Alabama, and from Choctawhatchee River in Florida. Bailey, *et al.* reported the Spotted Gar for the tidewater section of the Escambia River, Florida (*5*: 117). Gunter reported the capture of two from Copano Bay, Texas (*27*: 23), and Reid gave records of it for East Bay, Texas (*60*: [1955]: 431). All records cited above indicate that, of the four Gar considered, this species and the Florida Gar (*L. platyrhincus*) are the least tolerant of saline conditions.

Synonyms, with References to Occurrence in Brackish or Salt Water:

Lepisosteus oculatus Winchell, Proc. Acad. nat. Sci. Philad., *16*, 1864: 183 (Huron R., Michigan); Gunter, Publ. Inst. mar. Sci. Texas, *1* (1), 1945: *23* (Copano Bay, Texas); Bailey, Winn, and Smith, Proc. Acad. nat. Sci. Philad., *106*, 1954: 117 (in tidewater, Florida); Reid, Texas Sci., *7* (4), 1955: 431 (East Bay, Texas).

Cylindrosteus productus Cope, Proc. Acad. nat. Sci. Philad., *17*, 1865: 86 (San Antonio, Texas).

Cylindrosteus agassizii Duméril, Hist. Nat. Poiss., *2*, 1870: 347–348, 351 (St. Louis, Missouri).

Cylindrosteus bartonii Duméril, Hist. Nat. Poiss., *2*, 1870: 347–348, 356 (New Orleans, Louisiana).

Lepisosteus osseus (Linnaeus) 1758

Longnose Gar

Figures 13, 15

Study Material. Many specimens, including 42, 139–779 mm TL, used for the *Description*; from tributaries of the Gulf of Mexico from Florida to México; from the Mississippi River drainage, Louisiana to Indiana; in USNM, CNHM, UMMZ, UI, UL, UT, and TU collections; also, the head only of the type of *Lepidosteus leptorhynchus* Girard 1858, USNM 1002.

Distinctive Characters. Lepisosteus osseus is distinguishable from *L. spatula*, *L. oculatus*, and *L. platyrhincus* at a glance by its long narrow snout.

Description. Proportional dimensions in per cent of length, based on 42 specimens, 114–695 mm length, as listed under *Study Material.* Although the variability of most dimensions for a limited size range is not very great, the following figures nevertheless include allometric variation.

Body: depth 7.0–10; width 5.9–9.5.

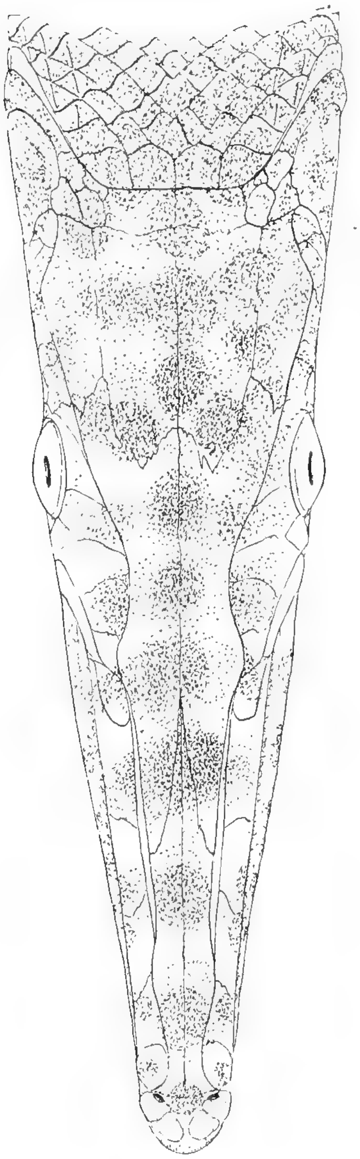
Caudal peduncle: length 9.4–13.0; least depth 3.7–5.1.

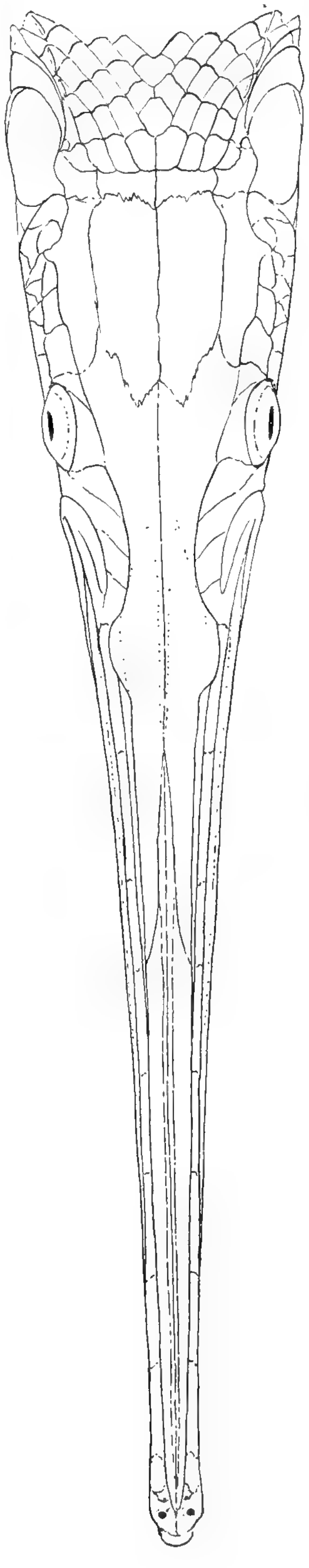
Head: mid-dorsal length 29.4–38.8; length 31.8–41.2; depth 5.4–7.2; width 5.3–7.6.

Snout: length 21.4–28.9; least width 1.1–2.1; width 2.6–3.7; very narrow.

Orbit: length 2.2–3.7.

Interorbital: least bony distance 3.8–5.2.





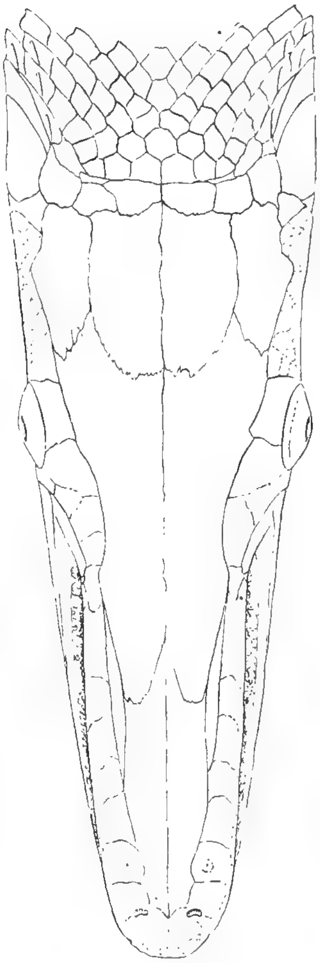


FIGURE 14. TOP. Mid-dorsal view of head (122.7 mm) of *L. oculatus* in Fig. 12. FIGURE 15. CENTER. Mid-dorsal view of head (165.0 mm) of *L. osseus* in Fig. 13. FIGURE 16. BOTTOM. Mid-dorsal view of head (102.3 mm) of *L. spatula* in Fig. 18.

Postorbital distance to: bony margin 6.6–8.9; fleshy margin 7.5–10.0.
Frontal bones: least width 1.7–2.5.
Lower jaws: width 3.6–5.2; least width 0.7–1.3.
Mandible: length 20.4–26.4.
Dorsal fin: depressed length 10.2–14.8.
Anal fin: depressed length 11.1–15.9.
Caudal fin: length 12.0–22.3.
Pectoral fin: length 2.6–10.3.
Pelvic fin: length 8.1–13.2.
Distance from tip of snout to: dorsal origin 84.8–89.3; pelvic insertion 56.1–62.1.
Distance from pelvic insertion to: anal origin 20.4–26.1; pectoral insertion 18.7–24.4; lateral line 3.3–4.7.
Distance from dorsal origin to: occiput 48.2–56.9; caudal base 10.6–15.2; lateral line 4.2–5.4.
Distance from anal origin to: caudal base 15.3–19.2.

Proportional dimensions in per cent of head length for 39 specimens, 114.1–695 mm length, with head lengths 81.8–272 mm, including head of type (see *Study Material*).

Snout: length 67.4–73.8; least width 3.1–4.5.
Orbit: length 6.3–9.1.
Interorbital: least bony distance 10.6–13.4.
Postorbital distance to: bony margin 17.7–23.6.
Lower jaws: least width 1.8–3.6.
Mandible: length 64.3–68.4.

Proportional dimensions in per cent of snout length.

Snout: least width 12.9–25.7.
Postsnout: distance 2.1–3.0.

Statistics of meristic characters: first number—number of specimens; second and third numbers—extremes in range of variation; fourth number—mean figure.

Scales: transverse rows between pelvic and dorsal origins 35, 31–35, 32.5; transverse rows 37, 19–24, 21.2; predorsal 38, 47–55, 50.8; lateral line 40, 57–63, 60.1.
Gill rakers: total 38, 14–31, 22.6.
Fin rays: dorsal 40, 6–9, 7.4; anal 40, 8–10, 8.8; caudal 40, 11–14, 12.8; pectoral on left 39, 10–13, 11.1, and on right 39, 10–13, 11.2; pelvic on left 40 and on right 40, all with 6 rays.

Color. In general, olivaceous brown above and white below, with specimens from clear water showing more contrast in coloration; their backs usually more greenish, those from turbid waters more brownish. Dark spots on median fins and on body, more clearly defined on specimens from clear water; darkened areas on body frequently appearing as blackened margins of scales (as if ink were dropped on the body and then wiped off, leaving traces in grooves between the scales); old individuals sometimes lacking dark spots on body or fins. Catesby has described and figured "acus maxima squamosa viridis" from Virginia as having a pink belly and pink fins (*13*: 30, pl. 30).

This peculiar coloration may be indicative of a hemorrhagic condition that is easily produced by exposure and rough handling before preservation.

Young individuals, colorful with various shades of brown to black, and white to cream. Broad dusky or dark brown band on the side of body, extending from snout through eye to base of caudal fin; upper margin of band scalloped, the elevated portions fusing into an interrupted stripe of reddish brown or cinnamon. A narrow mid-dorsal stripe of similar color. Ventral surface of small young chocolate colored on midbelly and bordered above on either side by a milky to cream stripe, the dark coloration disappearing in larger young and leaving only a narrow ventrolateral stripe. All fins more or less spotted or blotched with dark brown, the dark color of fins usually in the form of bars on pelvic, dorsal, and anal.

Size. The maximum size of *osseus* is about 1,500 mm TL. Abbott gave a length of five feet for a specimen speared in Crossweelssen Creek, New Jersey (*31*: 270). The 28 specimens collected from July 1953 to February 1955 from Lake Pontchartrain were 541–1,180 mm TL.

Spawning and *Development.* The early life history of *L. osseus* is quite well known (A. Agassiz, *1* [1878]; Mark, *45*). The more extensive studies were made by Wilder (*71*: 155–163; *72*: 1–12, 192, 195, 10 figs.), Balfour (*6*: chap. 6), Balfour and Parker (*7*), and Eycleshymer (*21*). Agassiz has described the spawning activities and early development of the Longnose Gar of Black Lake, New York (*1* [1879]: 65–75, 5 pls.), and many illustrations represent the developmental stages of the fins and adhesive organs. The adhesive organs on the ventral surface at the tip of the snout on newly hatched fry are used for attachment to objects above the bottom silt. Although larvae are relatively inactive until the yolk supply is absorbed, they are capable of very rapid movements when disturbed. At three weeks of age the yolk has been used, and the adhesive organs are reduced to a small swelling.

The following data give an approximation of the size of individuals at the time of atrophy of the fleshy caudal appendage projecting from the upturned end of the vertebral column. A caudal appendage has been observed at the following lengths: 191, 219, 233, 245, 260, and 271 mm.; but none was seen on specimens of these lengths: 266, 268, 271, 274, 284, and 286 mm. Wilder's observation of a 300-mm specimen with the caudal appendage nearly atrophied is in line with measurements given above. Our largest specimen (271 mm) is actually 323 mm TL when the caudal fin length is added. Apparently no one has yet determined the maximum age attained by Garfish, but numerous specimens have been kept in aquariums for a number of years. Mark, who kept *L. osseus* for nearly $3^1/_2$ years in aquariums at Cambridge, obtained the material from Black Lake, New York, when it was in early stages of segmentation (*45*: 5).

Food and Feeding. The Longnose Gar usually waits for its prey to get within "easy reach" and then, with a sudden thrust, grasps the victim (Abbott, *31*: 269, 270). The prey is often held crosswise in the mouth for several minutes before it is swallowed. In the brackish waters of Lake Pontchartrain, this Gar feeds on various fishes and crustacea; largescale menhaden (*Brevoortia patronus*), bay anchovy (*Anchoa mitchilli*), sea catfish (*Galeichthys felis*), and the blue crab (*Callinectes sapidus*) were found in the stomachs by Dr. Rezneat M. Darnell.

Relation to Man. In most areas the Longnose Gar is considered not only an obnoxious predatory fish but a destructive one as well, gill and trawl nets often being damaged by it in the brackish waters of Louisiana, and probably elsewhere. In some parts of the country it is used as food, although most fishermen throw it out on the banks, or mutilate it before release back into the water. Smith (*64*: 59) reported (after Earl, *18*: 485) that in 1880 this was one of the principal foodfishes in the New Bern market. The roe, being poisonous, is not used in caviar production as is that of the sturgeons and the paddlefishes.

Range. It frequents waters from Quebec to Florida along the Atlantic except for the eastern part of the New England states, and in the west it ranges from the Great Lakes region south to northern México.

The adult is frequently found in the brackish waters of Louisiana; Smith has stated that the Longnose Gar sometimes enters salt water and is not rare in Albemarle Sound (*64*: 59). In winter it frequents the deeper waters of Lake Pontchartrain, where, during a biological survey, several specimens were collected with trawl nets from dredge holes 30 feet in depth. Uhler and Lugger reported it as common in brackish water of the Potomac and Patapsco rivers (*66*: 154), but Hildebrand and Schroeder recorded it as not common in Chesapeake Bay (*32*: 77). Joseph and Yerger reported three specimens, 1,000–1,070 mm TL, for Alligator Harbor, Florida (*39*: 120).

The type of *Lepidosteus crassus* Cope 1865 was collected from brackish water at Bombay Hook, near the mouth of the Delaware River.

Synonyms, with References to Occurrence in Salt Water:

Esox osseus (in part) Linnaeus, Syst. Nat., 10th ed., 1758: 313; after Artedi, based on "Acus maxima squamosa viridis," Catesby, 1738: 30, pl. 30 (Virginia).

Esox virdis Gmelin *in* Linnaeus, Syst. Nat., 13th ed., *1* (3), 1789: 1389.

Lepisosteus gavialis Lacépède, Hist. Nat. Poiss., 5, 1803: 333 (lakes, rivers of both Indies).

Sarchirus vittatus Rafinesque, J. Acad. nat. Sci. Philad., *1* (2), 1818: 419, pl. 17, fig. 2 (based on juv.).

Lepisosteus oxyurus Rafinesque, Ichthyol. Ohiensis, 1820: 73 (Ohio R.).

Lepisosteus longirostris Rafinesque, Ichthyol. Ohiensis, 1820: 74 (Muskingum R., Ohio, descr. based on head).

Lepisosteus huronensis Richardson, Fauna Boreal. Amer., *3*, 1836: 237 (Penitanguishene, Lake Huron).

Lepidosteus rostratus Cuvier *in* Richardson, Fauna Boreal. Amer., *3*, 1836: 238 (Penitanguishene, Lake Huron).

Lepidosteus semiradiatus Agassiz, Rech. Poiss. Foss., *2*, 1836: 2, pl. 2.

Lepidosteus gracilis Agassiz, Rech. Poiss. Foss., *2*, 1836: 3.

Lepidosteus bison DeKay *in* Zool. N.Y., 1842: 271, pl. 43, fig. 139 (Lake Erie, Buffalo, New York).

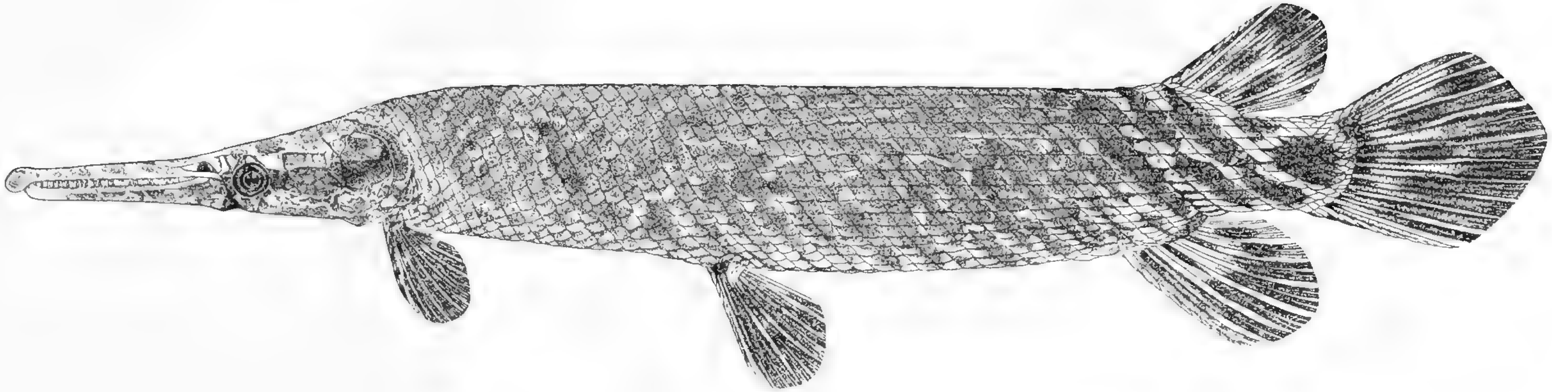
Lepisosteus lineatus Thompson, Hist. Vermont, 1842: 145 (ill., Winooski R., Burlington, Vermont; based on juv.).

Macrognathus loricatus Gronow *in* Gray, Cat. Fish. Coll. and Descr. by L. T. Gronow, in Brit. Mus., 1854: 148 (after Linnaeus).

Lepidosteus leptorhynchus Girard *in* Pacif. R. R. Surv., Fish., *10* (4), 1858: 351 (Devil R., Texas; head only, USNM 1002).

Lepidosteus otarius Cope, Proc. Acad. nat. Sci. Philad., *17*, 1865: 86 (Platte R. near Fort Riley).

Lepidosteus crassus Cope, Proc. Acad. nat. Sci. Philad., *17*, 1865: 86 (type from brackish water at Bombay Hook, near mouth of Delaware R.).



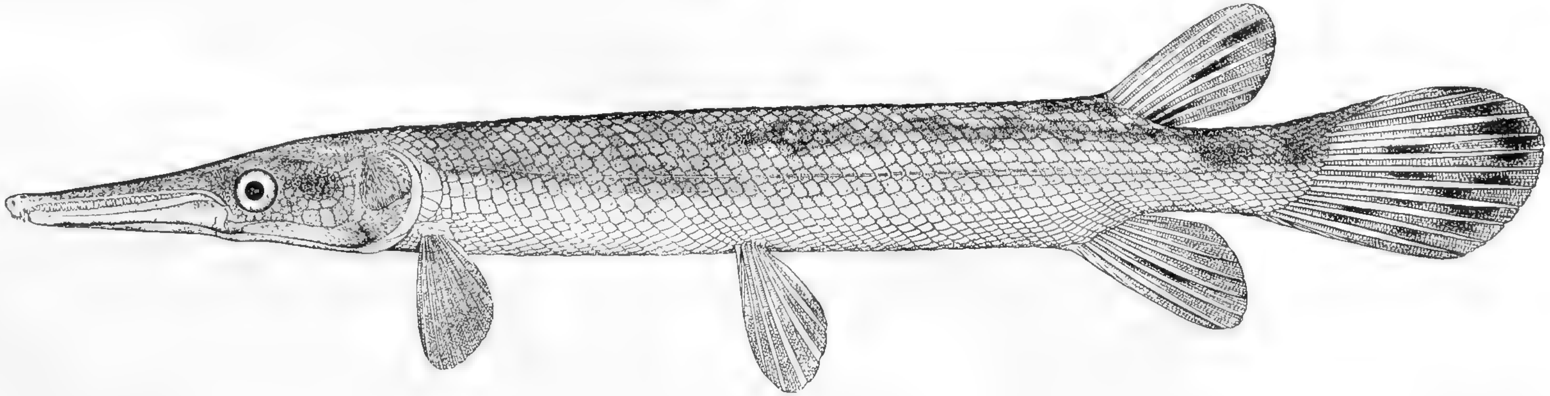


Figure 17. Top. *Lepisosteus platyrhincus*, 516 mm TL, from Tamiami Canal, Collier County, Florida, 2.7 miles W. of Collier and Dade County line, U. S. Hwy. 41, TU 16920.

Figure 18. Bottom. *Lepisosteus spatula*, 488.8 mm TL, from Lake Pontchartrain, Tangipahoa Parish, Louisiana, at mouth of Tangipahoa River, TU 8619.

Lepidosteus treculi Duméril, Hist. Nat. Poiss., *2*, 1870: 323–324, 327 (Mississippi R.).
Lepidosteus milberti Duméril, Hist. Nat. Poiss., *2*, 1870: 323–324, 328 (New York).
Lepidosteus harlani Duméril, Hist. Nat. Poiss., *2*, 1870: 323–324, 329, Atlas, pl. 21, fig. 1, 1 a, 1 b (Wabash R.).
Lepidosteus smithi Duméril, Hist. Nat. Poiss., *2*, 1870: 323–324, 330 (upper Mississippi R.).
Lepidosteus ayresii Duméril, Hist. Nat. Poiss., *2*, 1870: 323–324, 331 (Wabash R.).
Lepidosteus copei Duméril, Hist. Nat. Poiss., *2*, 1870: 323–324, 332 (n. North America).
Lepidosteus lesueurii Duméril, Hist. Nat. Poiss., *2*, 1870: 323–324, 335 (Wabash R.).
Lepidosteus elisabeth Duméril, Hist. Nat. Poiss., *2*, 1870: 323–324, 336 (no local.).
Lepidosteus lamarii Duméril, Hist. Nat. Poiss., *2*, 1870: 323–324, 337 (n. North America).
Lepidosteus clintonii Duméril, Hist. Nat. Poiss., *2*, 1870: 323–324, 338 (no local.).
Lepidosteus troostii Duméril, Hist. Nat. Poiss., *2*, 1870: 323–324, 339 (U.S.A.).
Lepodosteus piquotianus Duméril, Hist. Nat. Poiss., *2*, 1870: 323–324, 340 (Lake Erie).
Lepidosteus horatii Duméril, Hist. Nat. Poiss., *2*, 1870: 323–324, 341 (n. North America).
Lepidosteus thompsoni Duméril, Hist. Nat. Poiss., *2*, 1870: 323–324, 342 (upper Mississippi R.).
Lepidosteus louisianensis Duméril, Hist. Nat. Poiss., *2*, 1870: 323–324, 343, Atlas, pl. 22, fig. 3 (New Orleans, Louisiana).
Lepidosteus osseus Günther, Cat. Fish. Brit. Mus., *8*, 1870: 330.
Lepidosteus osseus Jordan and Evermann, Bull. U.S. nat. Mus., *47* (1), 1896: 109; Uhler and Lugger, Rep. Comm. Fish. Md., 1876: 154 (brackish water, Chesapeake Bay region); Smith, N.C. geol. econ. Surv., *2*, 1907: 59 (brackish and salt water, N. Carolina); Hildebrand and Schroeder, Bull. U.S. Bur. Fisher., *43*, 1928: 77 (Chesapeake Bay); Joseph and Yerger, Pap. oceanogr. Inst. Fla. St. Univ. Stud., *22*, 1956: 120 (brackish or salt water, Florida).

Doubtful Synonyms:

Lepisosteus stenorhynchus Rafinesque, Amer. Mon. Mag., *3*, 1818: 447; no description (Ohio, Wabash, Green rivers).
Sarchirus argenteus Rafinesque, Ichthyol. Ohiensis, 1820: 86 (Licking R., Slate Creek; brief descr. based on communication from Mr. Owings).

Lepisosteus platyrhincus DeKay 1842

Florida Gar, Florida Spotted Gar

Figure 17

Study Material. A total of 76 specimens, 187–516 mm TL; and type of *Cylindrosteus megalops* Fowler 1910, 369.4 mm length, 419.0 mm TL, ANSP 25371 (in alcohol); from peninsular Florida, in TU, ANSP, and AMNH collections.

Distinctive Characters. Like *L. oculatus*, *L. platyrhincus* differs from *L. osseus* and *L. spatula* by the presence of numerous dark spots on the anterior part of its body and head, but it is distinguished from *L. oculatus* primarily by its lack of plates on the ventral surface of the isthmus, by its wider snout, and by the wider lower jaws.

Description. Proportional dimensions in per cent of length, based on 30 specimens, 157.0–416.0 mm length; from peninsular Florida.

Body: depth 10.5–14.3; width 9.2–12.0.
Caudal peduncle: length 9.8–13.0; least depth 5.7–7.5.
Head: mid-dorsal length 24.5–33.1; length 27.4–36.2; depth 7.2–8.5; width 8.1–9.8.
Snout: length 15.8–22.5; least width 2.6–3.4; width 4.1–5.4.

Orbit: length 2.6–3.5.
Interorbital: least bony distance 5.0–5.9.
Postorbital distance to: bony margin 8.3–10.1; fleshy margin 9.5–11.5.
Frontal bones: least width 2.2–2.7.
Lower jaws: width 5.3–6.8; least width 2.3–3.5.
Mandible: length 13.7–19.6.
Dorsal fin: depressed length 13.9–16.4.
Anal fin: depressed length 14.3–16.5.
Caudal fin: length 15.1–19.3.
Pectoral fin: length 8.8–11.8.
Pelvic fin: length 11.4–13.8.
Distance from tip of snout to: dorsal origin 81.0–88.5; pelvic insertion 52.6–61.3.
Distance from pelvic insertion to: anal origin 24.9–32.0; pectoral insertion 23.5–28.1; lateral line 4.5–7.5.
Distance from dorsal origin to: occiput 53.8–61.3; caudal base 14.2–16.3; lateral line 5.4–7.5.
Distance from anal origin to: caudal base 16.0–19.8.

Proportional dimensions in per cent of head length for 30 specimens, 157–416 mm length, with head lengths 61.5–118.3 mm.

Snout: length 57.3–62.3; least width 7.5–12.0.
Orbit: length 9.0–11.2.
Interorbital: least bony distance 15.5–21.0.
Postorbital distance to: bony margin 28.0–32.2.
Lower jaws: least width 6.3–12.6.
Mandible: length 49.3–54.8.

Proportional dimensions in per cent of snout length (sl) and mandible length (ml).

Snout: least width 4.8–8.2 in sl.
Postsnout: distance 1.3–1.6 in sl.
Lower jaws: least width 4.0–8.5 in ml.

Statistics of meristic characters: first number—number of specimens; second and third numbers—extremes in range of variation; fourth number—mean figure.

Scales: transverse rows between pelvic and dorsal origins 76, 30–33, 31.7; transverse rows 76, 21–25, 22.3; predorsal 76, 47–51, 48.6; lateral line 76, 54–59, 56.5.
Gill rakers: 30, 19–33, 24.9.
Fin rays: dorsal 30, 7 or 8, 7.3; anal 30, 7 or 8, 7.6; caudal 30, 12 or 13, 12.7; pectoral on left 30, 9–11, 9.9 and on right 30, 9–11, 9.7; pelvic 30, all with 6 rays on both sides.

Sexual Dimorphism. As in the case of *L. oculatus*, sexual dimorphism is apparent in this species also, i.e. females attain a larger size and proportionally have a longer snout than males. In length of snout, the females of *platyrhincus* overlap the males of *oculatus*.

Color. General coloration on back darker than in *L. oculatus*; coloration and pattern on ventral surface highly variable, with specimens taken from the same place and at the same time exhibiting variation from immaculate to solid black. Many specimens with a pattern of two or four or more dark stripes on ventral surface. Two other color phases also, a brown and an orange (Phillips, *53*: 331).

Young, similar in coloration to color given for *L. oculatus* (pp. 73, 74).

Size. Kilby reported observations on specimens taken off Bayport, Florida, a mile from shore in the Gulf of Mexico (*41*: 91); and three specimens, 169, 445, and 495 mm, were collected from the coastal marsh near Bayport. Hammett and Hammett reported a maximum of 1,330 mm TL in a sample of 225 specimens (*30*: 197).

Development. In this species the development is probably similar to that in *L. oculatus* (p. 74).

Habits. The diet of this species in brackish and marine waters is unknown.

Relation to Man. Kilby reported that this species is a nuisance to fishermen (*41*: 191).

Range. L. platyrhincus ranges from the southern tip of peninsular Florida northward into the lowlands of Georgia. The paucity of records for salt water seems to indicate little tolerance of this species for saline conditions, but there may be a lack of collections from the areas of its occurrence.

Synonyms, with Reference to Occurrence in Salt Water:

Lepisosteus platyrhincus DeKay, Zool. N.Y., *1*, 1842: 273, p. 43, fig. 137 (Florida); Kilby, Tulane Stud. Zool., *2* (8), 1955: 151 (salt water, off Florida).

Cylindrosteus castelnaudi Duméril, Hist. Nat. Poiss., *2*, 1870: 347–348, 355, Atlas, pl. 21, figs. 2, 2 a, 2 b (Lake Lafayette, Florida).

Cylindrosteus megalops Fowler, Proc. Acad. nat. Sci. Philad., *62*, 1910: 609, pl. 38, figs. 15, 16 (Bayport, Florida).

Lepisosteus spatula Lacépède 1803

Alligator Gar

Figures 16, 18

Study Material. A total of 29 specimens: 28, 187–2,159 mm TL[10] (dry mounts or preserved in alcohol), from western Florida along the Gulf coast to México; including the type of *Lepidosteus berlandieri* Girard 1858, from Matamoros, Tamaulipas, México, USNM 1003; 1, 49.5 mm length, 57.3 mm TL, from Hildebrandt Bayou near Port Acres, Jefferson County, Texas, TU 22288; all in TU, UMMZ, USNM, ANSP, AMNH, CNHM, and UT collections.

Distinctive Characters. Lepisosteus spatula is separable from *L. osseus* and *L. oculatus* by its large size and broad, short snout. The young of *spatula* are distinguishable from the young of *oculatus*, *osseus*, *platyrhincus*, and *platostomus* by the light dorsal stripe.

Description. Proportional dimensions in per cent of length, based on 25 specimens, 156.5–1,760.0 mm length; also the 49.5-mm specimen [with measurements enclosed in brackets].

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[10] The largest specimen is now at Tulane University (TU Osteol. Coll. 360).

Body: depth 9.8–14.2 [12.5]; width 9.1–14.0 [9.0].

Caudal peduncle: length 11.7–14.2 [10.9]; least depth 5.8–7.5 [6.2].

Head: mid-dorsal length 21.5–32.4 [31.5]; length 28.4–36.5 [35.7]; depth 8.2–10.6 [9.4]; width 9.4–12.9 [9.4].

Snout: length 15.7–21.4 [19.5]; least width 3.9–5.1 [5.0]; width 5.3–6.7 [6.8].

Orbit: length 2.5–4.1 [5.6].

Interorbital: least bony distance 7.2–9.0 [7.2].

Postorbital distance to: bony margin 9.7–11.1 [10.5]; fleshy margin 10.5–12.8 [11.1].

Frontal bones: least width 3.7–4.4 [4.8].

Lower jaws: width 6.1–9.8 [7.8]; least width 4.5–5.5 [4.6].

Mandible: length 13.7–18.5 [15.9].

Dorsal fin: depressed length 13.4–18.4 [15.1].

Anal fin: depressed length 13.0–17.9 [14.5].

Caudal fin: length 13.6–19.0 [16.7]; filament [19.3].

Pectoral fin: length 9.1–13.3 [5.0].

Pelvic fin: length 11.1–15.0 [8.0].

Distance from tip of snout to: dorsal origin 82.8–86.0 [82.0]; pelvic insertion 53.5–59.4 [56.7].

Distance from pelvic insertion to: anal origin 23.2–30.7 [25.2]; pectoral insertion 21.0–32.9 [21.4]; lateral line 5.3–8.2.

Distance from dorsal origin to: occiput 51.9–59.8 [50.9]; caudal base 14.5–17.5 [16.9]; lateral line 5.8–7.5.

Distance from anal origin to: caudal base 17.0–20.8 [18.1].

Proportional dimensions in per cent of head length for 27 specimens, 156.5–1,760.0 mm [49.5], including 2,159-mm specimen, TU Osteol. Coll. 360 (see ftn. 10), with head lengths 54.6–562.0 mm [17.7].

Snout: length 54.1–59.7 [54.7]; least width 13.0–15.3 [14.1].

Orbit: length 5.4–12.1 [15.8].

Interorbital: bony distance 23.0–30.5 [20.3].

Postorbital distance to: bony margin 28.6–36.5 [29.3].

Lower jaws: least width 13.5–19.2 [12.9].

Mandible: length 46.7–52.4 [44.6].

Proportional dimensions in per cent of snout length (sl) and mandible length (ml).

Snout: least width 3.7–4.5 [3.9] times in sl.

Postsnout: distance 1.2–1.5 [1.2] in sl.

Lower jaws: least width 2.7–3.8 [3.4] times in ml.

Statistics of meristic characters: first number—number of specimens; second and third numbers—extremes in range of variation; fourth number—mean figure.

Scales: transverse rows between pelvic and dorsal origins 24, 34–38, 35.3; transverse rows 27, 23–32, 26.3; pectoral 27, 49–54, 51.1; lateral line 27, 58–62, 60.3.

Gill rakers: total 20, 59–66, 62.7.

Fin rays: dorsal 22, 7–10, 7.7; anal 22, 7–10, 7.8; caudal 22, 12–14, 12.9; pectoral 22, 11–15, 12.7 on left and 22, 8–16, 12.6 on right; pelvic 22, all with 6 rays except 1 with 5 on left.

Color. In general, dark olivaceous brown above and white to yellowish beneath, but some nearly black dorsally; this coloration not unusual for specimens kept in aquariums. Two small specimens (156.5 and 170.5 mm length) dark brown except for light flesh-color on belly, breast, and throat regions. Skin between mandibles finely speckled with brown; numerous dark spots on sides—only below lateral line anteriorly, but above, below, and along lateral line on peduncle posteriorly. Rays of all fins dark brown, the dorsal, anal, and caudal having noticeably darker spots. Individuals of about 500 mm have few dark spots on sides, and then usually on peduncle; although only a few dark spots are present, there are numerous places where the groove between the scales is markedly darker than the surface of the scale; a few dark spots on dorsal, anal, and caudal fins; some large individuals from Lake Pontchartrain devoid of spots on fins as well as on body.

Color of 49.5-mm specimen. Light median dorsal stripe extending from tip of snout to origin of dorsal, and from posterior insertion of dorsal to upper base of caudal fin; this light stripe bordered on either side by a broad dark brown area extending about a third of the way down the sides and reaching to dorsal rim of orbit. Dark lateral band from anterior tip of mandible to anterior rim of orbit, thence posteriorly from posterior rim of orbit to base of caudal. Dark lateral band extending posteriorly along mandible from its anterior tip to anterior rim of orbit, and from posterior orbit to base of caudal; this dark band on body composed of close-set mottlings, forming irregular borders dorsally and ventrally. Venter light except for dark strip along inside of rami of lower jaws, thus leaving a light midventral band. All fins with dark brown blotches.

Size. The smallest Alligator Gar seen is the 49.5-mm specimen described above. The largest one on record, a female taken from Belle Island Lake, Vermilion Parish, Louisiana, was 9 feet 8.5 inches long and weighed 302 pounds; statistics on other large individuals are given by Gudger (*26*: 118–120), Weed (*69*: 5, 6), and Hussakof (*34*: 2). During a recent biological survey of Lake Pontchartrain and adjoining brackish waters, 21 specimens, 410–1,472 mm TL,[11] were collected. Additional specimens were taken from the Gulf of Mexico at Grand Isle, Jefferson Parish, Louisiana.

Spawning and Development. Practically nothing is known of the spawning and development of the Alligator Gar, but according to the unpublished writings of George Powers Dunbar (Wortman, *75*: 385), it spawns during December and January. The egg is enveloped in gelatinous material, and the egg strands are draped on snags and vegetation; by the end of August the young fish has reached 14 inches in length. These notes by Dunbar need verification. [Recent observations prove the foregoing to be incorrect. The Alligator Gar spawns in April, May, and June in the Louisiana

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[11] The remains of several taken from the Gulf side of Breton Island as well as the head of a specimen (*ca.* 6 ft.) taken from the Gulf of Mexico at Destin, Florida, are in the Tulane University osteology collection.

area. The description of the eggs probably was of some amphibian, as suggested by Dr. Edward C. Raney (personal communication)].

The 49.5-mm specimen (see *Description* and *Color* above) has neither scales nor lateral line developed, the pelvics and pectorals are relatively much shorter than in older fish, and in the head region, the lower jaws, mandible, and interorbital dimension are relatively shorter while the orbit is much larger, as is common in the young of many species. In coloration it is distinguished by the light median stripe from the snout to the upper caudal except for its interruption by the dorsal.

Specimens 156.5 and 170.5 mm length have the caudal appendage but lack scales in the mid-dorsal region and on the midventral surface except for a partially developed anal plate. The rays of the pectoral as well as those of the other fins are fully developed.

Food and Feeding. L. spatula is credited with eating large numbers of game fishes in fresh water (Gudger, *26*: 120), but little has been published about its diet in brackish and salt water. Raney reported that it ate ducks and water turkey (*Anhinga anhinga*) in Cuartez, Resaca, Texas (*57*: 50), and Gunter found mullet (*Mugil*) in the gut tract of 12 out of 24 specimens (*27*: 24). No other food items were mentioned by these authors. Those examined during the Lake Pontchartrain studies contained striped mullet (*Mugil cephalus*) and blue crabs (*Callinectes sapidus*).

Jordan (*35*: 313), Weed (*69*: 9), and Gunter (*27*: 24) have given evidence that the Alligator Gar is a scavenger.

Relation to Man. It is sold at present for human consumption in the French Market in New Orleans, and its scales were used by the Indians (Gowanloch, *24*: 389–392) and by the late Mr. Percy Viosca in his jewelry industry. Many unauthenticated accounts of Gar attacks on humans have appeared in both popular and semipopular literature, but swimmers probably need have very little fear of them (*24*: 389–392; *26*: 120, 121). With the recent development of underwater spear-fishing, all of the Gars are desirable targets. Gar fishing rodeos are common annual events in Louisiana.

Range. The Alligator Gar is a frequent invader of brackish and marine waters, and of the four species it is the most tolerant to higher salinities. It occurs in fresh water in the Mississippi River and lower parts of its major tributaries from the Ohio and Missouri rivers southward to the Gulf of Mexico, and in brackish and salt waters along the Gulf coast from Choctawhatchee Bay, Florida, to northern México (*26*: 118–120; *69*: 5, 6; *34*: 2). Gunter recorded Alligator Gars from Copano Bay, Aransas Bay, and from a Gulf beach, Texas (*27*: 24), and Reid reported the capture of one from East Bay, Texas (*60* [1956]: 302). Bailey, *et al.* gave catch records for the tidewater section of Escambia River, Florida (*5*: 117), and specimens frequently on display at the Gulfarium at Ft. Walton, Florida, are captured in Choctawhatchee Bay.

Synonyms, with References to Occurrence in Salt Water:

Lepisosteus spatula Lacépède, Hist. Nat. Poiss., *5*, 1803: 333 (no local.); Bailey, Winn, and Smith, Proc. Acad. nat. Sci. Philad., *106*, 1954: 117 (tidewater, Florida); Reid, Texas J. Sci., 1956: 302 (salt water, Texas).

Lepisosteus ferox Rafinesque, Ichthyol. Ohiensis, 1820: 73 (Ohio River).

Lepidosteus berlandieri Girard *in* Pacif. R. R. Surv., Fish., *10* (4), 1858: 353 (Tamaulipas, México).

Atractosteus lucius Duméril, Hist. Nat. Poiss., *2*, 1870: 360, 364 (Tampico, México).

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Order Isospondyli[1]

COMPOSITE AUTHORSHIP

Characters and Keys to Suborders and Families

HENRY B. BIGELOW
Museum of Comparative Zoology
Harvard University

Acknowledgments. Special thanks are due the following persons for their invaluable help and cooperation in preparing the text and keys of this section: William W. Anderson, James E. Böhlke, Daniel M. Cohen, J. R. Dymond, Robert H. Gibbs, Jr., W. A. Gosline, Marion Gray, N. B. Marshall, Giles W. Mead, James E. Morrow, Jr., George S. Myers, Albert E. Parr, and Robert R. Rofen.

Characters of Living Isospondyli. Both premaxillary and maxillary bones are present in most, but in a few these bones are greatly reduced or lacking (among Argentinoidea, Part 4). In most the maxillaries form a part of the border of the mouth (see also pp. 11, 12, 17, 92, 95). The premaxillaries are only slightly protractile, if at all so, except in the Phractolaemidae,[2] some Alepocephalidae, and some Stomiatoidea (see Bertin and Arambourg, *18*: 2247), where they are protractile. The bone in the ethmoid position above the vomer is unpaired in most but paired in a few (pp. 95, 96).

There are four gill clefts, and in a few there is an open slit between the mandible and the hyoid arch (Malacosteidae).

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[1] With accounts of the included Suborders, Families, Genera, and Species by various authors as listed in the Table of Contents. In this series of volumes, the Iniomi, treated as a Suborder of the Isospondyli by some authors, is given the rank of Order and is dealt with in Memoir I, Part 5.

[2] A family of the Chanoidea, or so-called milkfishes, of the tropical Pacific.

Typically the fins have no supporting spines,[3] most of the rays being branched; however, in a few the rays are unbranched at the origin. Typically the pectorals[4] are posterior to the gill openings, but in the genus *Asquamiceps* (Alepocephalidae) they are well inside the gill cover; in the more primitive genera their line of insertion is low down on the side near the ventral profile, but in some of the alepocephalids and argentinoids they are inserted higher up on the sides; the pectoral bases are far below the upper end of the gill openings except in some of the bathylagids, where the upper end of the gill opening is greatly restricted. The pelvic fins,[5] if present, are posterior to the pectorals, their positions ranging from abdominal to thoracic. In most there is only one dorsal fin with jointed bony or membranous rays (lacking in a few); in some there is a fleshy "adipose" dorsal fin with unjointed horny rays between the rayed dorsal and caudal fins; also, in a few (some Astronesthidae) there is a second adipose fin close in front of the anus. The rayed dorsal, or the adipose dorsal if present, is separated from the caudal by a definite gap, and in most the anal fin is similarly separated from the caudal.[6] The caudal fin is about the same in width both above and below the projected longitudinal axis of the trunk,[7] and the rear boundary of its fleshy base is symmetrical relative to the axis of the trunk; in most, the rear outline of the caudal is more or less deeply forked, or at least concave, but in some it is more nearly truncate transversely, and in a few it is either rounded or has two or three of the middle rays extending almost equally beyond the others (genus *Pantodon*).

The radialia of the pectoral fins are articulated basally with the pectoral girdle. In the great majority the pectoral girdle has a mesocoracoid element firmly attached above to the auditory (otic) region of the skull (see also pp. 2, 6). In the pelvic fins the basal radialia are reduced to a few small nodules, and the pelvics are not attached to the pectoral girdle. The number of skeletal supports equals the number of rays in the dorsal and anal fins.

The head, though naked in the great majority, is clothed with smooth scales among the Esocoidea and in the genus *Lepogenys* (Alepocephalidae) and with prickly scales in *Gonorhynchus*; in no living representative of the Order[8] is the head armored with bony plates. And in no living family are the margins of the caudal fin armed with more than one enlarged "fulcral" scale, such as is characteristic of the caudal of the sturgeons[9]

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[3] Among the Idiacanthidae the base of each dorsal and anal ray bears on its anterior side a pair of short sharp spurs that project through the skin (for details, see Beebe, *3*: 152, 213). Among the Sternoptychidae, the rayed dorsal is preceded by the projecting spine-like tips of approximately 1–7 of the neural processes of an equal number of vertebrae (for an early account, see Cuvier and Valenciennes, *15*: 395, 402, 419).

[4] The stomiatoid genera *Idiacanthus*, *Photostomias*, and *Tactostoma* (described by Bolin, *6*: 39), are said to have no pectorals; likewise some specimens of *Eustomias* and *Photonectes*.

[5] Among many families, such as the salmonids, specimens occasionally lack one or both pelvics, but this is an individual anomaly (see Myers, *29*: 600–601; *28*: 41).

[6] Not in the freshwater Notopteridae of Africa and the East Indies, or in the genus *Coilia* (Engraulidae) of the tropical warm-temperate Indo-Pacific.

[7] Most of the fin rays, however, are "attached to the lower spines of the hinder vertebrae, which are greatly enlarged, and at the same time inclined backwards so as to be more or less parallel to the axis of the body" (Norman, *31*: 61).

[8] In the fossil Leptolepidae the dermal bones of the skull were covered with an enamel-like substance.

[9] These fulcral scales were "present, but usually small" among the fossil Pholidophoridae (Boulenger, *7*: 545).

and gars (Fig. 3). The body scales, lacking in only a few,[10] are thin and overlap each other in most instances, but in some they are thick and bony; the exposed surface is smooth or only finely striate except in a few where it is either granular and sculptured with a network of low ridges[11] or has fine[12] or coarse[13] prickles; in most the exposed edges are even, or nearly so, but in a few[14] they are pectinate; the exposed portion of the scale is not enamel-like in any living family.[15]

A lateral line is either present or absent, as are luminescent organs.

The swim bladder, if present, is dorsad in position[16] and is either closed or connected to the anterior part of the alimentary tract by an open duct; it is not connected to the inner ear by a chain of bonelets (Weberian ossicles). The oviducal tracts along which the ova pass to the exterior consist either of closed tubes (oviducts complete) or of membranous channels that are open above but are enclosed by longitudinal folds of the peritoneum (oviducts incomplete).[17] The inner wall of the intestine in a few has a series of circular ridge-like thickenings which suggest the spiral valve of elasmobranchs, chimaeroids, and polypteroids; however, they are probably not homologous (Cohen, *10*: 96).

The last few vertebrae are turned upward in a few (Salmonidae). If present, the lateral processes (parapophyses) that bear the pleural ribs are simply set in pits in the vertebral centra in some but are fused with the centra in others.

Nomenclature. The names Isospondyli[18] and Malacopterygii[19] have been used interchangeably as ordinal names by various authors for nearly a century. More recently the name Clupeiformes, proposed for this Order by Berg (*4*: 216, 417), has been accepted by Bertin and Arambourg, but in this series of publications the name Isospondyli is preferred, following Cope (*11*: 454, 455).

[10] Among the Alepocephalidae, Stomiatoidea, and Galaxiidae.

[11] Among freshwater osteoglossids of South America, Malaya, and Australia.

[12] In at least two species of *Argentina* (see Smitt, *50*: fig. 229).

[13] In the genus *Gonorhynchus* of the warm-temperate Indian Ocean and western Pacific. For an excellent illustration, see Cuvier and Valenciennes (*13*: pl. 568).

[14] In the genus *Brevoortia*, p. 342.

[15] The exposed surface of the scales was covered with an enamel-like substance (ganoine) in the fossil family Leptolepidae, which was abundantly represented from the Upper Triassic to the Middle Cretaceous, and in the Pholidophoridae of the Jurassic.

[16] The ventral "sole" of *Opisthoproctus*, interpreted by Trewavas as a swim bladder (*53*: 610), appears to be part of a light organ (Bertelsen, *5*: 862).

[17] The original idea (Rathke, *37*) "that the salmonoids have no oviducts and that the ova are deposited free in the abdominal cavity has been handed down to the present day in all literature pertaining to the subject" (Kendall, *24*: 190). Similarly, according to Cuvier, the ovaries in *Argentina* discharge the eggs into the abdominal cavity "comme dans les autres Salmonoides" (*14*: 410). Trewavas could trace no oviduct in a specimen of *Opisthoproctus* cleared in glycerine and caustic potash before dissection (*53*: 610, 611), nor could Beebe do so in a mature female of *Dolichopteryx* (*2*: 78). It has been reported similarly that the ova are discharged into the body cavity in the Galaxiidae, the Haplochitontidae, the Hyodontidae, and the Notopteridae. However, Kendall showed from his own dissections that the actual situation, in both the Salmonidae and the Osmeridae, is as summarized in the text above, and that the ova cannot be extruded if they be displaced in the abdominal cavity. Probably this is equally true of the other bony fishes that have been reported as lacking oviducts.

[18] Proposed in 1871 by Cope (*11*: 454–455).

[19] First proposed in 1738 by Artedi (*1*: 1), it was given its first post-Linnaean definition in 1893 by Gill (*17*: 130–131), as was Cuvier's "Malacopterygiens abdominaux" (*12*: 159), which also included the Ostariophysi. Malacopterygii was adopted by Boulenger in 1904 (*7*: 543).

The Order Isospondyli, as defined under *Characters of Living Isospondyli*, corresponds to: the Order Isospondyli of Cope;[20] the Suborder Isospondyli in part of Woodward (*54*: xxxvi; *55*: xvii); the Suborder Malacopterygii plus the Suborder Haplomi in part of Boulenger (*7*); the Suborders Clupeiformes and Esociformes of Goodrich (*25*: 386, 397); the Orders Isospondyli (excluding the Mormyriformes) and Haplomi of Regan (*38*: 77–78); the Orders Clupeiformes plus Galaxiiformes of Berg (*4*: 216, 254, 256, 417, 436, 437); the Order Isospondyli of Romer (*45*: 581, 584) plus the Suborder Esocoidea, which he referred to the Order Mesichthyes of Hay (*20*: 397); and the Order Clupeiformes of Bertin and Arambourg (*18*: 210).

The members of the Order Isospondyli include some of the most generalized of living bony fishes, and the fossil record for some of them reaches as far back in geologic time as the Lower Cretaceous (p. 15). The Order is accepted here as a matter of convenience, since the interrelationships of its included units still remain obscure.

Suborders. The heterogeneous assemblage that is grouped together in Part 5 as the Order Iniomi has been treated as a Suborder of the Isospondyli by some authors (Schultz and Stern, *47*: 233; Bertin and Arambourg, *18*: 2269) but as a separate Order by Regan (*38*: 77–78; *41*: 314), Jordan (*22*: 153), Norman (*30*: 317), Berg (*4*: 242, 256, 429, 437—as Scopeliformes), and Marshall (*26*: 305–336). In accord with present-day tendencies based on evolutionary grounds, discussed below, the Iniomi are here classed as a separate Order.

In 1929 Regan (*41*: 313, 314) set the Iniomi apart from the Isospondyli as a separate Order on the following grounds:

1a. Maxillaries (typically) forming a part of upper border of mouth; pectoral girdle with mesocoracoid element in the great majority. Isospondyli.
1b. Maxillaries not forming a part of upper border of mouth; pectoral girdle without mesocoracoid element. Iniomi.

Unfortunately, the separation between Iniomi and Isospondyli is not as clear-cut as the foregoing implies. Thus the mesocoracoid is lacking: in some of the Argentinoidea (*53*: 609, 612); in the Salangidae (Salmonoidea); in the Retropinnatidae, the systematic relationships of which remain uncertain; in the Esocoidea (Part 4), the Bathylaconoidea (*35*: 52), and the Aplochitonidae (*40*: 290), which have sometimes been grouped with the Salmonoidea but which seem to deserve the rank of a separate Suborder. Furthermore, the Iniomi share the withdrawal of the maxillary bone from the upper border of the mouth with some fishes that are isospondylous in other respects: i.e. the genus *Albula* (Albulidae), the Pterothrissidae (here rated as a separate family), *Nematalosa* (*44*: 465, fig. 127, as "*Chaetoessus*"), and the genus *Chanos*.

Such members of the Order Isospondyli as are known to occur in the western North Atlantic are distributed in Parts 3 and 4 among the Suborders Elopoidea, Clu-

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[20] The systematic position of Cope's (*11*: 454) Scyphophori (freshwater families Mormyridae—distinguished especially by the enormous cerebellum—and Gymnarchidae) remains controversial.

peoidea, Stomiatoidea (including its subdivisions Gymnophotodermi, Heterophotodermi, and Lepidophotodermi, named by Parr [*33*: 15–17; *34*: 136]), Salmonoidea, Argentinoidea,[21] Esocoidea, and Bathylaconoidea.

These Suborders correspond to: the Suborders Clupeoidei, Salmonoidei, Stomiatoidei, Opisthoproctoidei, and Esocoidei of Berg (*4*); the Suborders Clupeoidei, Salmoniformes, Opisthoproctoidea, Stomiatoidea, Gymnophotodermoidea, and Esociformes of Schultz and Stern (*47*); the Suborders Clupeoidea, Stomiatoidea, and Salmonoides, plus the Order Haplomi, of Norman (*31*); the Suborders Elopoidei, Clupeoidei, Salmonoidei, Opisthoproctoidei, Alepocephaloidei, Stomiatoidei, Bathylaconoidei, and Esocoidei of Bertin and Arambourg (*18*: 2211); and the Suborders Elopina, Albulina, Esocina, Clupeina, Chanina, Gonorhynchina, Salmonina, Opisthoproctina, and Stomiatina of Matsubara (*27*: 178–227).

One major area of uncertainty as to the relationships among the groups of isospondylous fishes centers around the position of the Elopidae, Albulidae, and Pterothrissidae. Indeed, within recent years it has been questioned whether *Elops* is even of the same lineage as other living teleosts. Thus Saint Seine has derived it from the Halecostomi (*46*: 297), a group known otherwise from fossils only (*18*: 2195–2201), and Nybelin has emphasized the holostean nature of certain characteristics of *Elops*,[22] embodying a similar point of view.

Both the Elopidae and the Albulidae, to be sure, have characteristics that are considered archaic by both palaeontologists and neozoologists alike; among these are: the retention of the gular plate and of the numerous branchiostegal rays in *Elops* and *Tarpon*; the arrangement of the mucous canals on the top of the snout in *Elops* (*32*: 454, fig. 1); the presence of close-set teeth on the parasphenoid bone in the roof of the mouth (Elopidae, Albulidae, and Pterothrissidae); the presence of roofed post-temporal fossae; and the persistence in *Albula*, *Pterothrissus*, and *Megalops* (but not in *Elops*) of two rows of valves in the arterial cone of the heart.[23]

On the other hand, the elopids and the albulids differ widely and conspicuously from living members of *Lepisosteus* and *Amia* in the narrow rod-like nature of their branchiostegal rays and in the nature of the skeleton of their caudal fin; this latter difference is a conspicuous one, externally, for while the rear boundary of the fleshy base of the caudal is symmetrical relative to the main longitudinal axis of the trunk in the elopids and albulids, it slopes upward-rearward in *Lepisosteus* (Fig. 3, p. 16) and *Amia*. Further features worth mention are: (1) the invariable presence in the elopoids of a median supraoccipital bone, which, to a greater or lesser degree, is involved in the roof-complex of the skull; (2) the absence of coronoid teeth in the mandible; (3) a one-to-one relationship between the principal caudal rays and hypurals of *Amia* and *Lepisosteus* compared with the considerable consolidation of the hypural elements in the elopids; (4) the absence in elopids of the rigid attachment of the premaxillaries to the skull, which

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[21] The reason for using this name rather than Opisthoproctoidea is given in Suborder Argentinoidea, Part 4.

[22] "Les Elopidae m'apparaissent etre des Holosteens aussi bien qu'*Amia* ou *Lepidosteus*" (*32*: 458).

[23] See Senior for account of the cone for *Tarpon* (*48*: 146–151), for *Elops* (*48*: 150), and for a summary (*49*: 83–84).

characterizes the living holosteans; and (5) a well-developed articulation with the autopalatines in elopids. Indeed, in the development of the whole upper jaw mechanism, the elopoids are considerably in advance of the holosteans.

However, though we accept the traditional view that the elopids and albulids (with *Pterothrissus*) do belong among the Isospondyli, there is much uncertainty as to their disposition within that Order. For example, Jordan and Evermann (*23*: 407), followed by Norman (*31*: 63), rated them as families within the Suborder Clupeoidea; Berg (*4*: 221, 222; 419, 420) defined them as superfamilies (Elopoidae and Albuloidae), each to include two families; Fowler (*16*: 151) and Poll (*36*: 8) rated them as families of Isospondyli (Clupeiformes of Poll) without the intervention of Suborders. However, as early as 1893, Gill (*17*: 127–128) made them the basis of a separate Suborder, Elopoidea, in which he was followed by Bertin and Arambourg (*18*: 2211), who stressed in particular the primitive nature of their caudal fin skeleton.[24] Jordan (*22*: 117–118), proceeding a step further, proposed the Suborder Elopoidea for the elopids and the Suborder Albuloidei for the albulids as contrasted with the clupeoids and with other Suborders of Isospondyli; Matsubara[25] has also accepted this arrangement.

Exclusion of the elopids and albulids from the clupeoids clearly seems demanded, for among living fishes they appear to stand much lower on the evolutionary tree than any other teleosts that are at all well known. But it still remains an open question whether the features in which the elopids and albulids agree, balanced against those in which they differ, are better represented by placing them in two separate Suborders or by uniting them in one, as is done here.

The isospondylids as here defined include the ladyfishes or bigeye herrings, the tarpons, the bonefishes, the true herrings, the anchovies, and the salmons, all of which have been familiar for generations to seaside dwellers in general in one part of the world or another. They also include such of the pikes as enter brackish or salt water, and an assemblage of oceanic fishes, many of which have luminescent organs and are bizarre in appearance; the latter are seldom seen by ordinary seafarers, commercial fishermen, or anglers, and little is known about their mode of life.

Key to Suborders. Although the general characteristics are now tolerably well known for the elopoid, herring-like, salmon-like, and pike-like fishes, we still have so much to learn about the internal anatomy of the less familiar groups of Isospondyli that their natural affinities remain obscure in many respects. Areas of continuing uncertainty are, for example: the relative weights to be accorded one character or another from the evolutionary standpoint; the breadth of coverage to be allotted to the herring-like fishes and the salmon-like fishes; and the disposition to be made of various outlying families such as the Bathylaconidae (Part 4), which do not readily fit in any of the major subdivisions that are recognized generally. Furthermore, Suborders

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[24] For accounts of the caudal fin skeletons of *Elops*, *Albula*, and *Megalops*, see Regan (*39*: 355, 356, fig. 1); see Hollister (*21*: 260–276) for *Elops* and *Albula*.

[25] Elopina and Albulina, Suborders of Order Clupeida (equivalent to Isospondyli) (*27*: 180–182).

that are easily separable typically may intergrade with one another marginally. For instance, the presence of parietal bones among the Clupeoidea and not among the Stomiatoidea has been invoked as an alternative between these two Suborders, but this is not strictly so, since some stomiatoids do have parietals (see Regan and Trewavas, *43*: figs. 6, 9, 10; Günther and Deckert, *19*: 244). Neither is the arrangement of the photophores on the sides in definite longitudinal rows reliably diagnostic for the Stomiatoidea, since they are not so in one species of *Neonesthes*, while in one other species the linear arrangement is to be recognized only with difficulty,[26] as is true of some species of *Astronesthes* as well.[27] And Mrs. Marion Grey contributes the information that some species of *Cyclothone*, *Gonostoma*, and *Malacosteus* have no photophores at all on the sides of the body.

Under these circumstances the construction of a satisfactory key to the Suborders of Isospondyli that would withstand the test of time is not to be hoped for at present.

Tentative Key to Suborders of Isospondyli of the Western North Atlantic

1a. Parasphenoid bone on roof of mouth with low close-set teeth; larval stage ribbon-shaped (leptocephalus-like). Elopoidea, Part 3, p. 107.

1b. Parasphenoid bone without teeth; larval stage in most not ribbon-shaped.[28]

  2a. Premaxillary bones minute; maxillaries forming almost entire length of upper jaw; branchiostegal rays plate-like, the edge of the uppermost attached to lower margin of subopercular bone and thus taking part in formation of gill cover. Bathylaconoidea, Part 4.

  2b. Premaxillary bones well developed; branchiostegal rays not plate-like; the edge of upper branchiostegal ray not joining subopercular and interopercular bones and thus not taking part in formation of gill cover.

    3a. Luminescent organs (photophores) absent in most; never present on head, but present on eye-tube in a few (*Dolichopteryx* of Argentinoidea); if present on sides of body they are in nonlinear arrangement except along base of anal fin (*Binghamichthys* of Alepocephalidae); some with a tubular papilla on each shoulder that connects with a voluminous sac beneath the skin (Searsiidae).

    4a. No adipose fin between rayed dorsal fin and caudal.

      5a. Snout noticeably flattened dorsoventrally (depressed), in duck-billed form; teeth along rear part of lower jaw large, formidable, conspicuous; premaxillary bones far apart in front; mesethmoid (proethmoid) bone paired. Esocoidea, Part 4.

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[26] Information contributed by Robert H. Gibbs.

[27] According to Zugmayer (*56*: 4), the photophores are distinguishable only with difficulty in *Astronesthes niger* (as *A. myriaster*), but Regan and Trewavas (*42*: 20, fig. 12) picture them clearly for the type specimen of that species.

[28] Certain of the Stomiatoidea have ribbon-shaped larvae; Part 4.

5b. Snout not flattened dorsoventrally, its dorsal contour convex; teeth along rear part of lower jaw small and inconspicuous; premaxillary bones close together in front; mesethmoid (proethmoid) bone not paired. Clupeoidea, Part 3, p. 148.

4b. Adipose fin between rayed dorsal fin and caudal present in most, but lacking in a few (see 6b).

6a. Swim bladder connected to oesophagus throughout life by an open pneumatic duct (physostomic); premaxillary bones well developed; jaws with well developed teeth except in the Coregonidae, which are either toothless or have minute teeth; eyes of ordinary type; oviducts incomplete (p. 455), so far as is known. Salmonoidea, Part 3, p. 455.

6b. Swim bladder not connected to oesophagus during late stages of growth (physoclystic);[29] premaxillary bones small or lacking; jaws toothless; eyes tubular in some but not in others; oviducts incomplete in some,[30] perhaps complete in others. Argentinoidea,[31] Part 4.

3b. Luminescent organs (photophores) present on head, on body, on tail sectors, or on all three; their arrangement in longitudinal rows on sides extending anterior to anus as well as along base of anal fin; no tubular papilla on shoulder. Stomiatoidea (including Suborders Gymnophotodermi and Lepidophotodermi[32]), Part 4.

Families. The Isospondyli plus the Iniomi include about 55 families on a worldwide basis, about 45 of which are known to occur in the western North Atlantic. At first glance, this may seem an appalling number among which to choose when one has to run down a given specimen to its proper family, the more so because there is no one conspicuous character or combination of characters visible from the outside on which anyone but a professional taxonomist can rely to tell him whether his fish belongs among the Isospondyli or among the Iniomi. The task, however, is not as difficult as one might expect, for nearly all of the western Atlantic families (or subdivisions of families) of the two Orders combined are separable, one from another, by features that are visible from the outside, that are susceptible of rather precise definition, and that are mutually exclusive, or nearly so.

However, in numerous instances a family, because of the diverse characters of its genera and species, has been split into two or more parts. Hence the same family

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[29] Cuvier and Valenciennes seem to have been the first to record this fact for *Argentina* (*14*: 411). Trewavas' interpretation of the ventral "sole" of *Opisthoproctus* as a swim bladder is now known to have been erroneous (*53*: 610).

[30] This is the case for *Argentina*, *Opisthoproctus*, and *Dolichopteryx* (Part 4). For *Macropinna*, however, Chapman reported that a "fine duct" extends from the posterior end of each ovary, but he could not determine whether these ducts open into the urinary bladder or into the rectum (*8*: 293).

[31] For a detailed comparison of the Argentinoidea and Salmonoidea, see Argentinoidea, Part 4.

[32] Proposed by Parr, *33*: 15–17.

may be referred to in different parts of the same key or in one or more of the other keys. For example, such of the Bathypteroidae as have no adipose dorsal fin are found in Key A while those with an adipose fin are found in Key B.

General Key to Families of Isospondyli, Iniomi, and Giganturoidei of the Western North Atlantic; Adolescents and Adults[33]

1 a. Eyes (if any) of the usual sort, i.e. not at tips of slender stalks or with pupil above center, and not capable of being directed upward.
  2 a. No luminescent organs (photophores) either on sides of body, or on head.
    3 a. No adipose fin between rayed dorsal fin and caudal. Key A, below.
    3 b. Adipose fin present between rayed dorsal and caudal. Key B, p. 99.
  2 b. Luminescent organs (photophores) present on head, or on body, or on both; or with eyes on top of head. Key C, p. 101.
1 b. Eyes at tips of slender stalks, or with pupil above the center and capable of being directed upward. Key D, p. 103.

KEY A. NO DORSAL ADIPOSE FIN; NO PHOTOPHORES ON SIDES OF HEAD OR BODY.

1 a. Rays in posterior half of dorsal and in rearmost part of anal much longer than those in anterior part of these fins. Macristiidae.[34]
1 b. Not more than one dorsal ray (if any) and no anal ray much longer than the others.
  2 a. Bony (gular) plate present in chin region between branches of lower jaw. Elopidae, Part 3, p. 111.
  2 b. No bony (gular) plate in chin region.
    3 a. Upper jaw reaching rearward far beyond eye.
      4 a. Snout overhanging mouth noticeably. Engraulidae (western Atlantic saltwater species), Part 3, p. 152.
      4 b. Snout not overhanging mouth.
        5 a. Pectoral fin longer than head; either uppermost pectoral rays or outermost pelvic rays much longer than the others; lower lobe of caudal much longer than upper in some. Bathypteroidae in part, Part 5.[35]
        5 b. Pectoral fin shorter than head; none of pectoral or pelvic rays prolonged; lower lobe of caudal little, if any, longer than upper.
          6 a. A fleshy ridge present along back anterior to dorsal fin. Alepocephalidae in part (*Anomalopterus*), Part 3, p. 250.[36]
          6 b. No fleshy ridge on back anterior to dorsal fin.

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[33] For larval stages of a few, see Key D, 1 b. In this key no attempt is made to present the author's views as to phylogenetic relationship.

[34] Occur in the vicinity of the Azores, hence may be taken sometime in the western Atlantic.

[35] See Key B, 4 a for those with adipose fin.

[36] See also Key A, 11 a; Key C, 15 a.

7a. Eyes minute, about same diameter as nostril.
Ipnopidae in part (*Bathymicrops*, *Bathytyphlops*), Part 5.[37]

7b. Eyes well developed, much larger than nostril.
Bathysauridae in part, Part 5.[38]

3b. Upper jaw reaching rearward little (if any) past eye, and ending considerably short of rear edge of eye in most.

8a. Snout overhanging mouth; parasphenoid bone rearward along mid-roof of mouth thickly set with low teeth.

9a. Base of dorsal occupying only about 24–25% of distance between gill openings and origin of caudal. Albulidae, Part 3, p. 132.

9b. Base of dorsal occupying about 80% or more of distance between gill openings and origin of caudal. Pterothrissidae.[39]

8b. Snout not overhanging mouth; parasphenoid bone without teeth.

10a. Rear end of base of dorsal fin separated from upper origin of caudal by a distance much shorter than head.

11a. Upper jaw not reaching rearward beyond front of eye; teeth inconspicuous.
Alepocephalidae in part, Part 3, p. 250.[40]

11b. Upper jaw reaching rearward about as far as rear edge of eye; teeth along rear half of lower jaw large and formidable. Esocidae, Part 4.

10b. Rear end of base of dorsal fin separated from upper origin of caudal by a distance at least as long as head, and longer in most.

12a. Midline of abdomen in front of anal fin armed with a double series of stiff, pointed scales (scutes).
Clupeidae in part (Clupeinae, pp. 274–411; Pristigasterinae, pp. 411–438; Chirocentrinae, pp. 438–442; Dorosomatinae, pp. 443–451), Part 3, Key pp. 259–262.[41]

12b. Midline of abdomen in front of anal fin rounded; not armed with a double series of scutes.

13a. Origin of dorsal fin considerably anterior to mid-length of trunk; pelvics posterior to dorsal; maximum depth of trunk equal to about 30% of distance from gill opening to base of caudal; head about 25% as long as distance from snout to origin of caudal. Clupeidae in part (Dussumierinae, pp. 262–274), Part 3, Key pp. 259–262.[42]

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[37] See also Key C, 1a.

[38] For those with adipose fin, see Key B, 13b.

[39] Sometimes included among the Albulidae. It has not yet been reported for the western side of the Atlantic, but it may be expected there because it is plentiful at moderate depths along the coast of tropical West Africa. For details and description, see Poll (*36*: 16–25, 28, fig. 9).

[40] See also Key A, 6a; Key C, 15a.

[41] See also Key A, 13a.

[42] See also Key A, 12a.

13b. Origin of dorsal fin considerably posterior to mid-length of trunk; pelvics below or anterior to dorsal; maximum depth of trunk only about 15% as great as distance from gill opening to base of caudal; head between 17–20% as long as distance from snout to base of caudal.
Argentinidae in part (Microstomatinae), Part 4.[43]

KEY B. A DORSAL ADIPOSE FIN PRESENT CLOSE IN FRONT OF CAUDAL; NO PHOTOPHORES ON SIDES OF HEAD OR BODY.

1a. Well-developed rayed dorsal fin and adipose dorsal fin present.
  2a. A narrow, posteriorly-pointing fleshy lobe close above base of pelvic fin on each side.
    3a. Teeth in jaws well developed, easily felt; 19 or more scales in a transverse series from origin of dorsal to lateral line. Salmonidae, Part 3, p. 457.
    3b. Teeth in jaws minute, if present; not more than 13 scales in a transverse series from origin of dorsal to lateral line. Coregonidae, Part 3, p. 547.
  2b. No fleshy lobe on side above base of pelvic fin.
    4a. Some of upper pectoral rays longer than others and separate from lower part of fin, thus forming a separate division.
    Bathypteroidae in part, Part 5.[44]
    4b. Pectorals not divided into an upper and lower division.
      5a. Dorsal high, sail-like, its base extending from close behind gill openings nearly to adipose fin. Alepisauridae, Part 5.
      5b. Dorsal not high and sail-like, its base occupying not more than about half the distance between level of gill openings and adipose fin.
        6a. Upper jaw not reaching rearward as far as front of eye.
          7a. Mouth at least twice as long as eye; eye not more than about 17% of hl (less than this in most); anal base at least 1.5 times longer than base of dorsal; teeth well developed, long and fang-like in some. Paralepididae, Part 5.
          7b. Mouth not longer than eye; eye 27–40% of hl; anal base not appreciably longer than dorsal base; teeth minute, if detectable at all.
            8a. Lateral-line scales not extending out onto caudal fin; adipose dorsal anterior to rear end of base of anal fin.
              9a. Gill membranes separate; branchiostegal rays 5 or 6. Argentinidae in part (Argentininae), Part 4.[45]

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[43] See also Key B, 8b and 9a; Key D, 4b.

[44] For those without dorsal adipose fin, see Key A, 5a.

[45] See also Key D, 4b.

9b. Gill membranes broadly united; branchiostegal rays 2. Bathylagidae, Part 4.[46]

8b. Lateral-line scales extending out onto caudal fin; adipose dorsal fin over or posterior to rear end of base of anal fin. Argentinidae in part (*Nansenia*, Microstomatinae in part), Part 4.[47]

6b. Rear end of upper jaw reaching beyond front of eye.

10a. Some of jaw teeth large, fang-like, conspicuous.

11a. Eye about 33% or more of hl; origin of anal posterior to origin of dorsal by a distance less than 50% of hl. Omosudidae, Part 5.

11b. Eye only about 15% of hl; origin of anal posterior to origin of dorsal by a distance nearly equal to hl. Evermannellidae in part, Part 5.[48]

10b. None of jaw teeth much enlarged or fang-like.

12a. Upper jaw extending rearward past eye for a distance at least twice the length of eye.[49]

13a. Rear end of base of dorsal anterior to origin of anal by a distance at least 50% of hl. Synodontidae, Part 5.

13b. Rear end of base of dorsal only slightly anterior to origin of anal. Bathysauridae in part, Part 5.[50]

12b. Upper jaw extending rearward past eye for a distance no longer than length of eye, and relatively shorter than this in most.

14a. Dorsal profile of head deeply concave close in front of eye; insertion of pelvics anterior to origin of rayed dorsal by a distance nearly or quite as long as eye. Scopelosauridae, Part 5.

14b. Dorsal profile of head close in front of eyes only weakly concave at most; insertion of pelvics under or posterior to origin of rayed dorsal.

15a. Upper jaw extending rearward beyond eye for a distance about as long as eye; dorsal profile of head weakly concave; body deepest about at gill opening. Neoscopelidae in part (*Scopelengys*), Part 5.[51]

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[46] See also Key A, 13b; Key B, 8b; Key D, 4b.

[47] See also Key D, 1b.

[48] For species having eyes with pupil above center and capable of being directed upward, see Key D, 5b.

[49] In small specimens of some species of *Trachinocephalus* the upper jaw does not extend rearward as far as this.

[50] For those without adipose fin, see Key A, 7b.

[51] For those with photophores, see Key C, 14b.

15b. Upper jaw not extending rearward appreciably beyond eye; dorsal profile of head straight to weakly convex; body deepest about at dorsal fin.

  16a. Origin of rayed dorsal nearer to gill opening than to adipose dorsal by a distance of slightly less to considerably more than head length.

    17a. Pupil round; entire posterior edge of opercular flap formed by subopercular bone.
    Aulopidae, Part 5.

    17b. Pupil keyhole-shaped; posterior edge of opercular flap formed by opercle above, and by subopercle below.
    Chlorophthalmidae, Part 5.

  16b. Origin of rayed dorsal almost or quite as near to adipose dorsal as to gill opening, and much nearer to adipose dorsal in some.
  Osmeridae, Part 3, p. 553.

1b. No rayed dorsal fin; only an adipose dorsal fin. Anotopteridae, Part 5.

KEY C. PHOTOPHORES PRESENT ON HEAD, OR ON BODY, OR ON BOTH; OR WITH EYES ON TOP OF HEAD.

1a. Eyes without lenses, covered by frontal bones, and consisting of large and flat plates that occupy more than half of dorsal surface of head.
Ipnopidae in part, Part 5.[52]

1b. Eyes with lenses, not covered by the frontal bones and, if dorsally directed, occupying less than half of dorsal surface of head.

  2a. One or more barbels on chin, usually long and fleshy but sometimes very small.

    3a. Dorsal fin mostly or wholly anterior to anal, its origin near midlength of trunk.

      4a. Dorsal base extending behind pelvics, its origin behind or only slightly before pelvic base; first dorsal ray not prolonged.
      Astronesthidae, Part 4.

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[52] For those without these organs, see Key A, 7a.

4b. Dorsal base completely in front of pelvic bases; first dorsal ray much prolonged. Chauliodontidae, specimens up to about 50 mm long,[53] Part 4.

3b. Dorsal fin opposite anal, its origin far posterior to midlength of trunk.

5a. Sides of body with scales, or marked by hexagonal pigment patterns resembling scales. Stomiatidae, Part 4.

5b. Sides of body scaleless, either unmarked or with parallel vertical lines, never with hexagonal areas.

6a. Dorsal fin with more than 50 rays and beginning well before middle of body; base of each dorsal and anal ray flanked on either side by a sharp bony spur that penetrates the skin; length of trunk posterior to head more than 20 times greater than greatest depth of body. Idiacanthidae in part (adults), Part 4.[54]

6b. Dorsal fin with 30 rays or less, its origin well behind middle of body; no bony spurs flanking bases of dorsal and anal rays; length of trunk posterior to head not more than 15 times greater than greatest depth of body.

7a. Mouth with a membranous floor; isthmus attached to mandibular symphysis; dorsal corner of gill opening behind posterior margin of eye. Melanostomiatidae, Part 4.

7b. Mouth without a floor; isthmus attached to mandibular symphysis by a muscular cord; dorsal corner of gill opening above or in advance of posterior margin of eye. Malacosteidae in part, Part 4.[55]

2b. Chin without fleshy barbel.

8a. Each shoulder with a tubular papilla open at the tip and connected to a voluminous sac beneath skin. Searsiidae, Part 3, p. 254.

8b. Shoulders without tubular papilla or sac beneath skin.

9a. Dorsal fin preceded by the protruding, spine-like tips of from one to several of the neural processes of a like number of vertebrae. Sternoptychidae, Part 4.

9b. Dorsal fin not preceded by the protruding spine-like tips of the neural processes of any vertebrae.

10a. Branchiostegal rays plate-like, conspicuously exposed, the uppermost connected to subopercular and interopercular bones. Bathylaconidae, Part 4.

10b. Branchiostegal rays not plate-like, the uppermost not connected to subopercular and interopercular bones.

11a. Dorsal adipose fin present.

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[53] For larger specimens, see Key C, 12a.

[54] See also Key D, 1b.

[55] See also Key C, 15b.

12a. Teeth enormous, conspicuous even when mouth is closed; first dorsal ray greatly prolonged.
Chauliodontidae in part, Part 4.[56]

12b. Teeth small to moderate in size; first dorsal ray not greatly prolonged.

13a. Upper edge of mouth formed by both maxillaries and premaxillaries; upper jaw teeth extending outside lower jaw when mouth is closed; photophores generally present on branchiostegal membrane.
Gonostomatidae in part, Part 4.[57]

13b. Upper edge of mouth formed by premaxillaries only; upper jaw teeth contained within mouth; no photophores on branchiostegal membranes.

14a. Distance from pelvics to anal origin not more than twice the length of eye.
Myctophidae in part, Part 5.[58]

14b. Distance from pelvics to anal origin at least 3 times longer than eye.
Neoscopelidae in part, Part 5.[59]

11b. No dorsal adipose fin.

15a. Body with at least 20 longitudinal rows of scales; mouth not widely distensible; gape not extending past eye; teeth small.
Alepocephalidae in part, Part 3, p. 250.[60]

15b. Body without scales; mouth enormously distensible; gape extending beyond eye by a distance 3 or more times the length of eye; teeth large and conspicuous. Malacosteidae in part, Part 4.[61]

KEY D. EYES EITHER TUBULAR (TELEOSCOPIC), OR WITH PUPIL ABOVE CENTER AND CAPABLE OF BEING DIRECTED UPWARD, OR WITH EYE SITUATED AT THE TIP OF A SLENDER STALK.

1a. Eyes not at tips of slender stalks.

2a. Lower lobe of caudal much longer than upper lobe; gill openings minute; base of pectorals wholly above gill openings. Giganturidae, Part 4.

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56. See also Key C, 4b.
57. Exceptions: in *Ichthyococcus* the upper jaw is formed by the maxillaries alone, and in *Triplophos* it is almost entirely bordered by the premaxillaries.
58. See also Key D, 1b.
59. See also Key B, 15a.
60. See also Key A, 6a; Key A, 11a.
61. See also Key C, 7b.

2b. Lower lobe of caudal about as long as upper lobe; gill openings broad; base of pectorals not wholly above gill openings.
  3a. Upper jaw falling far short of eye; teeth minute, if detectable at all.
    4a. Either an adipose fin between rayed dorsal and caudal, or a dome-shaped luminescent organ on eye tube. Opisthoproctidae, Part 4.
    4b. No adipose fin, and no luminescent organ on eye tube.
    Argentinidae in part (*Xenophthalmichthys*, Microstomatinae in part), Part 4.[62]
  3b. Upper jaw reaching rearward beyond front of eye; teeth fang-like, conspicuous.
    5a. Body strongly compressed sidewise, covered with scales; pectorals with 19–21 rays, their line of insertion oblique, wholly above articulation of lower jaw with skull (quadrate bone).
    Scopelarchidae, Part 5.
    5b. Body not much compressed, without scales; pectorals with only 12 rays, their line of insertion nearly horizontal, close to ventral outline of body, entirely below articulation of lower jaw.
    Evermannellidae in part, Part 5.[63]

1b. Eyes at tips of slender stalks.
  Stalk-eyed larval stages of Bathylagidae in part (Part 4);[64] of Idiacanthidae in part (Part 4);[65] of Myctophidae in part (Part 5);[66] and probably others of unknown parentage.

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[62] See also Key A, 13b; Key B, 8b; and Key B, 9a.

[63] See also Key B, 11b.

[64] See also Key B, 9b.

[65] See also Key C, 6a.

[66] See also Key C, 14a.

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Suborder Elopoidea[1]

COMPOSITE AUTHORSHIP

Characters and Key to Families

HENRY B. BIGELOW[2]
Museum of Comparative Zoology
Harvard University

Characters. Silvery, herring-like isospondylous fishes with the Parasphenoid bone on posterior part of roof of mouth thickly set with low Teeth,[3] extending nearly to posterior end of basioccipital or beyond, without lateral processes for articulation with the mesopterygoid. Temporal foramina present. Parapophyses not fused with vertebral centra, but simply wedged in pits. Proethmoids not paired (see Esocoidea, Part 4). Pectoral girdle with mesocoracoid element. A Bony (gular) plate in chin region between branches of lower jaw in some (Elopidae, including the Megalopidae of Matsubara) but not in others (Albulidae, Pterothrissidae). Luminescent organs absent. Adipose fin lacking between rayed dorsal and caudal. Pelvic fins abdominal, standing from about 30% to about 45% of distance rearward from gill slit toward lower origin of caudal. Anal fin originating from about 50% to about 68% of distance between pelvics and caudal. Caudal deeply forked. Rearmost dorsal ray greatly prolonged in some (*Tarpon*, *Megalops*); the Rearmost anal ray prolonged as well in a few (*Dixonina*); none of the other fin rays prolonged. A single large, narrow, fleshy Axillary scale above pectorals and pelvics. Scales thin, cycloid. Eyes circular, of the ordinary type. Upper jaw extending rearward far beyond eye in most,

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1. With families Elopidae and Albulidae by Samuel F. Hildebrand, pp. 111 and 132, respectively.
2. The assistance of Dr. W. A. Gosline is gratefully acknowledged.
3. Ridewood, who described their skulls in detail, has recorded this peculiar dentition (*3*: 39, for *Elops*; 44, for *Megalops*; 40, for *Albula*; 53, for *Pterothrissus*). These observations have been verified for *Pterothrissus* by Poll (*2*: 222, fig. 7), and for *Tarpon* by original examination.

and tip of LOWER JAW projecting as far as tip of upper jaw or slightly beyond it; upper jaw in others (*Albula*, *Dixonina*, *Pterothrissus*) falling far short of front of eye, and tip of snout overhanging mouth. MAXILLARIES forming part of margin of upper jaw in most but excluded from gape in a few (*Albula*, *Pterothrissus*). BRANCHIOSTEGAL RAYS slender, rod-like, not forming a part of opercular system. One to three lateral sensory CANAL-BEARING BONELETS on either side of snout in front of lacrimals. Some with two rows of valves in cone of HEART (*Albula*, *Pterothrissus*, and *Megalops*, but not *Elops*).

There is a ribbon-like (leptocephalus-like) larval stage.

Families. Three families are recognized here within the Suborder as defined above: Elopidae, Albulidae, and Pterothrissidae, the last of which is extralimital and is included only in the Key to Families.

Fossil History. The Elopidae are known from as far back in geologic time as the Lower Cretaceous, the Albulidae (including the Pterothrissidae) from as far back as the Upper Cretaceous.

Key to Families

1a. A bony (gular) plate in chin region between branches of lower jaw; upper jaw extending rearward considerably beyond eye; tip of lower jaw projecting at least as far as tip of upper jaw, or a little farther; 23–35 branchiostegal rays.
Elopidae (including Megalopidae of Matsubara), p. 111.

1b. No gular plate; upper jaw falling short of front of eye; tip of snout overhanging mouth; only about 11–15 branchiostegals.

  2a. Base of dorsal occupying only about 25% of distance between gill opening and base of caudal. Albulidae, p. 132.

  2b. Base of dorsal occupying about 80% of distance between gill opening and base of caudal. Pterothrissidae.
  Plentiful off tropical West Africa in depths of 100–250 m and reported down to 500 m;[4] also Japan.

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[4] According to Cadenat (*1*: 365) and Poll (*2*: 23). Not yet reported for the western Atlantic but may be expected there.

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Editorial Comments on the Hildebrand Manuscripts

The following manuscripts by Dr. Hildebrand had not been worked on by him for some years prior to his death in 1949. The Sears Foundation is therefore grateful to Dr. George S. Myers for having undertaken the task of bringing some manuscripts up-to-date in such ways as he thought necessary, and to the U.S. Fish and Wildlife Service for having made this possible through the kind offices of Dr. L. A. Walford. Dr. Myer's work, which was both time-consuming and extensive, was confined principally to the insertion of recently described genera and species, the rewriting of certain keys, and research on the classification or nomenclature of certain genera (notably *Pristigaster* and *Ilisha*) which required changes in the names originally used by Dr. Hildebrand. Revisions that departed radically from what he believed Dr. Hildebrand would have included have been inserted as initialed footnotes.

Some years ago Dr. John Tee-Van, because of the pressure of administrative duties at the New York Zoological Society, was no longer able to continue as Editor-in-Chief; Dr. Bigelow was subsequently chosen by the Editorial Board as his successor. Upon receipt of the Hildebrand manuscripts from Dr. Myers, Dr. Bigelow made extensive revisions and additions in many of the accounts, mainly in the sections dealing with life history. Thus Dr. Bigelow added much information to that originally contributed by Dr. Hildebrand; his major revisions occur primarily in the sections dealing with the Elopidae (p. 111), Albulidae (p. 132), and Clupeidae (p. 257). The taxonomy remains essentially as it was written by Dr. Hildebrand or revised by Dr. Myers, excepting minor changes for conformance with general format. The value of Dr. Bigelow's contributions to the Hildebrand papers, and indeed to Part 3 in many other respects as well, can be measured only by the usefulness of this volume to those who will have occasion to refer to it. I have made such emendations as seemed desirable for publication.

Explanations of Dr. Hildebrand's procedure of measuring and counting are given on pages 154, 258, 343. Dr. Hildebrand's taxonomic accounts are as complete as the material and original sources of information permitted. In most instances they are based upon his study of extensive material available to him at the U.S. National Museum and elsewhere, and perhaps equally important, upon his broad and extensive knowledge acquired over the years from firsthand observations in both field and laboratory. Whether one agrees or disagrees with his treatment of relationships and such, there can be no question of the care and meticulousness of his basic work.—
Y. H. Olsen.

Family Elopidae[1]

SAMUEL F. HILDEBRAND[2]

Characters. BODY slender, more or less compressed laterally; belly rounded; ordinary scales covering median line. EYE large, with adipose tissue in large examples. MOUTH large, terminal, or superior. MAXILLARIES large, in about three pieces, extending far beyond eye in adults. PREMAXILLARIES not protractile. LOWER JAW with an elongate bony plate between its branches. TEETH all small, often bluntly villiform; teeth present on jaws, vomer, palatines, pterygoids, tongue, and basibranchials. BRANCHIOSTEGALS about 23–35. GILL MEMBRANES separate, free from isthmus. OPERCULAR BONES with membranous borders. GILL RAKERS moderately long. Last several segments of SPINAL COLUMN directed upward toward base of upper lobe of caudal. LATERAL LINE present. SCALES large or small, with membranous borders; missing on head; the median row in front of dorsal neither enlarged nor modified. DORSAL fin over or somewhat behind pelvics. CAUDAL forked. PECTORALS and PELVICS similar, each with a rather long axillary scale.

Remarks. The members of this family are characterized by the presence of the bony gular plate between the arms of the lower jaw, the numerous branchiostegals (23–35), and the large terminal or superior mouth.

The genera *Tarpon* and *Elops* (pp. 112, 123) sometimes have been assigned to two families, Megalopidae and Elopidae. However, the two genera agree in so many seemingly basic characters—the gular plate, numerous branchiostegals, the dentition, the large maxillaries, and the primitive character of the caudal skeleton—that it seems desirable to treat them as one family.

The members of the Elopidae generally are considered to be among the most archaic of existing teleosts. Their antiquity, particularly as indicated by their skulls, has been fully discussed (ftn. 3).

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[1] Edited and emended by George S. Myers, Henry B. Bigelow, and Yngve H. Olsen.

[2] August 15, 1883–March 16, 1949.

The young pass through a leptocephalus stage, similar to that of the eels.

Range. The members of this family are widely distributed in the warmer seas.

Key to Western Atlantic Genera

1a. Body moderately deep, rather strongly compressed laterally; mouth superior, with tip of mandible entering dorsal profile; last ray of dorsal and anal produced, filamentous; scales large, about 41–48 in a lateral series; anal with about 22–25 rays. *Tarpon* Jordan and Evermann 1896, below.

1b. Body very slender, not greatly compressed laterally; mouth terminal or nearly so; last ray of dorsal and anal not produced into a filament; scales small, generally more than 100 in a lateral series in American species; anal with fewer than 20 rays. *Elops* Linnaeus 1766, p. 123.

Genus *Tarpon* Jordan and Evermann 1896

Tarpon

Tarpon Jordan and Evermann, Bull. U.S. nat. Mus., 47 (*1*), 1896: 409; type species by original designation, *Megalops atlanticus* Cuvier and Valenciennes, Hist. Nat. Poiss., *19*, 1846: 398.

Generic Synonyms:

Clupea Bloch, Naturg. ausland. Fische, Pt. 9, 1794: 32; in part, for *C. cyprinoides* Bloch; Shaw, Genl. Zool., 5 (1), 1804: 173, for *C. gigantea* Shaw.

Megalops Lacépède, Hist. Nat. Poiss., 5, 1803: 289; in part, for *M. giganteus* Voigt *in* Cuvier, Das Thierreich (German transl.), *2*, 1832: 423.

Characters.[3] Body oblong, rather strongly compressed. Vertebrae about 55. Pseudobranchiae undeveloped. Branchiostegals about 23. Mouth quite oblique, superior, with prominently projecting mandible. Lateral line decurved, with branched tubes. Scales large, not especially primitive, their characters similar to those of *Elops* (cf. Cockerell, *17*: 122); scales extending somewhat onto base of anal and caudal but not onto dorsal. Dorsal fin high anteriorly, its last ray produced and filamentous. Anal similar to dorsal but longer, its last ray produced in large examples, its origin not far behind dorsal base. Pelvics inserted well in advance of dorsal fin. Last several Vertebrae clearly out of line with main axis, being directed toward the tip of upper lobe of caudal. Air bladder large and opening into gullet; within bladder a considerable amount of cellular, lung-like tissue; two large and two small strands adhering to bladder wall (bladder serving somewhat as an air-breathing organ, much as in gars [pp. 64, 67]; for description and figures of the modified bladder, see Babcock, *1* [1936]: 50). Alimentary canal much shorter than body; the stomach large, reaching far back

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[3] The skull has been fully described and figured by Gregory, who regarded it as a little less primitive than that of *Elops* (*30*: 137–142, figs. 31–33). The characters of the tail of *Tarpon* and related genera have been described by Regan (*59*: 354), and in more detail by Hollister (*39*: 264).

into abdominal cavity as a sort of blind sac, the two orifices rather close together. Pyloric caeca numerous, short and branched, held together by connective tissue.

Remarks. This genus is close to *Megalops* Lacépède, the oxeye herring represented by *M. cyprinoides* of the Indian Ocean and adjacent Pacific, but it differs from *Megalops* mainly in the more anterior position of the pelvic fins—well in advance of the dorsal fin in *Tarpon* but inserted under the base of the dorsal in *Megalops.* Thus the difference is in the position of the pelvic fins rather than in the dorsal as stated in the original description of *Tarpon.* Hollister, who compared specimens, has stated that *Tarpon* has only 57 vertebrae whereas *Megalops* has 68, and that *Tarpon* has 12–15 dorsal rays whereas *Megalops* has 19–21 (*42*: 449). Also, *Tarpon* grows to a much larger size. American ichthyologists generally have accepted *Tarpon* as a valid genus while Old World students have rejected its separation from *Megalops.* Perhaps in consideration of the additional differences now known, the separation may seem better founded. Compared to *Elops*, *Tarpon*'s body is not as slender, its scales are larger, and its dorsal and anal fins have long filaments attached to the last ray of each fin.

Species and Range. A single species is known, ranging from Cape Cod, Massachusetts, to southern Brazil. It has been reported also for tropical West Africa.

Tarpon atlanticus (Cuvier and Valenciennes) 1846

Tarpon, Tarpum, Sabalo Real, Cuffum, Silverfish, Silverking, Grand Ecaille, Jewfish, Palika

Figure 19

Study Material. A total of 25 specimens: 14, 78–1,175 mm TL (57–837 mm SL), measured in the laboratory, from Boggy and Boca Grande, Florida; Fajardo, Puerto Rico; "Cuba"; "West Indies"; and "Amazon River," Brazil; 11 adults, 100–1,990 mm TL, from Gatun and Miraflores locks, Canal Zone, examined for food, sex, and spawning condition.

Distinctive Characters. See *Remarks*, above.

Description. Proportional dimensions in per cent of standard length, and counts, based on at least 14 specimens in the *Study Material* unless stated otherwise, specimens 57–837 mm SL.

Body: depth 23.5–29.
Head: length 25–31.
Snout: length 4.5–6.2.
Eye: diameter 5.3–9.5.
Maxillary: length 15.5–18.
Anal fin: length of base 18–20.
Pectoral fin: length 19–22.8.

Scales: 41–48 series.
Gill rakers: 19–21+36–40.
Fin rays: dorsal 13–15;
anal 22–25; pectoral 13 or 14.
Vertebrae: 53–57 (4 specimens).

Body with almost vertical sides; the dorsal outline of head nearly straight and horizontal, the back somewhat elevated, with ventral outline strongly curved anteriorly; depth 3.4–4.3 in SL. Scales large, firm, with crenulate membranous border. Lateral line complete, decurved anteriorly, the pores branched. Head moderately short and deep, its depth at middle of eye not quite twice its width at the same place, 3.2–4.7 in SL. Snout to rim of upper jaw considerably shorter than eye in small specimens, gradually becoming equal to and finally longer than eye during growth, 4.5–5.5 in head. Eye 3.3–4.7 in head, much nearer to dorsal than to ventral profile, wholly in anterior half of head in adults. Gill rakers rather long and slender, scarcely denticulate. Mouth superior. Mandible projecting far beyond the gape, entering dorsal profile in advance of mouth. Maxillary broad, strongly curved, extending under posterior part of eye in young (80–100 mm) but far beyond eye in large examples, 1.5–1.9 in head.

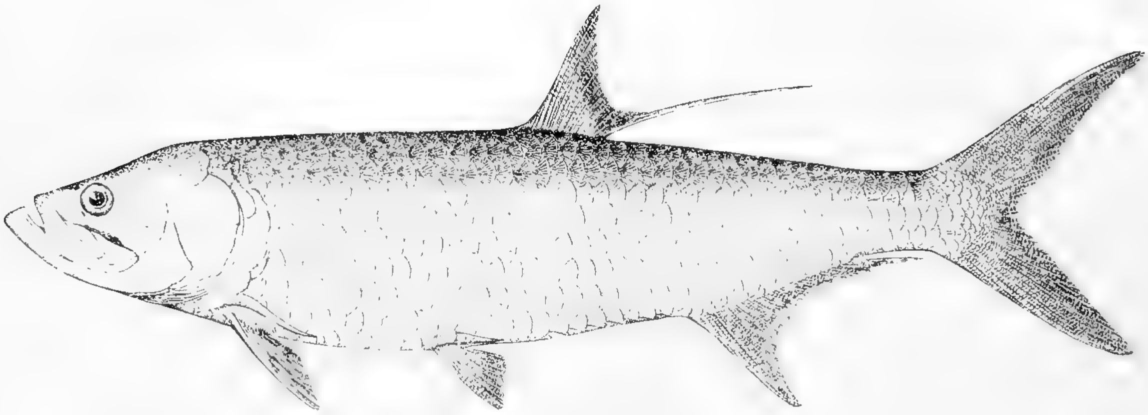

Figure 19. *Tarpon atlanticus,* from off New Jersey, USNM 14924; from Goode. Drawn by H. L. Todd.

Dorsal fin high anteriorly, its last ray produced in specimens over 100 mm long, quite long in large specimens, reaching to end of base of anal fin in some specimens seen; its origin about equidistant between base of caudal and anterior margin of eye. Caudal deeply forked, the lobes of about equal length, generally somewhat longer than head. Anal somewhat elevated anteriorly, its last ray produced in adults, sometimes reaching the base of lower rays of caudal, its origin at least an eye's diameter behind end of dorsal base, its base 4.6–5.6 in SL. Pelvic rather large, inserted more than an eye's diameter in advance of origin of dorsal, and somewhat nearer to base of pectoral than to origin of anal in large specimens. Pectoral rather long, extending to base of pelvic in small specimens, not nearly to pelvic in large ones, 1.2–1.4 in head. Axillary scale of pectoral rather small, only about a third of the fin length, 2.7–3.4 in head.

Color. Preserved specimens bluish silvery above, sides and lower parts bright to pale silvery. Pectorals and pelvics pale; other fins all more or less dusky. Longley remarked, "The large eye falls below the level of the dorsal green and its iris blends with the silvery side. As seen by the diver this great fish appears unsubstantial, a gray ghost floating in gray water" (*49*: 5).

Size. The Tarpon reaches a very large size; an individual a little over eight feet having an estimated weight of 350 pounds has been reported for Hillsborough River Inlet, Florida. A fish up to six feet in length, having a weight of perhaps more than 100 pounds, is not very rare.

Development. The exceedingly large number of eggs produced by a Tarpon indicates extreme prolificness. For example, a female 80 inches long, weighing 142 pounds (caught and reported by Babcock, *1* [1936]: 41), contained 12,201,984 eggs according to a close estimate made by John T. Nichols of the American Museum of Natural History. This great number far surpasses the classic example of the prolificness of the large codfish often mentioned, which contained 1,839,581 eggs.

Ovarian eggs, taken from both unripe and spent fish, measured 0.6–0.75 mm in diameter, a small size for so large a fish. They sank slowly when placed in sea water, suggesting that they may be demersal, not buoyant.

Tarpon eggs that have been spawned naturally and are positively identifiable as such have not yet been described, nor have the early stages after hatching. But it has been assumed from analogy with its smaller relative (*Megalops cyprinoides*) of the East Indies that the Tarpon, like the ladyfish (*Elops saurus*, p. 124) and the bonefish (*Albula vulpes*, p. 134), passes through a ribbon-shaped leptocephalus stage during its larval development. This assumption has been corroborated by the capture at Beaufort, North Carolina, of a leptocephalus 20 mm long, near the transition stage; this, from comparison with the corresponding growth stage in *Elops* and *Albula* (*35*: 45) and in the East Indian *Megalops* from Java, probably was a Tarpon.[4] (One 18 mm long, recently pictured and described by Gehringer, certainly was [*27*: 290].—H.B.B.)

The smallest fry definitely reported as Tarpon have ranged between 16 and 19.6 mm SL (*32*: 6, fig. 5, pl. 1; see also pl. 2 for fry up to 36–38 mm; for earlier accounts of 37 and 77 mm fry, see *13*: 229 and *63*: 72). Breder's painstaking study of extensive series of various sizes from the western coast of Florida has shown that little alteration takes place in the body proportions with subsequent growth.

Rate of Growth. Analyses of the number of checks on the scales of Tarpon from the western coast of Florida, where it may be assumed that growth is interrupted during the cold months, suggest that in open waters it averages about 3,050–3,060 mm in length at one year, about 510–640 mm at two years, and about 1,270–1,525 mm at three years. Earlier scale studies (*1* [1936]: 68) suggest that a Tarpon averages about 1,376 mm or four feet six inches when it is nine or ten years old, that a fish of 70 pounds is about 12 years old, and a fish of 100 pounds is perhaps 13–16 years of age.

Tarpon kept in the old New York Aquarium grew more slowly than those reported above, from less than 500 to only 1,220 mm in five years, perhaps as a result of

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[4] For an account of the leptocephalus stages of *Elops* and *Albula*, see pp. 125 and 136; for the East Indian *Megalops*, see especially Chadabaram and Menon (*18*: 756–759) and Hollister (*42*: 449).

confinement (*13*). Present indications are that a Tarpon does not ordinarily mature sexually until it is about four feet long, i.e. until after the sixth or seventh winter (*13*: 229–247).

Spawning. Ripe or nearly ripe Tarpon have been captured at Boca Grande, Florida, June 5–22 (*1* [1936]: 41), and several fish containing large roe have been taken from the Panama Canal Zone during February, March, and April (*37*: 25, 30, 35). These observations indicate that at least some of them spawn there during the spring. Captures of both green and spent fish have shown that "the time of spawning on the west coast of Florida is from May to September" (*1* [1936]: 43; *13*: 226).

The general belief that spawning takes place along shore, mostly in shoal water, is borne out by Babcock's report that ripe females as well as males ejecting milt were caught near Boca Grande (*1* [1936]: 41, 43) and that he received an eyewitness account of pairs of Tarpon spawning in Charlotte Harbor, near Fort Myers, Florida. The presence of very young fish at points as widely distributed as Texas, Alabama, Florida, the Bahamas, Puerto Rico, Haiti, Cuba, and Trinidad seems sufficient evidence that the breeding range is extensive—along the shores of both continent and islands from the Gulf of Mexico eastward through the West Indies and Caribbean Sea areas. To what extent it breeds farther southward is not known. The well-known presence of young as well as large Tarpon in Lake Nicaragua also makes it likely that this fish spawns there in fresh water. No evidence, however, has been found that the Tarpon breeds in the lakes of the Panama Canal (*36*: 240). It seems probable, therefore, that the ripe fish there migrates to sea to spawn, using the locks of the Canal as a passageway.

Habits. The Tarpon does not school, at least not habitually like the menhaden, for example. When it does congregate in considerable numbers, as at the foot of the spillways of the dams in the Canal Zone, it does so presumably because food is abundant there. In other places it sometimes congregates in pursuit of schools of fish. The fish apparently is sensitive to cold water and will move away from it if possible. Even in southern Florida it disappears from the inshore waters during cool weather (*34*: 211). If it migrates out to sea, as it probably does at times to escape from cold water, it seems highly probable that it remains at or near the surface where the water generally is warmest and where it can utilize the modified air bladder for breathing. The Tarpon more or less habitually ascends freshwater streams, and in some places, in the tropics at least, it occupies freshwater lakes more or less permanently (*36*: 240; see also *Habitat*).

The rolling movements of the Tarpon at the surface of the water are familiar to all fishermen. As these movements reveal its presence, anglers watch for this activity. Why the fish practices such movements habitually was not understood until it was discovered that it possesses an air bladder supplied with a large amount of lung tissue (*36*: 246). After the fish has rolled at the surface and descended, bubbles appear at the surface, these presumably being air exhaled below the surface.

It has been suggested by several writers that the great leaps often executed by the Tarpon seem to serve a different purpose from rolling movements: to escape from enemies, to shake off remoras or irritating parasites, or to play. Also, it often executes great leaps when hooked, evidently trying to free itself; as most Tarpon fishermen know from experience, these efforts are frequently rewarded with success.

Habitat. The Tarpon, a coastal fish, is seldom if ever seen more than a few miles out from the land. To be sure, it has been credited with extensive seasonal offshore migrations, even across the Gulf of Mexico (p. 118), but not with any definite supporting evidence. The Tarpon may be taken in either salt or brackish water, and not infrequently it lives in freshwater streams and lakes. It has long been known to inhabit Lake Nicaragua, a body of water a hundred feet above sea level, and more recently it has been reported as plentiful in the rapid San Juan River, via which the Lake discharges into the Gulf of Mexico (*1* [1936]: 19–20). This fish is exceedingly abundant, sometimes at least, in fresh or virtually fresh water at the base of the spillway of Gatun Dam and also in Gatun Lake below Madden Dam. It occurs regularly also in other parts of Gatun Lake and in the small freshwater lake between Pedro Miguel and Miraflores locks (*36*: 240). To reach these lakes the fish must pass through the locks of the Canal. The smaller fish also abounds in fresh and slightly brackish streams, as around southwestern Florida. The young fry is often reported as occurring in great numbers in very stagnant brackish pools and lagoons that were not connected to the sea when the collections were made (*22*: 80; *3*: 145; *5*: 34; *12*: 154).

Migrations. Knowledge of this aspect of the Tarpon's life is scanty. It is probable that the great majority of the larval Tarpon passes through the metamorphosis close to the land, and many do so in estuaries, such as the Grande Añasco River, Puerto Rico (*21*: 146), and the Indian River, Florida (*32*: 1). However, some drift so far offshore that they almost certainly are lost to the Tarpon population: one, for example, was taken about 150 miles to the east of Brunswick, Georgia, well out in the Gulf Stream (*27*: 236).

The reported scarcity of fish less than three feet or so off the open coast, contrasted with their abundance in estuarine situations, even in drainage ditches, suggests that most of them tend at first to work inshore. Indeed, great numbers of small fry have repeatedly been encountered in brackish pools in mangrove swamps, in landlocked lagoons, and in small pools around Florida, Puerto Rico, Haiti, Jamaica, and on Andros Island in the Bahamas, access to which is possible only during periods of very high water. Many of the fish that are trapped in this way are no doubt lost to the population when the pools dry up. (For an interesting summary of recorded instances of this sort, see Babcock, *1* [1936]: 24, 32–46.) But many of them probably find their way out again. It is only in situations of this sort that the Tarpon fry has ever been taken in any great numbers, at least around Florida (information from Dr. J. E. Randall). It is to be found in such situations around southwestern and southern Florida throughout the year. The postlarval stages have recently been taken in such numbers in the salt marshes of the Indian River on the eastern coast of Florida as to show that this is an important center of dispersal for them (*32*: 9). Little Tarpon 1–1.5 feet long are very plentiful in the narrow headwaters of brackish and freshwater streams, and even in drainage ditches. But the growing fish tends to move down to the broader waters as it grows.

There is no apparent reason to credit the older Tarpon with any extensive migrations, whether inshore-offshore or along shore, in the southern part of the range, for large fish are found there within rivers and along the open coast at all times of the year.

In the northern part of its range, however, the large Tarpon drops out of sight with the onset of autumn, not to reappear until the following March or later, according to locality. It has often been credited with extensive seasonal migrations, "northward along the Florida coast and down the Texan coast, and back across open waters" (*13*: 234). But a more plausible explanation is that the autumnal disappearance of the Tarpon from the open coasts of the northern-northeastern periphery of the Gulf of Mexico represents nothing more extensive than a temporary withdrawal; it probably moves far enough offshore and deep enough to escape winter chilling, such as killed many of all sizes along the western coast of Florida in 1885, 1894–95, 1905, and 1935 (*74*: 123; *1* [1936]: 21; *66*: 640). Appearance of the Tarpon off North Carolina in summer and autumn (as happens more or less regularly), and even farther north (p. 120), evidently represents so extensive a journey from the nearest wintering ground available for a warm-water nonoceanic fish that it seems unlikely that any of those ever find the way back to their southern home.—H.B.B.

Food. The Tarpon, so far as known, is wholly carnivorous. A specimen nearly six feet long from Boca Grande, Florida, examined by me, had the remains of six marine catfish in its stomach; and a 12-inch specimen from the same place had ingested a silverside. The Tarpon has been reported as feeding almost exclusively on cutlassfish, e.g. in Calcasieu Pass, Louisiana (*73*: 170–172). At times it gathers in great abundance at the foot of the spillway of Gatun Dam in the Canal Zone and at the spillway of Madden Dam in the upper part of Gatun Lake, presumably for the purpose of feeding on small fish that are carried over the spillways. Various observers have reported that it will follow schools of mullets, anchovies, and other fish, apparently feeding on them at will. Young Tarpon, ranging from about two to eight inches in length, taken in an isolated lagoon at Port-au-Prince, Haiti, had fed exclusively on "aquatic hemiptera which filled the waters of the lagoon" (*5*: 36). Blue crabs constitute a favorite bait in Florida.

Enemies. The chief natural enemy of the large Tarpon is undoubtedly the shark, and it has been reported that the porpoise attacks it too (*1* [1936]: 64); the small Tarpon quite certainly falls prey to many predators in the sea. The Tarpon's chief protection from enemies is apparently its great swimming speed, whereby it escapes.

Variation. Whether geographical variations exist can be determined only from study of a larger number of specimens, collected from many localities, than have been available to me.

Relation to Man. As a gamefish, the Tarpon scarcely is surpassed. Its reputation is world-wide and much has been written about the requirements for capturing and subduing this powerful, hard-fighting fish. Its great strength became evident to the writer one day when he was helping to land a Tarpon 80 inches long. A man standing nearby saw the great fish leap ashore from the seine, and wishing to prevent it from jumping back into the water, he threw himself on it, evidently believing that he had enough strength and weight to manage the fish. However, with one stroke of the tail the fish lifted the man, who weighed at least 150 pounds, and threw him a distance of about 12–15 feet. It is understandable, then, why considerable strength, skill, patience, and determination are required to land a large Tarpon and why Tarpon fishing is exciting.

About angling for Tarpon, Miss Francesca LaMonte has provided the following information (personal communication). The hard-fighting Tarpon, either large or small, is a prized catch wherever it occurs in western Atlantic waters, from Nova Scotia to Argentina, or in the eastern South Atlantic off Lagos, Nigeria, and at the mouth of the Volta River, Ghana. The most famous western North Atlantic grounds for both numbers of fish and facilities are: the Florida Keys, centering around Islamorada and Marathon; the western coast of Florida, especially in the passes near Boca Grande and Useppa Island; the Rio Pánuco, México; and the Rio Encantado, Cuba.

The number of Tarpon caught is always small in comparison with the number present, for the fish puts up a violent and often successful fight. A large one is usually fished from outboard motor boats (with the motor cut) by casting, trolling, drifting, or still fishing, on 12-pound line or less, with plugs or with either live or dead bait, and with or without a drag on the reel. The first problem is to set the hook in the Tarpon's hard mouth, then to prevent the fish from throwing it or breaking the line, both of which it will try to do. First it will make a fast, powerful run and a series of high, twisting leaps, shaking its head with violence. Failing to throw the hook, it will then try to break the line either by charging at the boat if the line is too tight, or, if too loose, taking off into the mangroves where the line will eventually break on the roots. The small young Tarpon is caught in rivers and canals on fly-fishing or spinning tackle with light monofilament line. Though small, it fights just as hard as the adult and is by no means sport for an inexperienced angler.

There is wide diversity of opinion as to the edible qualities of Tarpon flesh. On our own shores "large ones at least are not edible" (Babcock, *1* [1936]: 63), but in Panama it is highly esteemed by the natives and West Indian immigrants (*36*: 239); there the size of the fish receives no consideration, for an 80-inch Tarpon seemed as acceptable as a small one; as stated by me in the paper just cited, a small fishery for Tarpon was in operation in Gatun Lake in 1935. It has been reported that it is highly prized as food by the Indians of the Caladonia Bay (Panama) region (*10*: 152). In the United States the commercial value of the Tarpon is so slight that it has not been listed in the statistical reports of the commercial fisheries by the former Bureau of Fisheries or by the present U.S. Fish and Wildlife Service.

Range and Abundance. The regular range of the Tarpon extends from North Carolina to central Brazil, and it is probable that the Tarpon frequents the Brazilian coast southward to Pernambuco, or even to Bahia,[5] though the most southerly definite record is for Lake Papary, Rio Grande do Norte, in the general vicinity of Natal (*65*: 8). Thence northward the range is evidently unbroken around the South American coast, where it has been recorded for: Marajó Island at the mouth of the Amazon (*8*: 298); French Guiana (*57*: 164); Trinidad, where it has been reported as very plentiful (*69*: 26); and Lake Maracaibo, Venezuela, and its tributary Rio Concha, where several were seen rolling and a school was reported (*62*: 33). It is equally omnipresent in suitable situations all along the Central American littoral, including: the Panama Canal to Gatun Lake; the San Juan River (p. 117); and Lake Nicaragua, where it is so plentiful that a recent writer reported seeing "more than a dozen rolling at the surface at one time" (*52*: 184). As every angler knows, the Tarpon abounds near river mouths and in so-called "passes" along the coasts of México and Texas. Indeed, it is not unusual to find a Tarpon 80 or 100 miles up from the sea in some Mexican rivers (*13*: 219). In fact, the Bay of Campeche, just west of Yucatán, was the site of a more or less regular fishery for it as early as about 1675 (Capt. Wm. Dampier, cited from Gowanloch, *29*: 145–146). Proverbial centers of abundance are the mouth of the Pánuco River, near Tampico, México, and Aransas Pass, Texas. The Tarpon, as Gowanloch (*29*: 154) expressed it, is to be found near almost any coastal island or bay of Louisiana, Alabama, the western coast of Florida, and the eastern coast of Florida, northward in summer about to the vicinity of Daytona. Especially renowned fishing grounds are: the Calcasieu River, some 30 miles east of the Texas boundary; Grand Isle, Louisiana; Boca Grande and Captiva, western Florida; the waterways and rivers among the Thousand Islands, and the interior waterways of the Florida Keys (see also p. 119).

The Tarpon is widespread but seemingly not very abundant except perhaps locally throughout the West Indian region in general. More than a century ago it had been reported in scientific literature for Guadeloupe, Martinique, Santo Domingo, and Jamaica (*20*: 399). It has been reported for Haiti (*3*: 143) and is common around the Barbados and Puerto Rico. In some rivers of Cuba it is so abundant that a party of anglers has reported hooking 105 large ones in a day in the Rio Encantado (*33*: 205). Among the Bahamas a few are seen, and an occasional one is taken off Bimini (*33*: 207; also personal communication from Vladimir Walters); it is common around Andros Island (*11*: 66), and is taken or seen occasionally around Bermuda.

The Tarpon ranges in small numbers northward to North Carolina in some summers, and perhaps every summer; but large schools are sometimes seen as far north as Cape Lookout. A five-foot fish has been taken off Hatteras, and the North Carolina State Museum has one of 119 pounds from Beaufort, and another of 176 pounds from Wilmington (*64*: 115). But it appears only as a straggler and at irregular intervals farther north. It has been reported for the lower part of Chesapeake Bay by fishermen (*38*: 80); there are odd records of it for New Jersey, near Sandy Hook (*23*:

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[5] The first published account of the Tarpon, by Marcgrave (*50*), was probably based on examples from Recife (Pernambuco) or Salvador (Bahia).—G. S. Myers.

264), for the eastern end of Long Island, New York (*55*: 33), and for Rhode Island (*68*: 72). The Tarpon has been reported as being taken in small numbers almost every year in the vicinity of Woods Hole, Massachusetts (*67*: 741). But the Tarpon has been reported only once for the Gulf of Maine, when a specimen was taken at Provincetown at the tip of Cape Cod on July 25, 1915 (*6*: 91). Northward from Cape Cod there are only five records of it, all for Nova Scotia—one from Isaac Harbor (*31*: 45), one from Harrigan Cove (*70*: 53), one of about three feet caught near Terrence Bay, September 6, 1947, and two taken near Halifax on August 3–4, 1953 (information from Dr. A. H. Leim). The Tarpon is common on the coast of tropical West Africa (*25*: 154; *43*: 106; *1* [1951]: 18–19).

Synonyms and References:[6]

Clupea gigantea Shaw (in part), Genl. Zool., *5* (1), 1804: 173 (no type or type local. design., diagn., genl. acct., habitat).[7]

Megalops giganteus Voigt *in* Cuvier, Das Thierreich (German transl.), *2*, 1832: 423 (refs.; cf. Amer. *M. giganteus* and east. *M. filamentosus* Lacépède); "Disciples' edition" of Cuvier's Règne Anim., *1*, 1836: 559 (same as above with somewhat more extended descr.); Eng. ed., *10*, 1834: 442 (design. Amer. species as *M. cyprinoides*, with ref. to Bloch's pl. 403; pelvics under anterior part of dorsal are as in *Megalops cyprinoides* Broussenet as now understood, but 15 rays in dorsal suggest *Tarpon*).

Megalops atlanticus Cuvier and Valenciennes, Hist. Nat. Poiss., *19*, 1846: 398 (orig. descr., type local. Guadeloupe, Santo Domingo, Martinique, Puerto Rico; types in Paris); Poey, Repert. Fisico-Nat. Cuba, *2*, 1868: 423 (diagn., brackish water of Cuban rivers, attains 5 feet); An. Soc. esp. Hist. Nat., *4*, 1875: 146 (Cuba, Jamaica, Puerto Rico, Santo Domingo, Martinique, Trinidad, México, British Guiana); *in* Gundlach, An. Soc. esp. Hist. Nat., *10*, 1881: 343 (Puerto Rico, Cuba, Santo Domingo, Martinique, México); Henshall, Bull. U.S. Fish Comm. (1889), *9*, 1891: 385 (effect of cold water); Boulenger, Ann. Mag. nat. Hist., (6) *20*, 1897: 298 (Marajó I., Brazil); Gill, Smithson. misc. Coll., *48*, 1905: 35 (descr., habitat, game qualities, life hist., common names, etc.); Regan, Ann. Mag. nat. Hist., (8) *5*, 1910: 354 (caudal skel. cf. *M. cyprinoides*); Fowler, Proc. biol. Soc. Wash., *33*, 1920: 147 (Cape May, Monmouth and Ocean counties, New Jersey); Proc. Acad. nat. Sci. Philad., *80*, 1929: 609 (Barnegat Inlet, Atlantic Highlands, and Atlantic City, New Jersey); Copeia, 1931: 46 (sport fish, Port Aransas and Point Isabel, Texas); Bull. Amer. Mus. nat. Hist., *70* (1), 1936: 154, fig. 61 (African recs.; descr. based on Amer. specimens); Puyo, Bull. Soc. Hist. nat. Toulouse, *70*, 1936: 65, 163 (diagn., habitat in French Guiana); Cadenat, Rev. Trav. Off. Pêches marit., *10*, Fasc. 4, Liv. 4, Pt. 2, 1937: 441, figs. 5, 6 (refs., remarks); Norman and Fraser, Giant Fishes, 1938: 93, fig. 34 (semipopular acct.); Puyo, Faune Emp. Franç., 12, Poiss. Guijane Franç., 1949: 151, fig. 75 (descr., Fr. Guiana).

Megalops elongatus Girard, Proc. Acad. nat. Sci. Philad. (1858), 1859: 224 (orig. descr., type local. Long Island, New York; type not preserved).

Megalops thrissoides Günther (not of Bloch and Schneider, which probably is *M. cyprinoides*), Cat. Fish. Brit. Mus., *7*, 1868: 472 (diagn., Jamaica, Cuba, Trinidad, Brit. Guiana); Goode, Bull. U.S. nat. Mus., *5*, 1876: 68 (rare in Bermuda); Yarrow, Proc. Acad. nat. Sci. Philad., 1877: 215 (Ft. Macon, North Carolina); Steindachner, Denkschr. Akad. Wiss. Wien, *39*, 1878: 69 (Magdalena R., Colombia); Jordan

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6. The Tarpon has been discussed in so many popular books and periodicals that it does not seem practical to list all references to them. Therefore, only some popular accounts are cited, and only those citations in scientific periodicals that seem to contain substantial information. African records have been omitted except for references to Fowler (*25*) and Cadenat (*14*), whose publications contain important references to African literature treating the species.

7. This name was based by Shaw upon Marcgrave (*50*), who dealt entirely with the Atlantic Tarpon, and upon *Clupea cyprinoides* of Bloch, which is a composite of the Tarpon and the Pacific *Megalops cyprinoides* (Broussonet). Since Shaw's account is thus a composite, it devolved upon a subsequent revisor to assign the name *gigantea* to one of the included species. This was done by Cuvier (*19*: 324), who definitely assigned the name *gigantea* to the American Atlantic species. It would thus appear that the correct name of the Tarpon should be *Tarpon giganteus* (Shaw), but the name *atlanticus* is so well established that its conservation, under suspension of the International Rules, would seem to be worthwhile.—G. S. Myers.

and Gilbert, Bull. U.S. nat. Mus., *16*, 1883: 262 (descr., distrib.); Willcox, Bull. U.S. Fish Comm. (1886), *6*, 1887: 123 (effects of cold); Henshall, Bull. U.S. Fish Comm. (1894), *14*, 1895: 211 (abund. in Florida; food and game qualities; size; etc.).

Megalops — Gill and Bransford, Proc. Acad. nat. Sci. Philad., *29*, 1877: 187 (Toro Rapids, below Lake Nicaragua; eaten by natives).

Tarpon atlanticus Jordan and Evermann, Bull. U.S. nat. Mus., 47 (*1*), 1896: 409 (descr., range, synon.); 47 (*4*), 1900: fig. 177; Smith, Bull. U.S. Fish Comm. (1897), *17*, 1898: 90 (Woods Hole, Massachusetts); Evermann and Kendall, Rep. U.S. Comm. Fish. (1899), 1900: 54 (Florida); Linton, Bull. U.S. Fish Comm. (1899), *19*, 1901: 437 (parasites); Evermann and Marsh, Bull. U.S. Fish Comm. (1900), *20* (1), 1902: 80, fig. 10 (descr., small specimens from Puerto Rico); Gregg, Where to Catch Fish. E. Cst. Fla., 1902: 31, fig. (descr., fishing instruct., nonedible or barely so); Eigenmann, Bull. U.S. Fish Comm. (1902), *22*, 1903: 222 (20–192 mm specimens, no descr., Pinar del Rio, Cuba); Bean, Bull. N.Y. St. Mus., *60*, Zool. 9, 1903: 177 (synon., descr., New York); Hargraves, Fish. Brit. Guiana, 1904: 4 (local name Cuffum; used but not appreciated as food; fresh and brackish water); Smith, N.C. geol. econ. Surv., *2*, 1907: 114, fig. 36 (synon., descr., feed., range, North Carolina); Meek, Field Mus. Publ., Zool., *7*, 1907: 99, 111 (Lake Nicaragua); Fowler, Proc. Acad. nat. Sci. Philad. (1910), *62*, 1911: 599 (New Jersey); Eigenmann, Mem. Carneg. Mus., *5*, 1912: 444 (Georgetown, Brit. Guiana); Sumner, Osburn, and Cole, Bull. U.S. Bur. Fish. (1911), *31* (2), 1913: 741 (Woods Hole, Massachusetts); Cockerell, Bull. U.S. Bur. Fish. (1912), *32*, 1913: 122 (scales descr.); Gudger, Proc. biol. Soc. Wash., *26*, 1913: 104 (North Carolina); Halkett, Check List Fish. Canada, 1913: 45 (Isaac's Harbor, Nova Scotia); Starks, Stanf. Univ. Publ., Univ. Ser., 1913: 8 (Lake Papary, Rio Grande do Norte, Brazil); Fowler, Proc. Acad. nat. Sci. Philad., *67*, 1915: 245 (various Florida locals.; color relative to habitat; cleaning of "spawning beds"); also 522 (Trinidad, B.W.I.); Coker, Copeia, 1921: 25 (small ones, Dauphin I., Alabama); Eigenmann, Mem. Carneg. Mus., *9*, 1922: 179 (fresh water, Magdalena R., Colombia); Meek and Hildebrand, Field Mus. Publ. Zool., *15* (1), 1923: 174 (synon., descr., range, Panama); Schroeder, Rep. U.S. Comm. Fish. (1923), Append. 12, 1924: 4 (commerc. val., Key West, Florida); Bigelow and Welsh, Bull. U.S. Bur. Fish. (1924), *40* (1), 1925: 91, fig. 38 (descr., range, rare in Gulf of Maine); Breder, Zoologica, N.Y., *4* (4), 1925: 140, 152 (numerous at spillway, Gatun Dam, C. Z.; enters Caladonia Bay, Panama, in schools; highly prized as food by local Indians); Nichols and Breder, Zoologica, N.Y. (1926), *9* (1), 1927: 33, fig. (distr., life hist., size); Beebe, Bull. N.Y. zool. Soc., *30* (5), 1927: 141 (young adults from brackish lagoon, Haiti); Hildebrand and Schroeder, Bull. U.S. Bur. Fish. (1927), *43* (1), 1928: 80, fig. 41 (synon., descr., range, Chesapeake Bay); Beebe and Tee-Van, Zoologica, N.Y., *10* (1), 1928: 33, fig. (descr., Port-au-Prince, Haiti); Whiton and Townsend, Bull. N.Y. zool. Soc., *31*, 1928: 170 (feed., food in Calcasieu R., Cameron Parish, Louisiana): Breder, Field Bk. Mar. Fish. Atl. Cst., 1929: 59, fig. (diagn., distr., habits, food value, size); Jordan, Manual Vert. Anim. NE U.S., ed. 13, 1929: 37 (diagn., range, size); Nichols, N.Y. Acad. Sci., *10* (2), 1929: 198, fig. (range, Puerto Rico; diagn., habits); Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish. (1928), *2*, 1930: 29 (common names, range, synon.); Burr, Bull. Texas Fish Game Comm., No. 5, 1932: 36 (numbers at Port Aransas and Point Isabel, Texas); Beebe and Tee-Van, Field Bk. Shore Fish. Bermuda, 1933: 33, fig. (descr., uncommon in Bermuda); Breder, Bull. N.Y. zool. Soc., *34*, 1933: 65–67 (small ones from pond, Andros I., Bahamas; food); Gregory, Trans. Amer. philos. Soc., *23* (2), 1933: 137–142, figs. 31–34 (skull descr., cf. *Elops* and prehist. relatives); Storey and Perry, Science, *73* (2022), 1933: 284 (young adults, Sanibel I., Florida, and elsewhere); Gowanloch, Bull. La. Conserv. Dep., *21*, 1932: 8, 54–65 (genl. acct.); Bull. La. Conserv. Dep., *23*, 1933: 144–168 (account of 1932 enlarged); Breder, Zoologica, N.Y., *18*, 1934: 58, 59 (fresh water, Andros I., Bahamas); Hildebrand, Copeia, No. 1, 1934: 45 (larval Tarpon descr.); Beebe and Hollister, Zoologica, N.Y., *19* (6), 1935: 211 (from Union I., Grenadines, B.W.I.); Vladykov and McKenzie, Proc. N.S. Inst. Sci., *19* (1), 1935: 53, fig. 26 (two Nova Scotian recs.); Babcock, The Tarpon, ed. 4, 1936: 1–175, illustrated (good genl. acct. and much scientific data on anat., habitats, breed., respir., etc.); Hollister, Zoologica, N.Y., *21* (4), 1936: 263 (caudal skel.); and *24* (4), 1939: 449–475 (caudal skel. and other characters cf. *Megalops cyprinoides*); Miller, Forest and Stream, *41* (1), 1936: 32–33 (fishery in Rio Frio, tributary of L. Nicaragua); Gudger, Amer. Mus. Novit., 944, 1937: 1, fig. 2 (albino descr.); Heilner, Salt Water Fishing, 1937: 195–210 (genl. acct.; abund. in Cuba and elsewhere); Hildebrand, Sci. Month., *44*, 1937: 239–248, 4 figs. (Panama Canal; locally prized as food by natives); Kaplan, Big Game Angler's Paradise, 1937: 89–136 (genl. acct.); Storey, Ecology, *18*, 1937: 12 (always hurt by freezes); Breder, Bull. N.Y. zool. Soc., *41*, 1938: 24 (irreg. in New York Harbor); *42*, 1939: 154–155 (habitat of small ones at Sanibel I., Florida); Butsch, J. Barbados Mus. hist. Soc., 7 (1), 1939: 18 (common locally); Heilner, Bk. of Fishes, Nat. Geogr. Soc., 1939: 202, 327–336 (color plate, genl. acct.); Hildebrand, Zoologica, N.Y., *24* (1), 1939: 19, 25, 30, 35 (in locks of Panama Canal; transit through Canal completed); Longley and Hildebrand, Publ. Carneg. Instn. Wash., 535, 1941: 5 (feed.; descr., especially as seen by a diver; Tortugas, Florida); Breder, Zoologica, N.Y., *27* (1), 1942: 1 (behavior and respir. in confinement, refs. to papers on same subject); Breder, Zoologica, N.Y., *29*, 1944: 217–252 (habitat, body proportions, growth, movements, refs.).

Genus *Elops* Linnaeus 1766

Ladyfish

Elops Linnaeus, Syst. Nat., ed. 12, 1766: 518; type and only included species, *Elops saurus* Linnaeus 1766.

Generic synonyms:

Argentina, in part, Linnaeus, Syst. Nat., ed. 12, 1766: 519, for *A. carolina* Linnaeus.

Mugilomorus Lacépède, Hist. Nat. Poiss., *5*, 1803: 398; type and only included species, *Mugilomorus anna-carolina* Lacépède equals *Elops saurus* Linnaeus.

Trachonotus Rafinesque, Anal. Nat. ..., 1815: 88; type species *Mugilomorus anna-carolina* Lacépède; *Trachonotus* proposed as a substitute for *Mugilomorus* Lacépède.

Characters.[8] BODY slender. VERTEBRAE about 75. PSEUDOBRANCHIAE large. BRANCHIOSTEGALS about 34. MOUTH nearly horizontal and almost terminal. LATERAL LINE straight, with simple tubes. SCALES small, not especially primitive (fully described by Cockerell, *15*: 3; *17*: 122), forming a sheath on base of dorsal and anal fins. DORSAL rather high anteriorly, the last ray not prolonged. ANAL similar to dorsal but smaller, placed far behind dorsal. PELVICS inserted near vertical from origin of dorsal. Last several segments of spinal column directed upward toward base of upper lobe of caudal fin.

AIR BLADDER slender, with very transparent walls, occupying full length of abdominal cavity, adhering to abdominal wall dorsally and to alimentary canal ventrally. ALIMENTARY CANAL, below air bladder, consisting of a straight tube except for a large elongated blind sac that projects forward to throat below, and parallel to, the main canal; a mass of coeca (firmly bound together) attached to distal end of blind sac and forming a close-fitting shield on right side of sac throughout its length; one lobe of liver forming a hood over blind end of sac, and another lobe shielding left side of sac.

Remarks. The gular plate distinguishes this genus from *Albula*. The very slender body, the small scales, and the absence of filaments attached to the last ray of the dorsal and anal fins distinguish it from *Tarpon*.

Range. About seven species have been recognized, but only *Elops saurus* comes within the range of this work. The species are widely distributed in the warmer seas, entering estuaries and tidal streams.

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[8] The characters of the skull have been discussed by Gregory (*30*: 138), who regarded it as rather more primitive than that of the tarpon. The ganoid character of the caudal skeleton has been well described and correctly figured by Hollister (*39*: 260–263).

Elops saurus Linnaeus 1766

Ladyfish,[9] Bigeye Herring, Tenpounder, Skipjack, Macabi, Matejuelo Blanco, Matejuelo Real, Long John, Benane

Figures 20, 21

Study Material. Many specimens, including an almost complete growth series ranging from larvae to adults 550 mm long.

Distinctive Characters. See *Remarks*, p. 123.

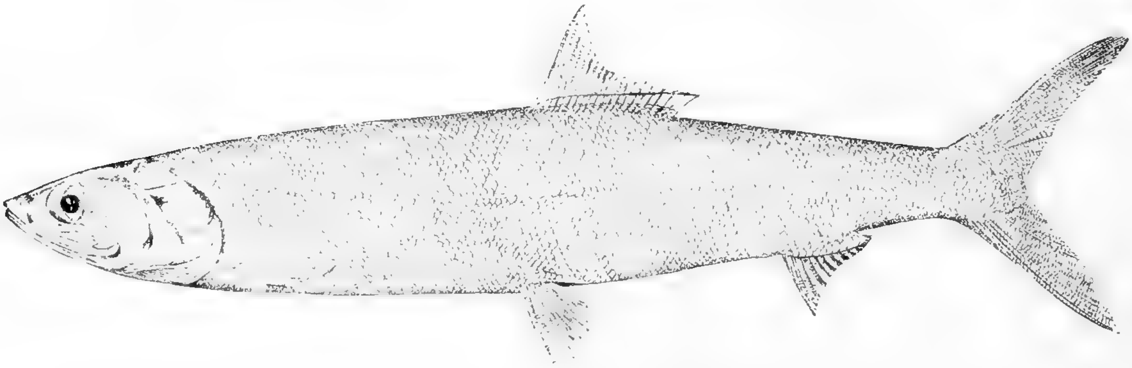

FIGURE 20. *Elops saurus*; U. S. National Museum specimen. Drawn by H. L. Todd.

Description. Proportional dimensions in per cent of standard length, based on study specimens.

Body: depth 14.5–19.3.
Head: length 25–31.
Snout: length 5.8–7.0.
Eye: diameter 5.0–6.3.
Maxillary: length 14.5–17.8.
Anal fin: length of base 9.8–11.8.
Pectoral fin: length 14–16.
Scales: 103–120.
Branchiostegals: 26–32.
Gill rakers: 6–8+10–15 (excluding rudiments).
Fin rays: dorsal 21–25; anal 14–17; pectoral 16 or 17.
Vertebrae: 73–80 (10 specimens).

BODY very slender, only moderately compressed, its depth 5.2–6.9 in SL. SCALES small, thin, with crenulate membranous border (fully described by Merriman, *51*: 113). LATERAL LINE nearly straight, extending onto base of caudal. HEAD low, flat above, 3.25–4.0 in SL. SNOUT rather long, usually a little longer than eye, 4.1–4.75 in head. EYE near upper profile, wholly in anterior half of head, 4.55–5.2 in head. INTERORBITAL flat, 5.7–8.4 in head. GILL RAKERS about 67% of the eye, scarcely denticulate, their entire surface rough, generally 1 or 2 rudiments in large specimens

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[9] In scientific literature, as well as in earlier popular books on American game fishes, the name Ladyfish was usually applied to *Albula vulpes* (p. 134). But to the angler, who alone takes much interest in either of them, "Ladyfish" means *Elops* while *Albula* is universally termed "Bonefish."

and 2 or 3 in small ones, on upper and lower limbs of first arch; the lower counts given, for this reason, are invariably based on the smaller specimens. MOUTH nearly horizontal, almost terminal, the lower jaw slightly included. MAXILLARY reaching somewhere under posterior half of eye in young adults, far beyond eye in large examples, 1.7–2.0 in head.

DORSAL fin rather high anteriorly, its longest rays usually reaching tip of last ray if deflexed, its outer margin rather deeply concave, its origin about equidistant between base of caudal and anterior margin of eye. CAUDAL very deeply forked, the upper lobe rather longer than the lower one, usually about as long as head. ANAL moderately small, far behind dorsal, its origin usually about equidistant between base of caudal and base of pelvic, its base 2.4–2.9 in head. PELVIC fin not much smaller than pectoral, inserted under, or slightly in advance of, origin of dorsal, scarcely nearer to origin of anal than to base of pectoral. PECTORAL fin rather broad, not falcate, reaching scarcely halfway to pelvic in large examples, somewhat more than halfway in small ones, 1.75–2.0 in head. AXILLARY SCALE of pectoral extending to about the midlength of fin, 3.0–3.9 in head.

Color. Preserved specimens uniform bluish gray above, silvery elsewhere; dorsal and caudal more or less dusky; other fins pale.

A large fresh specimen bluish on back, with sides silvery; slightly yellowish below. Dorsal and caudal dusky and yellowish; pelvics and pectorals yellowish with dusky punctulations (*38*: 78).

Size. Although a maximum of 900 mm (36 in.) TL has been reported (*45*: 410), the usual length probably is under 500 mm (20 in.). The largest individual seen by me was 730 mm (610 mm SL; 29.2 in.); this large fish occurred among hundreds of adults stranded in the Gatun Locks of the Panama Canal in 1935 when the Locks were drained. In my file is a record of another large one, 718 mm (28.75 in.), caught at Punta Gorda, Florida. Although one of the common names is Tenpounder, weight records indicate that this fish probably never weighs that much. A specimen 470 mm long (18.8 in.) weighed a pound, another of 550 mm (22 in.) weighed 1.6 pounds, and still another 625 mm (25 in.) weighed 2.7 pounds; 82 fish, ranging between 400–600 mm (16–24 in.), with an average length of about 450 mm (18 in.), weighed 100 pounds.

Development. The eggs and the earliest stages of the leptocephalus are unknown. Of the many leptocephalus larvae studied, the youngest ones, judging principally by the development of the fins, are 34, 35, and 37 mm long. Although the forked caudal is well developed, the other fins are virtually undifferentiated; the alimentary canal is very loosely attached to the abdomen, as in larval herrings and anchovies, and the vent is less than a head-length from the caudal base.

Two leptocephali, 34.5 and 36.5 mm long, are slightly more advanced; in these a thickening within the finfold where the bases of the dorsal and anal are developing has taken place, though rays are not yet definitely formed. The head is strongly depressed, the mouth is terminal and large, and the snout, viewed ventrally, is rather sharply triangular; these characters at once distinguish the leptocephalus of this species from that of *Albula vulpes*. The myomeres are mostly quite distinct, 78 having been counted in one of the specimens. A row of faint dark spots, which are much more distinct in older leptocephali, is present on each side just above the alimentary canal.

Three leptocephali, 42, 42, and 44 mm long, are the longest larvae in the collections studied and may represent about the maximum length attained in the leptocephalus stage. Here development has progressed somewhat beyond that of the specimens described above, for the rays are evident now in the dorsal and anal fins, though an accurate enumeration cannot be made. The anal fin is removed from the base of the caudal by a distance shorter than the head, and the primitive membrane has remained between the two fins. The pectoral fins are represented by tufts of membrane and the pelvics merely by thickened places in the abdominal wall where their bases are developing. Seventy-seven myomeres were counted in one of the specimens.

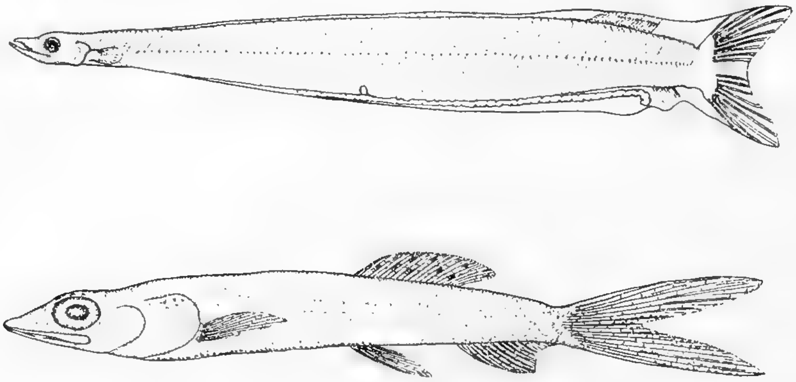

FIGURE 21. *Elops saurus*. ABOVE, leptocephalus, 35 mm long; BELOW, young fish, 20 mm TL, recently transformed.

In a considerably older specimen, reduced in length to 27 mm, the body, though still quite flat, has become much more substantial than in the younger stages described. The dorsal and anal fins are sufficiently developed to permit an accurate enumeration of the rays, and the anal fin is now well separated from the caudal. The primitive membrane has disappeared behind the fin, though a short section of it remains in front. The pectorals are rather well developed and show signs of rays. However, the pelvics are undifferentiated.

A virtually young adult only about 16 mm long (not in good condition) represents the maximum "shrinkage" in length during metamorphosis, among specimens studied. Though the body has become rather robust, the head and especially the snout remain depressed. The fins, except for the pelvics, are rather well developed. The intestinal canal remains loosely attached to the abdomen as in younger fish, and the primitive rows of dark dots on each side of the canal are distinct.

The state of development varies widely among the rather numerous young adults, 18 mm and upward. For example, a specimen scarcely 20 mm long is fully as well developed as others around 30 mm, and another specimen about 30 mm long is just as well developed as some between 35 and 40 mm. The small and exceptionally well developed specimens have advanced especially far in color. A specimen scarcely 20 mm long already has some of the silvery color of large adults and all the juvenile markings are missing, whereas a 32-mm specimen among the retarded ones is very pale and still retains the two rows of dark spots on the abdomen, as in the leptocephali. Even in the most retarded specimens, the fins are all well developed at a length of 22 mm, and the outline of the gular plate is visible under magnification. Scales begin to appear in at least some specimens at a length of 50 mm, and the teeth in the jaws are definitely in narrow bands. At a length of 60–65 mm, scalation generally is complete, and the fish are very similar to full-grown adults.

The environment probably affects the development profoundly, for the small, exceptionally advanced specimens described in the preceding paragraph were taken in brackish pools at Key West, Florida, whereas the notably larger and more retarded ones were taken at sea off Ocracoke and Beaufort inlets, North Carolina.

Spawning. There is relatively little information about the actual time and place of spawning. However, in 1939 I reported (*37*: 25) that 20 individuals, selected at random from among the many left stranded when the Gatun Locks (Panama Canal) were drained in February 1935, consisted of seven ripe or nearly ripe males (56.5–62 cm TL), and 13 females (63.5–73 cm TL) with large roe, indicating that spawning time in that vicinity was at hand. Although leptocephali of *Albula* have been taken in considerable seining during the winter and spring months on the Atlantic coast of Panama, no young of *E. saurus* have been reported. On the Pacific coast of Panama, leptocephali of the closely related *E. affinis* were taken during February, August, and "autumn." In the collections at hand there are leptocephali from Texas, mostly from the vicinity of Corpus Christi, collected in February, March, April, and November. Young adults were taken in Aransas Pass, Texas, during June, and at Key West, Florida, in March and November. Leptocephali are also at hand from the Florida Keys, taken in November, and from Cuba, caught during May. For Beaufort, North Carolina, there is a note in my files that a nearly ripe female of 604 mm was taken on October 3, 1912; leptocephali were collected there during January, February, March, April, May, October, November, and December; rather recently-transformed young adults were taken in the same vicinity during March, May, June, July, and August. Most of the many leptocephali studied were taken with tow nets on the bottom, at sea, in comparatively shallow water, though several captures were made in estuaries. The young adults, except for a few lots in the transition stage, were collected with seines in inside waters, partly in brackish ponds and pools.

Habitat. This is an active little fish, often traveling in schools, frequently skipping at the surface, and jumping when hooked. Its usual habitat is shallow salt and brackish water. The young adult has been taken in brackish lagoons and in ponds and pools, perhaps more or less recently and temporarily separated from the sea. In the Gatun Locks (see above) it occurred in large numbers and was most numerous in the middle chamber of the three flights, where the water, at least part of the time, is nearly fresh. No evidence of its entrance into the strictly fresh water of Gatun Lake was obtained; it seems improbable, therefore, that it uses the locks as a passageway; more probably the locks serve merely as a feeding ground. If it migrates to sea to spawn, as might be supposed since its young pass through a leptocephalus stage, the location of its spawning ground (or grounds) remains unknown.

Food. Its diet has not been thoroughly studied, but the short alimentary canal and the well-armored mouth surely suggest a flesh diet. A dozen or so adults taken in one catch at Beaufort, North Carolina, had fed exclusively on shrimp, and other examples from the same vicinity had fed on them also (*48*: 352; *64*: 116). It has been reported that an individual from Haiti had eaten a shrimp and two small fish of its own species (*5*: 33). A specimen taken in Connecticut had fed on two small fish, probably *Menidia* (*51*: 113). According to Kaplan, the Ladyfish feeds on shrimp, shiners, and squid (*46*: 91).

Parasites. The cestode parasite, *Rhynchobothrium bulbifer* Linton, has been found in the viscera of the adult Ladyfish (*48*: 352).

Relationships. This species is closely related to *E. affinis* Regan of the Pacific coast of tropical America, apparently differing only in the number of gill rakers: in 41 specimens of *E. saurus* examined, 9 had 6 rakers, 16 had 7, and 16 had 8, exclusive of rudiments, on the upper limb of the first arch; and in 88 specimens, 2 had 10 rakers, 7 had 11, 13 had 12, 28 had 13, 35 had 14, and 3 had 15 rakers, exclusive of rudiments, on the lower limb. In nine specimens of *E. affinis* examined, 4 had 10 and 5 had 11 rakers on the upper limb, and in 26 specimens, 2 had 16 rakers, 4 had 17, 6 had 18, 11 had 19, and 3 had 20 rakers, exclusive of rudiments, on the lower limb.

Elops saurus has been recorded for West Africa by Fowler (*25*: 155) and by others, but Regan (*58*: 38) has held that African specimens were distinct on the basis of fewer vertebrae—68 or 69 compared to 78 or 79 for American specimens—and on the basis of fewer scales—94–98 for African specimens and 102–118 for American specimens. According to counts made by me, these differences seem to be constant. Ten American specimens have 73, 74, 75, 75, 75, 77, 78, 79, 80, and 80 vertebrae, and nine American leptocephali have 77, 78, 78, 78, 79, 80, 82, 82, and 82 myomeres, whereas one adult from Ashantee, Africa, has only 67 vertebrae. Counts of scales in 22 American specimens resulted as follows: 1 specimen with 103, 2 with 105, 1 with 106, 2 with 107, 2 with 108, 1 with 109, 2 with 110, 1 with 111, 2 with 112, 1 with 113, 1 with 114, 1 with 115, 2 with 116, 1 with 118, and 2 with 120. The three specimens from Ashantee, Africa, examined by me have 92, 97, and 100 scales. Although the range of counts for American specimens is rather great, it does not overlap that given by Regan for African specimens. On the basis of the above data given by Regan and me, the African representatives, which Regan named *Elops senegalensis*, may still be considered distinct, though synonomized with *E. saurus* by Fowler.

Variations. No geographical variation in the number of gill rakers has been discovered, but there appears to be a slight increase in number with age, which seemingly may be attributed to the development of some of the rudiments into rakers as the fish grows. Thus, in 29 specimens 150 mm SL and under, 5 had 5, 14 had 6, and 10 had 7 rakers and 2 or 3 rudiments on the upper limb; among 20 specimens over 150 mm SL, 2 had 6, 4 had 7, and 14 had 8 rakers and 1 or 2 rudiments. Similarly, among 35 specimens 150 mm SL and under, 5 had 10, 14 had 11, 11 had 12, and 5 had 13 rakers and 2 or 3 rudiments on the lower limb; among 32 specimens over 150 mm, 4 had 12, 7 had 13, 18 had 14, and 3 had 15 rakers and 1 or 2 rudiments on the lower limb.

Relation to Man. For its size, the Ladyfish affords good sport to the light-tackle angler, but it is virtually of no value as food, its meat being dry and bony. It is seen from time to time in the market at Colón, Panama, where it is known as "bonyfish" to the West Indian Negro immigrants who speak English; however, the demand for it is small. When the Gatun Locks were drained in 1935, hundreds of Ladyfish became stranded, and it was estimated that more than 1,000 pounds perished. While the employees and the native residents eagerly accepted tarpon, crevalle jack (*Caranx hippos*), and other species, the Ladyfish was entirely neglected and had to be buried (*37*: 25).

Range and Abundance. Its range extends from Cape Cod to Brazil. The southernmost locality for which it has been recorded seems to be Rio de Janeiro (*60*: 90; *26*: 132). While *E. saurus* is not numerous in the West Indies, it is widespread in the Caribbean-Gulf of Mexico region, and is common along Atlantic Panama; the *Study Material* includes three specimens from the Gulf of Venezuela. It is common around Florida, especially in enclosed waters such as the Indian River and among the islands off the southwestern coast. The Ladyfish also occurs around Bermuda, though not in any great numbers. To the north, it is present irregularly off Beaufort, North Carolina, and it has been reported as common in the Chesapeake Bay region; farther to the north its appearances—always in autumn—are sporadic. Considerable numbers were taken near Sandy Hook in October 1923; for example, 13 out of one trap on the 19th (*55*: 33). It has been recorded for the eastern part of Long Island (Orient), New York, from October 6 to November 4. Also, it has appeared in considerable numbers at various localities in the Woods Hole region in some autumns (*67*: 741), but there is no dependable record for a Ladyfish north of the elbow of Cape Cod—there is no knowing whether one taken at Chatham, Massachusetts, in 1888 (*7*: 139) was from Nantucket Sound or the Gulf of Maine shore of Cape Cod. Nor is there any possibility of determining whether an "*Albula vulpes*," taken at Black's Harbor (Charlotte County, New Brunswick) and in poor condition when examined (*31*: 45), was actually a Bonefish or Ladyfish.

Synonyms and References:

Elops saurus Linnaeus, Syst. Nat., ed. 12, 1766: 518 (orig. descr.; type local. "Carolina"; type, a dried skin in BMNH; see Goode and Bean, Proc. U.S. nat. Mus. [1885], *8*, 1886: 205); Bloch and Schneider, Syst. Ichthyol., 1801: 430, pl. 82 (descr., refs.); DeKay, New York Fauna, Fishes (4), 1842: 267, pl. 41, fig. 131 (descr., New York Harbor); Storer, Synop. Fish. N. Amer., 1846: 211 (descr., refs.); Gronow, Cat. Fish., Gray ed., 1854: 168 (descr., refs., distr.); Poey, Repert. Fisico-Nat. Cuba, *2*, 1867: 423 (diagn., Cuba); Günther, Cat. Fish. Brit. Mus., *7*, 1868: 470 (synon., descr., Cuba, Jamaica, St.

Croix, "South America"; also several African and oriental locals. that probably are not this species); Yarrow, Proc. Acad. nat. Sci. Philad., 1877: 215 (Ft. Macon, North Carolina); Jordan and Gilbert (part not of Linnaeus), Bull. U.S. nat. Mus., *16*, 1883: 261 (diagn., range); Goode and Bean, Proc. U.S. nat. Mus. (1885), *8*, 1886: 205 (type, a dried skin cut in two pieces, in BMNH in Linnaean Soc. rooms); Willcox, Bull. U.S. Fish Comm. (1886), *6*, 1887: 123 (killed by cold, Florida); Henshall, Bull. U.S. Fish Comm. (1889), *9*, 1891: 373 (leptocephali, Marco, Florida); B. A. Bean, Proc. U.S. nat. Mus., *14*, 1891: 93 (Cape Charles, Virginia); Henshall, Bull. U.S. Fish Comm. (1894), *14*, 1895: 211 (Key West and Tampa, Florida; not as common as *Albula*; no econ. import.); Jordan and Evermann (part not of Linnaeus), Bull. U.S. nat. Mus., 47(*1*), 1896: 410 (descr., Amer. range includ. Pacif. cst., which has distinct species, *E. affinis* Regan); also 47 (*3*), 1898: 2806 (confusion of species); also *47* (*4*), 1900: fig. 178; Jordan and Rutter, Proc. Acad. nat. Sci. Philad., 1897: 94 (Jamaica, "sometimes 20 pounds" evidentally an error); Smith, Bull. U.S. Fish Comm. (1897), *17*, 1898: 90 (common in fall, Woods Hole, Massachusetts); Günther, Proc. linn. Soc. Lond., 1899: 25 (type in Linnaean Soc. coll.); Evermann and Kendall, Rep. U.S. Comm. Fish. (1899), 1900: 54 (Florida); Evermann and Marsh, Bull. U.S. Fish Comm. (1900), *20* (1), 1902: 81, fig. 11 (descr., Puerto Rico); Bean, Bull. N.Y. St. Mus., *60*, Zool. 9, 1903: 179 (refs., descr., New York); Schreiner and Ribiero, Arch. Mus. nac. Rio de J., *12*, 1903: 90 (Caravelas and Rio de Janeiro, Brazil; Woods Hole, Mass.); Hargraves, Fish. Brit. Guiana, 1906: 6 (local name "Long John"); Gill, Smithson. misc. Coll., *48*, 1905: 34 (skull figured, range; *Elops* cf. *Megalops*); Jordan and Thompson, Bull. U.S. Bur. Fish. (1904), *24*, 1905: 232 (Tortugas, Florida); Linton, Bull. U.S. Bur. Fish. (1904), *24*, 1905: 352 (food, parasites); Bull. Mus. comp. Zool. Harv., *50*, 1906: 156 (Gulf of Mexico at Progreso, Yucatán); Smith, N. C. geol. econ. Surv., *2*, 1907: 116, fig. 37 (refs., descr., range, North Carolina); Linton, Proc. U.S. nat. Mus. (1907), *33*, 1908: 86 (Bermuda); Regan, Ann. Mag. nat. Hist., (8) *3*, 1909: 37 (distr. limited to Amer. Atlant. cst.; Pacif. cst. represent. *E. affinis*; Afric. represent. *E. senegalensis*); Fowler, Proc. Acad. nat. Sci. Philad., *63*, 1911: 204 (Nantucket, Mass.; "South Carolina"; West Palm Beach, Florida; Santo Domingo; doubtfully from Jamaica, and Rio de J., Brazil); Weymouth, Proc. U.S. nat. Mus., *38*, 1911: 136 (Cameron, Louisiana); Nichols, Bull. Amer. Mus. nat. Hist., *31*, 1912: 181 (common in markets, Cuba); Sumner, Osburn, and Cole, Bull. U.S. Bur. Fish. (1911), *31* (2), 1913: 741 (Woods Hole area, Mass.); Starks, Stanf. Univ. Publ., Univ. Ser., 1913: 8 (coast of Brazil; Lake Papary, Rio Grande do Norte); Metzelaar, Trop. Atlant. Visschen, 1919: 9 (Curaçao, Dutch W. I., unimport. as food); Fowler, Proc. biol. Soc. Wash., *33*, 1920: 147 (Cape May, New Jersey); Breder, Zoologica, N. Y., *2* (15), 1922: 336 (Sandy Hook Bay); Meek and Hildebrand, Field Mus. Publ., Zool., *15* (1), 1923: 175 (synon., descr., range, Panama); Linton, Proc. U.S. nat. Mus., *64*, 1924: 59 (parasites); Bigelow and Welsh, Bull. U.S. Bur. Fish. (1924), *40* (1), 1925: 90, ftn. (questions Halkett's [1913: 45] ident. of New Brunswick specimen): Breder, Zoologica, N.Y., *4* (4), 1925: 141 (common at Gatun Dam Spillway, Canal Zone); Nichols and Breder, Zoologica, N.Y. (1926), *9* (1), 1927: 33, fig. (Sandy Hook, New Jersey; Orient and New York, N.Y.; Woods Hole, Mass.; a fall visitor); Hildebrand and Schroeder, Bull. U.S. Bur. Fish. (1927), *43* (1), 1928: 79, fig. 40 (descr., range, Chesapeake Bay); Beebe and Tee-Van, Zoologica, N.Y., *10* (1), 1928: 32, fig. (diagn., range, "apparently rather rare" at Port-au-Prince, Haiti); Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish. (1928), *2*, 1930: 39 (common names, range, synon.); Breder, Field Bk. Mar. Fish. Atl. Cst., 1929: 60, fig. (diagn., range, size); Fowler, Proc. Acad. nat. Sci. Philad., *80*, 1929: 609 (Atlantic City, New Jersey); Jordan, Manual Vert. Anim. NE U.S., ed. 13, 1929: 36 (diagn., range); Nichols, N.Y. Acad. Sci., *10* (2), 1929: 119 (probably not uncommon in Puerto Rican waters; diagn.; excellent sport fish with light tackle); Fowler, Copeia, No. 2, 1931: 46 (Corpus Christi, Texas; local name skipjack); also Proc. Acad. nat. Sci. Philad., *83*: 1931: 392, fig. 1 (Trinidad); Beebe and Tee-Van, Field Bk. Shore Fish. Bermuda, 1933: 33, fig. (descr., rare in Bermuda); Fowler (part not *E. saurus* Linn.), Bull. Amer. Mus. nat. Hist., *70* (1), 1936: 155 (synon., includ. Afric. refs. based on *E. senegalensis* Regan; descr. based in part on Afric. specimen); Hollister, Zoologica, N.Y., *21* (4), 1936: 260–263, figs. (caudal skel.); Hildebrand, Sci. Month., *44*, 1937: 243 (abund. in Gatun Locks, Panama Canal, when drained); Kaplan, Big Game Angler's Paradise, 1937: 91 (size, food, called Ladyfish in Florida); Storey, Ecology, *18*, 1937: 16 (often hurt by freezes); Breder, Bull. N.Y. zool. Soc., *41*, 1938: 24 (irregular, New York Harbor); Hildebrand, Zoologica, N.Y., *24* (1), 1939: 25 (Gatun Locks, Panama Canal, apparently feed. ground); Merriman, Copeia, 1939: 113, figs. A–D (scales); Bigelow and Schroeder, Copeia, 1940: 139 (Chatham, Cape Cod, Mass., northernmost definite rec.); Longley and Hildebrand, Publ. Carneg. Instn. Wash., 535, 1941: 4 (rare at Tortugas, Florida); Fowler, Arqu. Zool. estad. São Paulo, *3* (6), 1941: 132 (refs.); Hildebrand, J. Wash. Acad. Sci., *33* (3), 1943: 90–94, 3 figs. (notes on affinity, anat., develop.).

Argentina carolina Linnaeus, Syst. Nat., ed 12, 1766: 519 (orig. descr.; type local. "Carolina"; type lost).

Mugilomorus anna-carolina Lacépède, Hist. Nat. Poiss., *5*, 1803: 398 (orig. descr.; type local. "South Carolina"; type in Paris).

Elops inermis Mitchill, Rep. in part on Fish. New York, 1814: 14 (orig. descr.; type local. New York, specimen secured in market; type lost); Mitchill, Trans. Lit. philos. Soc. N.Y., 1815: 445 (descr., New York).

Albula vulpes Gregg (not *A. vulpes* Linnaeus, but *Elops saurus*), Where to Catch Fish E. Cst. Fla., 1902: 34 (descr., instruct. for angling, barely edible).

Doubtful Reference:

Elops saurus Halkett, Check List Fish. Canada, 1913: 45 (report. New Brunswick; ident. doubtful).

Negative References:[10]

Elops saurus Gregg, Where to Catch Fish. E. Cst. Fla., 1902: 33, fig. (*Albula vulpes*, not *E. saurus*); Bean, Bahama Islands: Fishes, 1905: 297 (determined as small *Jenkinsia lamprotaenia* on re-exam. by present writer; not *E. saurus*; USNM 53076).

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[10] To these may be added all mention of *Elops saurus* based on specimens not taken on the Atlantic coast of America, of which there are many.

Family Albulidae[11]

SAMUEL F. HILDEBRAND[12]

Characters. BODY slender, little compressed; belly rounded; ordinary scales on median line. HEAD rather low; flat above. SNOUT conical, projecting far in advance of mandible. EYE of moderate size, with much adipose tissue in adults. MOUTH moderately small, nearly horizontal. MAXILLARY generally reaching nearly to front of eye, or to some point underneath it, but never beyond eye. PREMAXILLARIES not protractile. GULAR PLATE lacking. TEETH small, present in bands on jaws, vomer, palatines, pterygoids, basibranchials, and sphenoid. BRANCHIOSTEGALS 13 or 14. GILL MEMBRANES separate, free from isthmus; a membrane across isthmus in front. OPERCULAR BONES with membranous borders. PSEUDOBRANCHIAE well developed. GILL RAKERS very short, stout, tubercular in large examples. Last several segments of SPINAL COLUMN directed upward toward base of upper lobe of caudal. LATERAL LINE present, straight. SCALES of moderate size, more or less quadrate, with membranous border, 3 (rarely 4) nearly parallel basal radii, and 4 or 5 coarse basal lobes (fully described by Cockerell, *15*: 3; *16*: 865; *17*: 122); scales extending onto the fins; a modified median row of enlarged scales in front of dorsal fin; no scales on head. DORSAL fin beginning in advance of pelvics. CAUDAL forked. ANAL very small, placed far behind dorsal. PECTORALS and PELVICS similar, each with an AXILLARY SCALE.

The young pass through a leptocephalus stage like the Elopidae and the eels.[13]

Remarks. The members of this family differ from those of Elopidae principally in the absence of a gular plate, and in having a conical snout as well as fewer bran-

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[11] Edited and emended by George S. Myers, Henry B. Bigelow, and Yngve H. Olsen.

[12] August 15, 1883–March 16, 1949.

[13] The heart of *Albula* is reminiscent of the ganoids in having a rudimentary conus arteriosus with two rows of valves (*9*: 548). Several fossil albulids are known, from as far back as the Eocene (*54*: 84).—G.S.M.

chiostegals (13 or 14). From members of the Clupeidae they differ in having a well-developed lateral line and undeveloped gill rakers.

Range. Only two living genera, *Albula* and *Dixonina*, are recognized.[14] The former has a world-wide distribution in warmer seas, and the latter is known from both coasts of tropical America.

Key to Western Atlantic Genera

1 a. Last ray of dorsal and anal not prolonged; snout only moderately conical, projecting only about a third of its length beyond mandible; maxillary not reaching eye. *Albula* Scopoli 1777, below.

1 b. Last ray of dorsal and anal much prolonged; snout sharply conical, projecting more than a third of its length beyond mandible; maxillary reaching nearly to middle of eye. *Dixonina* Fowler 1911, p. 143.

Genus *Albula* Scopoli 1777

Bonefishes

Albula Scopoli, Introd. Hist. Nat., 1777: 450; no species named, but based on *Albula* (name not binomial; followed by long description), in Gronow, Zoophyl., *1*, 1763: 102; type and only included species Albula s. salmo albula Meuschen, in Gronow, *3*, 1761, index (not paged), Mediterranean; binomial name given to Gronow's (1763) *Albula* (Whitley, *72*: 303) equals *Esox vulpes* Linnaeus, Syst. Nat., 1758: 313.

Generic Synonyms:

Esox, in part, Linnaeus, Syst. Nat., *1*, 1758: 313, for *E. vulpes* Linnaeus, Bahamas.

Argentina, in part, Forskål, Descr. Anim ..., 1775: 68, for *A. glossodonta* Forskål, Arabia.

Amia, in part, Bloch and Schneider, Syst. Ichthyol., 1801: 457, for *A. immaculata* Bloch and Schneider, South America.

Synodus, in part, Bloch and Schneider, Syst. Ichthyol., 1801: 398, for *S. argenteus* Bloch and Schneider, Tahiti; Lacépède, Hist. Nat. Poiss., *5*, 1803: 32, pl. 8, fig. 2, for *S. vulpes* Lacépède.

Clupea, in part, Bloch and Schneider, Syst. Ichthyol., 1801: 427, for *C. brasiliensis* Bloch and Schneider, Brazil; Lacépède, Hist. Nat. Poiss., *5*, 1803: 427, for *C. macrocephala* Lacépède, Martinique.

Butyrinus Lacépède, Hist. Nat. Poiss., *5*, 1803: 45; type by monotypy, *Butyrinus bananus* Lacépède equals *Esox vulpes* Linnaeus.

Glossodus Cuvier, Mem. Mus. Hist. nat. Paris, *1*, 1815: 232; genotype by monotypy, *Argentina glossodonta* Forskål equals *Esox vulpes* Linnaeus.

Engraulis Agassiz, L. *in* Spix and Agassiz, Selecta genera et species piscium...Brazil..., 1829: pl. 23, fig. 2, for *E. sericus* Agassiz; pl. 24, fig. 2, for *E. bahiensis* Agassiz, Brazil.

Conorhynchus Gill, Proc. Acad. nat. Sci. Philad., Suppl., 1861: 55; genotype by monotypy, *Butirinus vulpes* Storer equals *Albula vulpes*.

Characters. DORSAL and ANAL fins with the last ray not produced. MAXILLARY falling short of vertical from front border of eye. SNOUT projecting about a third of its

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[14] Dr. Hildebrand evidently excluded from the Albulidae the deep-water genus *Pterothrissus*, which is known from the coasts of Japan and West Africa and which may eventually be found in the western North Atlantic. *Pterothrissus* differs widely from *Albula* and *Dixonina* in the very long, many-rayed dorsal fin.—G. S. Myers.

length beyond tip of lower jaw. CAUDAL SKELETON (*39*: 269–275) exhibiting some ganoid characters, showing a relationship with that primitive group. VERTEBRAE: last 2 or 3 in *A. vulpes* out of line with central axis, directed somewhat dorsally; massive spines (neurals) attached to them and preceding segment, extending into base of upper lobe of caudal. ALIMENTARY CANAL appearing as a straight tube in larvae, becoming modified in the adult with development of a very large stomach that occupies fully 67% of the length of abdominal cavity if distended with food; stomach largely a blind sac; the cardiac and pyloric orifices rather close together. About 13 PYLORIC COECA, bound together, forming a sort of sheath over part of stomach. AIR BLADDER very long, extending backward far beyond vent, its walls very thin, without lung tissue (see tarpon) except for a pair of very small kidney-shaped cellular bodies attached ventrally at about midlength.

Remarks. This genus differs from *Dixonina* chiefly in that the last ray of both dorsal and anal is short and does not become prolonged in adults; see also Key, p. 133. From *Elops* it is distinguishable by the absence of a gular plate (p. 123).

Range. Only one modern species, *Albula vulpes*, is generally recognized; this occurs in virtually all warm seas.

Albula vulpes (Linnaeus) 1758

Bonefish, Grubber, Bananafish

Figures 22, 23

Study Material. An almost complete growth series ranging from leptocephali with virtually undeveloped dorsal and anal fins to adults 430 mm TL, from both Atlantic and Pacific. As the growth series was not complete in the material from the Atlantic, some specimens, especially the older stages of leptocephali and first stages of young adults, from the Pearl Islands in Panama Bay, were used in describing the young.

Distinctive Characters. See *Remarks*, above.

Description. Proportional dimensions in per cent of standard length, and counts, based on Atlantic adults only.

Body: depth at origin of dorsal 20–23 in large specimens, 14–19 in young adults.
Caudal peduncle: depth 6.9–8.9.
Head: length 27.5–32.
Snout: length 11.5–13.6 in large specimens, 8.5–10 in young adults.
Eye: diameter 5.5–8.0
Maxillary: length from tip of snout 9.1–12.7.
Anal fin: length of base 5.1–6.75.
Pectoral fin: length 15–19.
Scales: 65–71.
Gill rakers: 7 or 8+9 or 10.
Fin rays: dorsal 17 or 18, rarely 19; anal 8 or 9; pectoral 16 or 17, rarely 15.
Vertebrae: 72–74 (5 specimens).

Body slender, rounder and less compressed in large specimens than in young adults, its dorsal profile more convex than ventral profile, its depth at dorsal origin 4.35–4.9 in SL in large specimens, about 5.25–7.1 in the more slender, recently-metamorphosed young. Scales firm, with crenulate membranous edges. Head low, especially in large specimens, flat above, its depth exceeding its width at middle of eye by about diameter of pupil, 3.0–3.8 in SL. Snout rather long, conical, especially in large specimens, projecting about a third of its length beyond mandible, 2.2–2.5 in head, about 2.7–3.5 in young adults. Eye moderately small, 4.4–5.5 in head, its center nearer to margin of opercle than to tip of snout. Maxillary not quite reaching to eye in large specimens, but extending to, or slightly beyond, anterior margin of eye in young adults, 2.6–3.15 in head (measured from tip of snout).

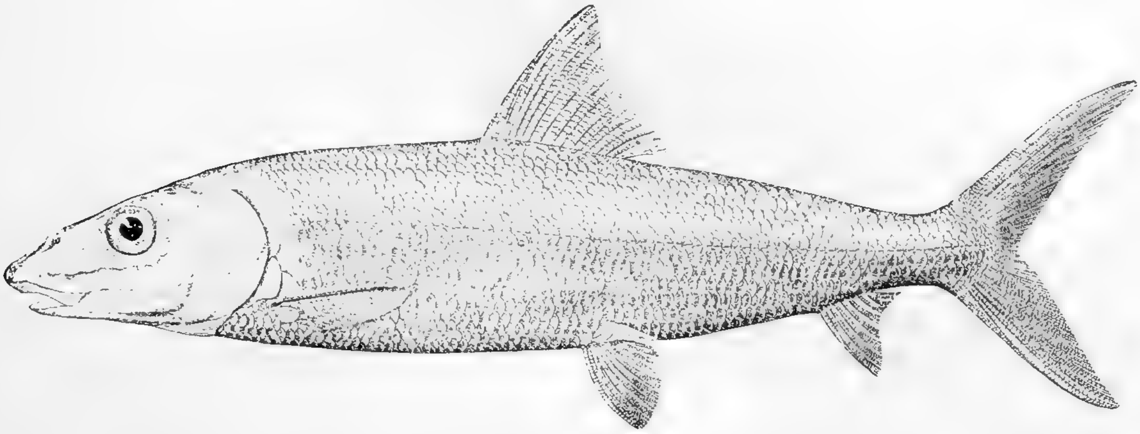

Figure 22. *Albula vulpes,* from off Newport, Rhode Island; from Goode. Drawn by H. L. Todd.

Dorsal fin somewhat elevated anteriorly, its longest rays not reaching to tip of posterior ray if deflexed, its origin a little nearer to tip of snout than to base of caudal. Caudal deeply forked, the upper lobe somewhat longer than the lower. Anal very small, its origin notably nearer to base of caudal than to base of pelvic, its last ray, though longer than the preceding one, not especially produced, its base 4.7–5.4 in head. Pelvic somewhat smaller than pectoral, inserted under or slightly behind middle of dorsal base. Pectoral with rounded margin, reaching notably less than halfway to pelvic, 1.7–2.0 in head. Axillary scale of pectoral about half as long as fin, adherent to body.

Color. Large specimens bluish above; bright silvery on sides and below; dark streaks between rows of scales, at least on dorsal half of side; dorsal and caudal with dusky margins, frequently entirely pale in preserved specimens. Very young adults (completely metamorphosed and about 30 mm) with a double series of dark spots on the back, each just off the median line; these spots soon uniting to form about nine dark crossbands on the back, extending down nearly or quite to lateral line; the third band crossing back at origin of dorsal; next two situated posteriorly under base of dorsal;

bands persisting until a length of about 75 mm. The dark longitudinal streaks of the adults appearing shortly before crossbands become obscure.

Size. Its maximum length is about 770 mm (31 in.) and its weight about 13 or 14 pounds.

Development.[15] The eggs and the earliest stages of the leptocephali remain unknown. The youngest at hand, that is, the least developed larva, is apparently somewhat younger than any yet described. It is 57 mm long (51 mm SL), was collected at Tortugas, Florida, and is the only one of the many that has the dorsal and anal fins entirely undeveloped. The pectoral fins appear as mere tufts of membrane and the pelvics only as a thickening of the body wall where the bases are developing. The caudal fin, however, is well developed with segmented rays, is broadly forked, and is about as long as the head. This larva is sharply compressed, though not more so than considerably older ones; its depth increases gradually backward from the head to about the beginning of the distal fourth of the body, where it is contained 11.8 times in SL. Myomeres are prominent, except anteriorly and posteriorly, and about 66 may be counted. The head is low and moderately broad and is contained 16.4 times in SL. The snout is conical and projects slightly beyond the mandible, the maxillary is not definitely formed, the slightly oblique gape extends under the anterior part of the eye, and the eye is scarcely as long as the snout, being contained in the head 4.1 times. The intestinal tract appears to be a straight tube, is rather loosely attached to the body, has a slight groove on each side, and extends nearly to the base of the lower lobe of the caudal. This old preserved specimen, collected in 1919, is now entirely without pigment. Several other specimens from Tortugas and Cuba are only slightly more developed.

Although leptocephali 75–87 mm long have been reported (*28*: 40),[16] the largest one now at hand among several hundred from many localities along the Atlantic and Pacific coasts of America is just 70 mm long (57 mm SL). In this specimen, one of a large collection from the Pearl Islands, Panama Bay, the dorsal and anal fins are developed (showing at least most of the rays), and the fulcra may be fairly accurately enumerated. The dorsal fin is placed over about the beginning of the distal fifth of the body. The anal is scarcely separated from the base of the lower caudal lobe. The pelvic fins are developed but do not have definite rays and are placed at about midbody length without the head, a position retained throughout life. The pectoral fins are fairly long, with definite indications of rays. The body is deepest somewhat in advance of the dorsal fin, and its depth there is contained 9.25 times in SL; 69 myomeres were counted. No prominent changes in the head region are evident. The head is contained 14.4 times in the SL. The snout and eye are of about equal length, being 3.6 in head. The jaws possess minute teeth that project somewhat forward. Two almost continuous dotted dark lines bound the intestinal tract from behind the pectoral fins to the vent, being

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[15] A detailed account of the development and distribution of young *Albula*, based on the DANA collections, has recently been published by Alexander (DANA Rep., *53*, 1961).

[16] The fact that *Albula* has a "leptocephalus" larva was first ascertained about 1896 by Prof. C. H. Gilbert of Stanford University. It seems he never published an account himself, but a synopsis of his findings, with his figures of the developmental stages, was made known by Jordan (*44*) and Gill (*28*: 43) — G. S. Myers.

interrupted only at the point of insertion of the pelvics; and a vertical series of dark dots is present on the caudal base. Living larvae of this size, and considerably older ones as well, are as transparent as glass. They appear as shining objects in the net and are easily overlooked, only the dark eyes being at all conspicuous.

Older larvae of 45 mm (39 mm SL), though still sharply compressed, are much more substantial than younger ones at a length of 70 mm or so. The dorsal and anal fins have moved forward considerably, the anal fin now being separated from the caudal by at least half the length of the head. The greatest body depth, at the origin of the dorsal, is contained 7.6 times in SL. The myomeres total 70–72. The head remains rather low and broad and is contained 6.0 times in the length; the snout projects beyond the mandible more prominently and is now rather longer than the eye, 4.0 times in head; and the maxillary is fairly well developed, extending well beyond the anterior margin of the eye, 2.4 in head. The color remains as in the younger fish described, except that a few dark chromatophores have appeared about the head, and a slightly broken dark line has developed on both upper and lower lobes of the caudal.

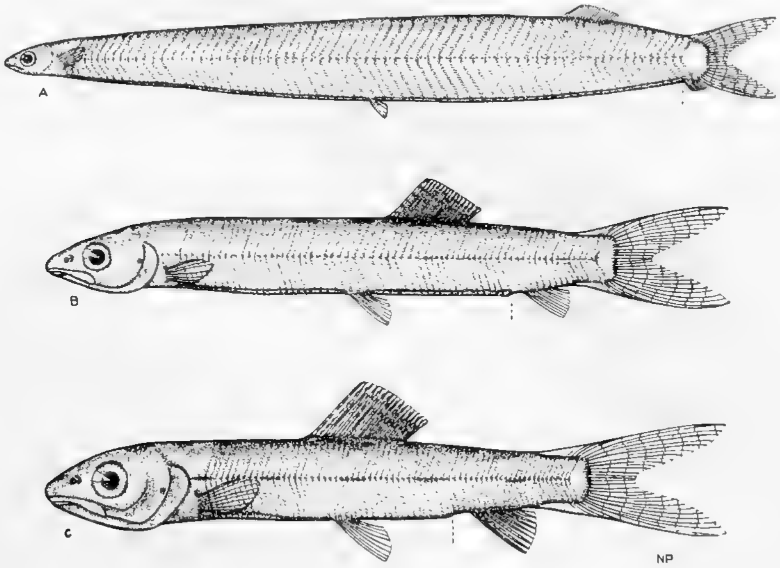

FIGURE 23. *Albula vulpes.* Pearl Island, Pacific Panama, USNM 128391. A Leptocephalus stage, 68 mm long; B older larva in transition stage, 76 mm TL; C older fry 30 mm TL. Drawn by Nancy D. Patton.

Larvae 32 mm long (26 mm SL) are the smallest in the study collections that may be classed as leptocephali. The body remains strongly compressed, though of course more robust and more substantial than in the 45-mm fish described above, and it has become more elongate, the depth at the dorsal origin being contained 8.4 times in SL. The dorsal and anal fins have continued to move forward, but they still remain more posteriorly placed than in the adult; the origin of the dorsal is somewhat nearer to the base of the caudal than to the tip of the snout and is approximately over the pelvic fins. The intestinal tract has become more fully invaginated and no longer remains merely attached, except posteriorly, as in younger fish; the vent, instead of being situated at the origin of the anal, is now well in advance of it, having moved forward rather more rapidly than the fin. The color markings remain about as in the younger fish described, but additional chromatophores have appeared, principally at the occiput, at the base of the dorsal, and on the dorsal.

The smallest specimen that may be classed as a young adult is 28 mm (21 mm SL), and its length is the least of the many *Albula* at hand. This fish is quite a little longer than the one that diminished from a leptocephalus to a young adult of only 20 mm, in an aquarium (*39*: 269; *40*: 109). The body remains more compressed in this and other young adults than in large adults, and it is also more slender, the depth at the dorsal origin 6.5 times in SL. The head is contained 3.45 times in SL and therefore does not differ in this proportion from large adults. The eye is rather small, 5.05 times in head, and is definitely shorter than the snout, which is contained 3.05 times in the head and projects rather prominently beyond the mandible; the maxillary extends to the anterior margin of the pupil and is contained 2.9 times in head. The dorsal and anal fins have continued to move forward, the origin of the dorsal now being equidistant between base of caudal and tip of snout; and the attachment of the pelvic fins is now only a little in advance of the middle of the dorsal base. At this stage, and even in ones a little older, the two dark lines along the sides of the intestinal tract in the leptocephali persist, two rows of dark spots on the back (described elsewhere) have appeared, there are indications of some elongate dark spots along the side, and some additional pigment has appeared on the base of the anal and ventrally on the caudal peduncle.

Scales first appear in young adults about 35 mm long. At a length of 40–45 mm, scalation generally is complete, except perhaps on the abdomen. At these stages the lateral line also is well developed. The dorsal and anal fins are situated approximately as in large adults; that is, the origin of the dorsal is somewhat nearer to the tip of the snout than to the base of caudal, and the anal is separated from the caudal by a distance somewhat greater than the length of the snout. The pelvic fins, which, from the time of their appearance in the leptocephalus, are inserted a little nearer to the head than to the base of caudal, retain that relative position and are now about under the middle of the dorsal base. The pectorals are long but not falcate and reach more than halfway to the pelvics. The vent has continued to move forward and is now in advance of the anal by a distance nearly equal to the length of the snout.

At 40 mm, pigmentation has become general and the nine crossbands on the back, described elsewhere, are prominent. But dark longitudinal stripes do not appear definitely until a length of about 75 mm is attained, at which size the crossbands have become obscure.

Spawning. The spawning season and the spawning grounds remain unknown. Most of the many larvae and young adults described herein were taken off the coast of Panama during February and March, but their occurrence at other seasons is not known, as no year-round collecting has been done there. Growth stages ranging from fairly young leptocephali of 70 mm TL to young adults 52 mm long were exceedingly numerous among some of the Pacific islands in Panama Bay in March 1937 (especially in the Pearl Islands). Somewhat similar stages, though less numerous, were taken in February and March on the Atlantic coast of Panama. Other leptocephali at hand were taken as follows: January 23 on the Pacific coast of Colombia, February 13 in Puerto Rico, March 13 in the Virgin Islands, April 8 in Cuba, April 23 and 28 in Haiti, May 19 in Cuba, June 30 at Beaufort, N.C., July 21 in Bermuda, and August 7 and November 25 at Tortugas, Florida. Beebe and Tee-Van (*5*: 37) have reported that on 34 evenings of collecting (between February 26 and April 30) with an electric light lowered from the gangway of a schooner in Port-au-Prince Bay, Haiti, larvae of *Albula* were absent only two nights and were very abundant 17 nights. With the capture of the leptocephali spread over most of the year and at widely spaced localities, there is little indication of where and when spawning takes place.

Although an advanced leptocephalus transformed rapidly in an aquarium under observation (*39*: 269; *40*: 109), it cannot be concluded that development before capture was equally fast, and that the rapid transformation under artificial conditions was normal, especially in the light of what is known about the slow development of the leptocephali of freshwater eels. At least the possibility exists that the rather advanced leptocephali that have been described may have been several months old and were caught far from the place where they had hatched.

Habits. The adult is usually caught in comparatively shallow water, but to what extent it enters deep water offshore apparently has not been determined. The larva has been taken at night at the surface under an electric light, by which it seems to be attracted, and during the day in the shallow water of bays and estuaries with seines, at least once in a creek with nearly fresh water (in Panama), and on one occasion in the surf on the outer shores of Bogue Banks, North Carolina. During March 1937, the larva and young adult were found in great abundance among islands in Panama Bay. In one very shallow tide pool with a muddy bottom, off San José Island in the Pearl Islands group, the water was literally "soupy" with fish and crustaceans. At the time there was an exceptionally low tide, and the concentration was so great and the water so shallow and warm that many small shrimp and fish perished, but the greater part of the aggregation seemed to endure the situation. It was possible to select from this pool a growth series ranging from leptocephali 70 mm long, the youngest present, to young adults 52 mm long.

Food. This fish, known as the Grubber in Bermuda (*40*: 104) grubs up some of its food from the bottom with its nose and sometimes turns somersaults in the process. In the West Indies and Florida it may be seen by day (*53*: 187), along shallow sandbanks and among underwater grasses, feeding during incoming tides on worms, mollusks, and crabs; but in Bermuda it apparently comes into the shallows at night to feed. Bivalves and small squid have been reported as its food (*5*: 37). In the Pearl Islands, young adults were gorged with small shrimp, but a few fish (small atherinids) had been eaten also.

Relationship and Variation. Only one species has been recognized. Insufficient material from its wide range has been studied, but the present study of specimens from the Atlantic and Pacific coasts of America has shown no constant differences or variations of importance.

Relation to Man. This species is not considered a good foodfish in most of its range in America. Schroeder, reporting on the fisheries at Key West, Florida, stated that "it is not highly regarded as a foodfish, and its commercial value is negligible" (*61*: 4). Similar statements are included in publications about the fishes of the West Indies. But Hollister, presumably reporting on observations made in Bermuda, stated to the contrary that "it surpasses its famous cousin, the Silver King, or tarpon, in possessing a combination of qualities, that of gaminess and of being a table delicacy" (*40*: 104). From the writer's own observations in Panama, the Bonefish is considered an inferior foodfish, whereas the tarpon is highly regarded as food by the native population. Thus tastes seem to differ in different localities.

However, the Bonefish ranks high with anglers, especially around Florida and the Bahamas, for it is so wary when feeding on the flats that careful stalking and long and delicate casting are called for; but once hooked, its runs are longer and swifter and its resistance far more vigorous and indefatigable than one might expect from such a comparatively small fish.

Miss Francesca LaMonte of the American Museum of Natural History, long acquainted with the sport fisheries, has generously offered the following information: This warm-water fish, which provides splendid angling with simple equipment, is caught on the flats and can be fished there either from a boat or while wading. The boat should be light as well as flat-bottomed and should be provided with an outboard motor, oars, and anchors for both bow and stern. The fish is taken by casting or still fishing, but the favorite method is casting. Light tackle with plug casting or saltwater fly rod provides good sport. As bait, anglers may use conch, crabs or crayfish, feathers, lures, or squid. Coming in with the tide, the Bonefish spreads out over the flats and among the mangrove stands; when the tide ebbs, it seeks deep holes. On the flats, the angler may chum or get his bait into the middle of a "mud" or group of Bonefish that is feeding, with tails uppermost while grubbing on the bottom.

When hooked, the Bonefish makes a very fast and strong run, taking out yards of line. In so doing it varies the straight dash by suddenly turning and coming toward the boat or by running into the mangroves where the line may be cut on the roots. After making several of these runs, the Bonefish usually begins to wear out, begins circling the boat, and can finally be picked up in a landing net.

For many years the angling record stood at $13^3/_4$ pounds for one caught on the famous Bonefish grounds off Bimini in the northern Bahama Islands, but this record was eventually beaten. The present record is for a fish of 18 pounds 2 ounces, caught off Kauai, Hawaiian Islands. In the western North Atlantic, the best known Bonefish grounds are the Florida Keys near Miami, the Islamorada-Marathon area, and the northern Bahamas.

Range and Abundance. The Bonefish is known from virtually all warm seas. On the Atlantic coast of America it is plentiful around southern Florida, among the northern Bahamas, and around Bermuda. But its area of chief abundance evidently does not reach much farther to the north, for it is rare even at Beaufort, North Carolina. However, odd specimens have been reported for the vicinity of New York (*2*: 183), Newport, Rhode Island (*68*: 74), the vicinity of Woods Hole, Massachusetts (*67*: 741), and perhaps even Charlotte County, New Brunswick, at the mouth of the Bay of Fundy (ftn. 15).

To the south it is present more or less regularly in the West Indies and on the Atlantic coast of Panama, though it does not seem to be numerous; it is known from as far south as Rio de Janeiro. On the Pacific coast of America it has been reported as occurring from San Francisco Bay, California, to Talara, Peru.

Synonyms and References:[17]

Esox vulpes Linnaeus, Syst. Nat., ed. 10, 1758: 313 (orig. descr.; based on *Vulpes bahamensis* Catesby, pre-Linnaean; type local. Bahamas; no type specimen).

Albula s. *Salmo albula* (nec *Salmo albula* Linnaeus) Meuschen, in Gronow, Zoophyl., *3*, 1781: index, unpaged (on "*Albula*" Gronow; type local. Mediterranean; type lost).

Clupea brasiliensis Bloch and Schneider, Syst. Ichthyol., 1801: 427 (orig. descr.; type local. Brazil; based on Marcgrave's MSS. in Berlin).

Albula conorhynchus Bloch and Schneider, Syst. Ichthyol., 1801: 432, pl. 86 (orig. descr.; based on Gronow, Plumier, and Marcgrave; no special type local. except Medit. and Amer.); Günther, Cat. Fish. Brit. Mus., *7*, 1868: 468 (descr., synon., Amer. locals.—West Indies, Jamaica, Belize, Puerto Cabello, Bahia, Natal, and Pacif. cst. of Centr. Amer.); Yarrow, Proc. Acad. nat. Sci. Philad., 1877: 215 (Ft. Macon, North Carolina).

Albula plumieri Bloch and Schneider, Syst. Ichthyol., 1801: pl. 86 (name on plate only; LAPSUS for *conorhynchus*).

Amia immaculata Bloch and Schneider, Syst. Ichthyol., 1801: 451 (orig. descr., after *Macabi* Parra [1787: 88, pl. 35, fig., nonbinomial]; type local. S. Amer.).

Clupea macrocephala Lacépède, Hist. Nat. Poiss., *5*, 1803: 426 (orig. descr.; type local. Martinique; after Plumier fig.).

Glossodus forskåli Agassiz, in Spix and Agassiz, Pisc. Brasil, 1829: 49; called *Engraulis sericus* on pl. 23 and *E. bahiensis* on pl. 24, fig. 2 (orig. descr.; type local. Bahia, Brazil; type probably in Munich).

Albula parrae Cuvier and Valenciennes, Hist. Nat. Poiss., *19*, 1846: 339 (orig. descr.; type local. Bahia and Rio de Janeiro, Brazil; type in Paris).

Butirinus vulpes Storer, Synop. Fish. N. Amer., 1846: 212 (diagn., refs.).

Albula rostrata Gronow, Cat. Fish., Gray ed., 1854: 189 (orig. descr.; type locals. Amer. and Indian oceans, Medit. Sea; type probably in London).

Conorhynchus plumieri Poey, Repert. Fisico-Nat. Cuba, *2*, 1867: 423 (descr., Cuba).

Albula vulpes Jordan and Gilbert, Bull. U.S. nat. Mus., *16*, 1883: 258 (descr., range); Bean, Bull. U.S. Fish Comm. (1888), *8*, 1890: 206 (not uncommon at Cozumel, Yucatán); Collins and Smith, Bull. U.S. Fish Comm. (1891), *11*, 1892: 104 (commerc. catch, Gulf coast, Florida, 1890); Eigenmann, Proc. U.S. nat. Mus. (1892), *15*, 1893: 135 (not abund. at San Diego, California); Henshall, Bull. U.S. Fish Comm. (1894), *14*, 1895: 211 (common at keys, passes, inlets of s. Florida, good food and game fish); Lönnberg, Ofvers. Svensk. Vet. Akad. Forh., 9, 1895: 662 (Cape Haitien, Haiti); Jordan and Evermann, Bull. U.S. nat. Mus., 47 (*1*), 1896: 411; 47 (*4*), 1900: fig. 179 (descr., range, synon.); Jordan and Rutter, Proc. Acad. nat. Sci. Philad., 1897: 94 (Jamaica); Smith, Bull. U.S. Fish Comm. (1897), *17*, 1898: 91 (rare at Woods Hole, Massachusetts); Evermann and Kendall, Rep. U.S. Comm. Fish. (1899), 1900: 55 (Florida); Gilbert, Proc. Wash. Acad. Sci., *2*, 1900: 163 (Pernambuco and Maceió, Brazil);

[17] Literature dealing with American specimens only, or in part, is cited. It does not seem necessary to cite Old World references here.

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Elops saurus Gregg (not *Elops saurus* Linnaeus, but *Esox vulpes* Linnaeus), Where to Catch Fish. E. Cst. Fla., 1902: 33, fig. (descr., habitat, feed., instruct. for angling, fairly edible).

Negative Reference:

Albula vulpes Gregg, Where to Catch Fish. E. Cst. Fla., 1902: 34 (not *Albula vulpes* Linnaeus, but *Elops saurus* Linnaeus).

Genus *Dixonina* Fowler 1911

Dixonina Fowler, Proc. Acad. nat. Sci. Philad. (1910), 1911: 651; type species by original designation, *Dixonina nemoptera* Fowler.

Characters. See species account below.

Remarks. Dixonina is easily distinguished from *Albula* by the produced last ray of both dorsal and anal fins. Furthermore, *Dixonina* has a somewhat longer and more conical snout and a larger mouth than *Albula*.

Range. A single species is known; this has been reported from the West Indies, Venezuela, northern Brazil, and from the Pacific coast of México and Central America.

Dixonina nemoptera Fowler 1911

Shafted Bonefish[18]

Figure 24

Study Material. One Pacific coast specimen, about 413 mm long, 334 mm SL, from Acapulco, México, USNM 75547, recorded by Myers.

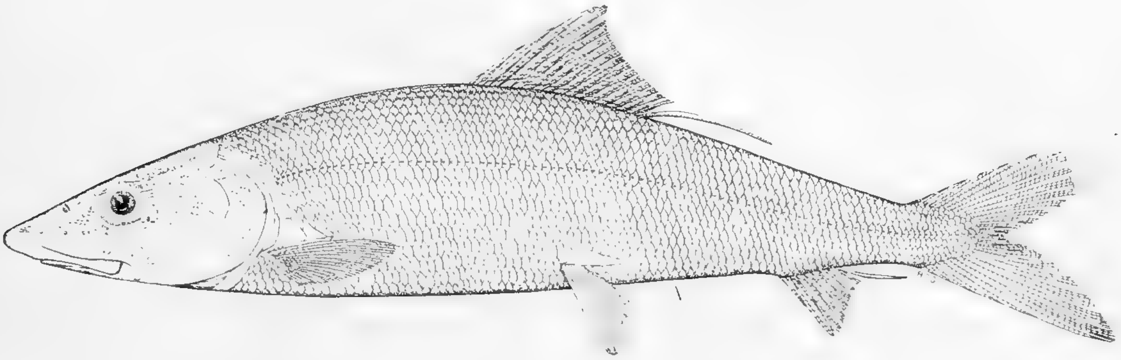

FIGURE 24. *Dixonina nemoptera,* 413 mm TL, Acapulco, Pacific coast of México, USNM 75547. From drawing by Ann S. Green.

Description. Proportional dimensions in per cent of standard length, and counts, based on Pacific specimen 334 mm SL.

Body: depth at origin of dorsal 23.
Head: length 29.5.
Snout: length 10.8.
Eye: diameter 5.4.
Maxillary: length from tip of snout 13.5.

Anal fin: length of base 5.5.
Pectoral fin: length 15.6.

Scales: 76.
Gill rakers: 5 + 10.
Fin rays: dorsal 19; anal 8; pectoral 16.

BODY slender, the back somewhat elevated, the ventral outline nearly straight; depth at origin of dorsal 4.3 in SL. SCALES firm, with crenulate membranous edges.

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[18] Name suggested by George S. Myers.

HEAD long and low, flat above, its depth at middle of eye exceeding its width at the same place by diameter of pupil, 3.4 in SL. SNOUT very long, projecting more than a third of its length beyond mandible, 2.7 in head. EYE moderately small, 5.4 in head, its center notably nearer to tip of snout than to margin of opercle. MAXILLARY extending nearly to middle of eye, 2.15 in head (measured from tip of snout).

DORSAL fin moderately high anteriorly, its longest anterior rays about as long as snout and eye, its last ray filamentous, almost reaching vertical from origin of anal, its origin about equidistant between tip of snout and caudal base. CAUDAL deeply forked, the upper lobe apparently longer than the lower (somewhat damaged). ANAL very small, its last ray produced, extending nearly to base of caudal fulcra, its origin equidistant between base of caudal and base of last dorsal ray, its base 3.5 in head. PELVIC not much smaller than pectoral, inserted about under middle of dorsal. PECTORAL not falcate, extending halfway to pelvic, 1.9 in head. AXILLARY SCALE of pectoral adherent to body, not very distinct.

Color. An old preserved specimen, slightly bluish above, silvery below; narrow dark streaks between rows of scales on upper part of side. Live specimens from the Pacific were described by Beebe (*4*: 44) as follows:

> Brilliant silver, appearing dark above in certain lights with dark green on the head; this dorsal pigmentation resolves into eight very dark lines along each side of upper half of the body, covering about one-fourth of each scale nearest to the adjoining line. Dorsal fin greenish, caudal dusky, anal silvery at base, a dusky spot at pectoral base, with yellow spot behind; basal membrane of pectoral apple green, rest of fin dusky. These colors fade at death. Iris silvery.
>
> In the young, at least up to 90 mm in length, two rows of dark spots extend along the side of body, the upper close to the mid-back. In a 115 mm fish the spots are less conspicuous and the dorsal dark lines begin to be distinct. The spots persist after death. In full-grown fish the dark scale lines are fainter than in fish of medium size.

Relationship. The specimen at hand from the Pacific agrees very well with two published accounts of Atlantic fish. Some Pacific coast specimens have been described as *D. pacifica* by Beebe (*4*: 43), who considered them specifically distinct from the Atlantic ones. On the basis of available descriptions (not specimens) of Atlantic fish, the differences between his Pacific specimens and those from the Atlantic were set forth as follows:

> In the former (*D. pacifica*) there is a greater number of lateral line scales (81 to 84, as compared with 76); increased number of vertical lines of scales on dorsal half (9 not 7) and on ventral half (9 not 7); decrease in predorsal scales (22 instead of 30); small eye (6.8 to 7, not 4.15); longer pelvic fins (2.2 and not 2.7); greater number of gill-rakers (7 + 11 instead of 4 + 9).

Most of the apparent distinctions between the Atlantic and Pacific specimens pointed out by Beebe become obscure or are of doubtful value in the light of measurements and enumerations based on the Acapulco fish. The number of scales in a longitudinal series seems to differ on the opposite sides of this fish; on the right side I counted 76 scales with pores (excluding greatly reduced ones on caudal base) and 79 on the left.

Again, I counted 77 oblique series (running upward and backward) just above the lateral line on the right side and 83 on the left. No variation in the number of longitudinal rows between the lateral line and origin of dorsal, and between the lateral line and origin of anal, occurs in the specimen studied, as these are respectively 8 and 6 full rows on each side. As to the number of scales in advance of the dorsal, the specimen before me has 21 modified scales in the median series, and 31 oblique series of ordinary scales (running upward and backward) on each side of the median row.

As neither Fowler (*24*: 652) nor Beebe stated which of the two was counted, I made inquiry of Mr. Fowler, who re-examined the type and found 21 modified scales in the median series, and 30–32 ordinary scales in the oblique series. As to the size of the eye in proportion to the length of the head, the specimen at hand is intermediate, the eye being contained in the head 5.4 times. The pelvic fin also is intermediate, its length 2.35 times in head. I have no doubt that the gill rakers in *Dixonina* become shorter and obscure with age, as they do in *Albula*, and that in large specimens it is difficult without dissection to see all of the bases, for that is all that remains of some of them. In the specimen from Acapulco, I find 5 + 10, including one in the angle with the lower limb count, a figure intermediate between counts given by Beebe and by Fowler.

It may be concluded, on the basis of the evidence presented, that *D. pacifica* for the present at least is a synonym of *D. nemoptera*.

Range. This albulid, as here understood, is known from the Atlantic from the type taken at Santo Domingo and from a specimen collected at Puerto Cabello, Venezuela.[19] For the Pacific it is known from a specimen taken at Acapulco, México (reported by Myers), and from 19 specimens taken off the coast of Costa Rica (reported as *D. pacifica* by Beebe). According to Walford (*71*: 119), the fish from the Gulf of California figured as *Albula vulpes* by Kumada and Hiyama (*47*: pl. 5) also is this species.

Synonyms and References:

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Albula nemoptera Metzelaar, Trop. Atlant. Vissch., 1919: 9 (descr.; Puerto Cabello, Venezuela).

Albula vulpes (not of Linnaeus) Kumada and Hiyama, Mar. Fish. Pacif. Cst. Mexico, 1937: 27, pl. 5 in color (descr., in part at least, and plate based on *Dixonina*).

Dixonina pacifica Beebe, Zoologica, *27* (8), 1942: 43, figs. 1–5 (orig. descr.; type local. Puerto Culebra, Costa Rica; SU 46486; cf. *D. nemoptera*).

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[19] One seen from Brazil.—G. S. Myers.

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Suborder Clupeoidea

COMPOSITE AUTHORSHIP[1]

Characters and Key to Families

HENRY B. BIGELOW
Museum of Comparative Zoology
Harvard University

Characters. EYES of the usual sort, i.e. not at the tips of short (tubular) cylinders or of slender stalks, nor with orbital cavity extended downward. ADIPOSE fin absent. PELVIC fins at least no farther forward than midlength of body and farther rearward than this in most, but lacking in a few. FIN RAYS jointed, and most of them branched. SCALES: the head naked, except in some Alepocephalidae; the trunk scaly in most, but naked in some of the Alepocephalidae (p. 250); scales large, thin, their free bony edge entire in most, often with crenulated membranous margin, but more or less strongly pectinate in a few genera (*Brevoortia*, p. 342, Fig. 85; and *Ethmidium*); exposed surface smooth or only weakly sculptured; midline of abdomen with scales of the ordinary shape in most, but with a double row of larger, sharp-pointed, and stiffer scales (scutes) in others (Clupeidae, pp. 257, 259, 260). BARBELS absent on chin or on throat. LUMINESCENT ORGANS lacking in most, but present in a few (some Alepocephalidae and all Searsiidae). LATERAL LINE well developed in most families (Engraulidae, Alepocephalidae, Searsiidae) but not visible in others (Clupeidae) though continuing rearward below scales to base of caudal except as it may occasionally perforate a few anterior scales (*10*: 957). GILL MEMBRANES wholly free from isthmus in the great majority.[2] BONY GULAR PLATE absent in chin region between branches of

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[1] With the late Samuel F. Hildebrand contributing the family Engraulidae as well as the family Clupeidae, except for the genera *Harengula* by Luis R. Rivas and *Dorosoma* by Robert R. Miller.

[2] Connected to the isthmus by a thin membrane in the anchovy *Cetengraulis* (p. 245).

lower jaw. Gill rakers present in all. Proethmoids not paired. Sides of snout without Sensory canal-bearing bonelets. Branchiostegal rays slender, rod-like, not forming part of the opercular system. Teeth, if any,[3] small in most, larger in a few (Chirocentridae); dental patterns various; teeth never present on the parasphenoid bone in midline of roof of mouth rearward. Premaxillaries not protractile, except in some Alepocephalidae and in the Phractolaemidae.[4] Maxillaries forming part of upper border of mouth in the great majority.[5] Lower jaw without predentary or supra-angular bones. Temporal foramina present.[6] Basal radialia of the pectoral fin in one row in most, articulating directly with the pectoral girdle; in two rows in a few (among the Chirocentridae, *II*: 9–11, fig. 23; *I*: 227, fig. 118, 424). Pectoral girdle with a mesocoracoid element. Pelvic girdle not connected to the pectoral girdle. Last few Vertebrae not evidently upturned in any; lateral processes bearing pleural ribs (parapophyses) simply wedged into pits in vertebral centra, not fused with the latter; a lower series of intermuscular bones well developed in many (notably among Clupeidae), connected basally to pleural ribs and lying between muscle blocks (myotomes).[7] Ovaries with complete Oviducts, so far as known. Swim bladder present in most,[8] dorsal in position, and connected throughout life to the alimentary tract via an open pneumatic duct. Stomach with numerous pyloric caeca. Intestine without spiral or circular folds in most, but perhaps not in all.[9] Arterial cone of heart never with two rows of valves. Larvae not leptocephalus-like.

Families. The following families fall within the Suborder as defined above: i Clupeidae, including Dussumierinae and Dorosomatinae, p. 257; ii Alepocephalidae, p. 250; iii Searsiidae, p. 254; iv Engraulidae, p. 152; v Chirocentridae (regarded by Regan [*8*: 313–314] and Norman [*5*: 72] as a subfamily of Clupeidae; by Berg [*I*: 227, 422] as a separate Suborder, Chirocentroidei), Indian Ocean, China, and Japan; vi Chanidae, tropical Indo-Pacific; vii Phractolaemidae, Niger and Congo rivers; viii Kneridae, rivers of tropical Africa; and ix Cromeriidae, the Nile.

Clupeidae, Alepocephalidae, Searsiidae, and Engraulidae are represented in the North Atlantic. The Dolichopterygidae and the Macristiidae have also been referred to the Clupeoidea by one author or another. But *Dolichopteryx* (Part 4) falls among the Argentinoidea, as has long been evident from Parr's excellent illustration of it (*6*: 37, fig. 14). And the affinities of the Macristiidae remain as doubtful today as was the case in 1911, when Regan (*7*: 204, 205) redescribed the only specimen of the family that has yet been seen.

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[3] The Chanidae lack teeth, at least as adults.

[4] A freshwater family.

[5] In *Nematalosa* the mouth is bordered above by the premaxillaries, with the maxillaries covered by the lip, as is pictured very clearly by Ridewood (*9*: 465, fig. 127 as "*Chaetoessus*").

[6] Shown clearly in Ridewood's illustrations; see ftn. 5.

[7] For a diagram showing the relative positions of the pleural ribs and of the lower intermuscular bones, see Bertin (*4*: 704, fig. 462).

[8] Lacking among the Alepocephalidae; probably among the Searsiidae also.

[9] A structure suggesting the elasmobranch spiral valve, but probably not homologous, has been reported in *Chirocentrus* (see especially Goodrich, *3*: 116, fig. 77) and in *Alepocephalus* (Cuvier and Valenciennes, *2*: 176).

Key to Families of Clupeoidea, Known or to be Expected in the Western North Atlantic

1a. Tip of fleshy snout overhanging mouth. Engraulidae, p. 152.

1b. Tip of fleshy snout not overhanging mouth; at most the upper jaw protruding a little beyond lower.

  2a. Shoulder close behind upper part of gill opening, with a conspicuous projecting tubular papilla, open at the tip. Searsiidae, p. 254.

  2b. Shoulder without projecting tubular papilla.

    3a. Rear end of base of dorsal fin in advance of origin of caudal by a distance as long as head (longer in most); sides silvery; swim bladder well developed. Clupeidae, p. 257.

    3b. Rear end of base of dorsal fin in advance of origin of caudal by a distance considerably shorter than head; sides not silvery; no swim bladder. Alepocephalidae, p. 250.

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Family Engraulidae[1]

SAMUEL F. HILDEBRAND[2]

Characters. BODY moderately slender, compressed. CHEST and ABDOMEN in American species often carinate, without bony serrae. MOUTH horizontal or nearly so. MAXILLARY extending well beyond eye, sometimes nearly or quite to gill opening. SNOUT blunt, generally projecting far beyond tip of mandible. EYE placed well forward, in anterior half of head, sometimes with well developed adipose tissue in adults. PREMAXILLARIES not protractile, embedded in tissue of snout anteriorly, widely separated medianly. TEETH typically minute (some on jaw enlarged in *Lycengraulis*); present on jaws, vomer, palatines, pterygoids, and hyoids. GILL COVERS generally separate and free from isthmus (connected by a thin membrane in *Cetengraulis*). PSEUDOBRANCHIAE present. GILL RAKERS generally slender, rarely short, broad, and spiny; increasing in number with age in some species (as in *Anchovia*). SCALES thin, cycloid (usually lost on preserved specimens), generally if not always forming a sheath on bases of dorsal and anal fins; an enlarged scale in axil of pectoral and pelvic fins in American species. LATERAL LINE absent. DORSAL fin usually median in position, rarely behind mid-length, with about 12–16 rays in American genera. ADIPOSE FIN lacking. CAUDAL FIN rather deeply forked. ANAL with various ray counts, about 15–40 in American species.

Genera. The division of the family into compact and clearly definable genera is difficult. Thus there is a divergence of opinion among students concerning the status of described genera. Seven genera have been recognized (*3*), all confined to American waters, excepting *Engraulis*, which, though not represented in the western North Atlantic, is very widely distributed in both hemispheres; 75 species have been recog-

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[1] Edited, with some revision and expansion, by George S. Myers, Myvanwy M. Dick, Henry B. Bigelow, and Yngve H. Olsen.

[2] August 15, 1883–March 16, 1949.

nized, 44 from the Atlantic and 32 from the Pacific, including one species common to both coasts of tropical America. For the Atlantic species that come within the scope of this work, see the Table of Contents.

Commercial Importance. Some anchovies, because of their tremendous abundance, are of considerable importance. Some are canned whole or are used in the production of anchovy paste, and larger species are commonly sold fresh in the market, as in South America; they are also used extensively as bait. But their value as a forage fish for water birds and creatures that frequent the sea far exceeds their direct value to man. Many of the larger commercially important fishes, such as the seatrout, bluefish, and mackerels, feed on them extensively.

Range. Representatives of the family occur in the warmer shore waters throughout the world. Some of the species ascend freshwater streams, and probably a few live entirely in fresh water. The Engraulidae are most numerous in tropical regions, but several species either range into temperate waters or live there permanently.

Key to Genera of the Western North Atlantic

1a. Gill covers not connected across isthmus by a membrane.
  2a. Teeth in jaws small or minute, all of about uniform size.
    3a. Origin of anal fin posterior to origin of dorsal; tip of pelvic fin usually below origin of dorsal.
      4a. Maxillary more or less sharply pointed distally, generally reaching well beyond joint of mandible, often to margin of opercle, or nearly so.
        5a. Gill rakers close-set, increasing in number with age, 40–50 in young, about 130 in adults, on lower limb of first arch; body depth usually more than 25% of length; maximum size about 250 mm. *Anchovia* Jordan and Evermann 1896, p. 155.
        5b. Gill rakers not close-set, only about 15–30 on lower limb, not known to increase in number with age; body depth usually less than 25% of length; maximum size generally under 150 mm. *Anchoa* Jordan and Evermann 1927, p. 162.
      4b. Maxillary square or rounded distally, rarely reaching joint of mandible. *Anchoviella* Fowler 1911, p. 204.
    3b. Origin of anal fin in advance of dorsal origin, rarely under it; tip of pelvic fin anterior to a vertical from dorsal origin by a distance equal to about 50% of head.
      6a. Distance of dorsal fin origin from tip of snout much less than twice the distance from dorsal origin to caudal base; gill rakers short and broad, only about 14 on lower limb of first arch; anal with 30–33 rays. *Pterengraulis* Günther 1868, p. 228.

6b. Distance of dorsal origin from tip of snout about twice the distance of dorsal origin from caudal base; gill rakers long, slender, about 33 on lower limb of first arch in young, probably more in adults; anal with about 25 rays. *Hildebrandichthys* Schultz 1949, p. 230.

2b. Teeth in jaws, especially the lower ones, notably large, usually unequal in size. *Lycengraulis* Günther 1868, p. 233.

1b. Gill covers broadly connected across isthmus by a thin membrane (easily torn). *Cetengraulis* Günther 1868, p. 245.

Explanation of Measurements and Counts for Engraulidae.

Total length: from tip of snout to vertical at rearmost point of longest caudal lobe.

Standard length: from tip of snout to base of caudal fin, i.e. to the last vertebra, as nearly as can be determined without dissection.

Caudal peduncle: least depth unless otherwise noted.

Length of head: from tip of snout to most distal part of bony opercular margin, regardless of whether the straight line between these points is horizontal or oblique.

Depth of head: vertical distance at joint of mandible.

Postorbital length: from posterior rim of eye to most distal part of bony opercular margin.

Maxillary: from its anterior embedded end (located by touch) to its posterior extremity.

Cheek (smooth bone below and behind eye): distance from rim of eye to its distal point; the degree of its posterior angle determined by a protractor.

Dorsal and Anal fins: the counts include all rays, whether simple and unsegmented, simple and segmented, or branched; the last ray of the anal, even though split to the base, was counted as one unless definitely separated at base.

Length of pectoral: from base of upper ray to tip of longest ray.

Pectoral axillary scale: distance from base of upper ray of pectoral to tip of the modified scale or process.

Splint: adhering to first ray of pectoral; not considered distinct and not counted.

Scales or Scale pockets: counted along the side from the upper anterior angle of the gill opening to the base of the caudal; as the scales are nearly always lost in preserved specimens, they are generally not shown in the illustrations, except for a small patch.

Gill rakers: the counts are given as a formula, e.g. 12–16 + 15–18 (as for *Anchoa spinifer*), meaning a range of 12–16 rakers on the upper limb of the first branchial arch and 15–18 on the lower limb. The counts include those rudiments, if present, that have a free tip but not those that are mere tubercles. The gill raker at the angle of the first arch generally has a plainly visible root, extending either upward or downward; if the root was directed upward, the raker was included with the upper limb count; if directed downward, it was counted with the lower limb count. Rarely, the raker at the angle has two roots, one directed upward and one downward; in such cases it was included with the lower limb count.

VERTEBRAE: total number, including hypural, as determined by dissections.

Genus *Anchovia* Jordan and Evermann 1896

Anchovia Jordan and Evermann, Bull. U. S. nat. Mus., *47* (1), 1896: 449; type species by original designation, *Engraulis macrolepidotus* Kner and Steindachner 1864.

Characters. BODY in adults compressed, its depth about 2.6–3.8 in SL. SCALES firm, rather adherent. TEETH small, not disappearing with age. GILL RAKERS numerous, increasing in number with age, about 40 on lower limb in young, 100 or more in large specimens. ANAL origin somewhere under anterior 66% of dorsal base. VERTEBRAE 41–43.

Size. A length of 175 mm and upward is attained by most of the species.

Species. The genus *Anchovia* is represented in the Atlantic by *A. clupeoides* and *A. nigra*, and in the Pacific by three species.

Range. In the Atlantic, from the West Indies southward to or beyond Pernambuco (Recife), Brazil, and in the Pacific from the Gulf of California to Ecuador.

Key to Species of the Western Atlantic

1a. Insertion of pelvic fins about equidistant between base of upper ray of pectoral fin and origin of anal; snout projecting beyond mandible by about half its length; anal fin with 30–35 rays, most frequently with 33; vertebrae 42 or 43.
clupeoides (Swainson) 1839, below.

1b. Insertion of pelvic fins nearer to base of upper rays of pectoral fin than to origin of anal; snout projecting beyond mandible by about 67% of its length; anal fin with 28–32 rays, most frequently with 29–31; vertebrae 39–41.
nigra Schultz 1949, p. 158.

Anchovia clupeoides (Swainson) 1839

Sardina Boca Torta, Bocón, Hachudo

Figure 25

Study Material. At least 29 specimens, 75–205 mm TL, from: Puerto Rico; Jamaica; Cuba; Trinidad; several places on the Atlantic coast of Panama; the Gulf of Venezuela; Laguna de Tacarigua, Venezuela; and Pará, Rio Grande do Norte, and Pernambuco (Recife), Brazil. Some small specimens, 48 mm TL and upward, are at hand, but their proportions are not included because they differ considerably from the larger ones, especially in having a more slender body.

Distinctive Characters. A. clupeoides is closely related to *A. rastralis* of the Pacific coast of Middle America, from which it differs in having a slightly longer anal fin, inserted a little farther forward with respect to the dorsal. In specimens of equal size, the maxillary is usually a little shorter and tapers more abruptly in *clupeoides*, and its body is somewhat more slender. *A. clupeoides* apparently grows to a larger size than *A. rastralis*, for none of the latter has been reported to be larger than 110 mm TL. See also *A. nigra*, p. 161.

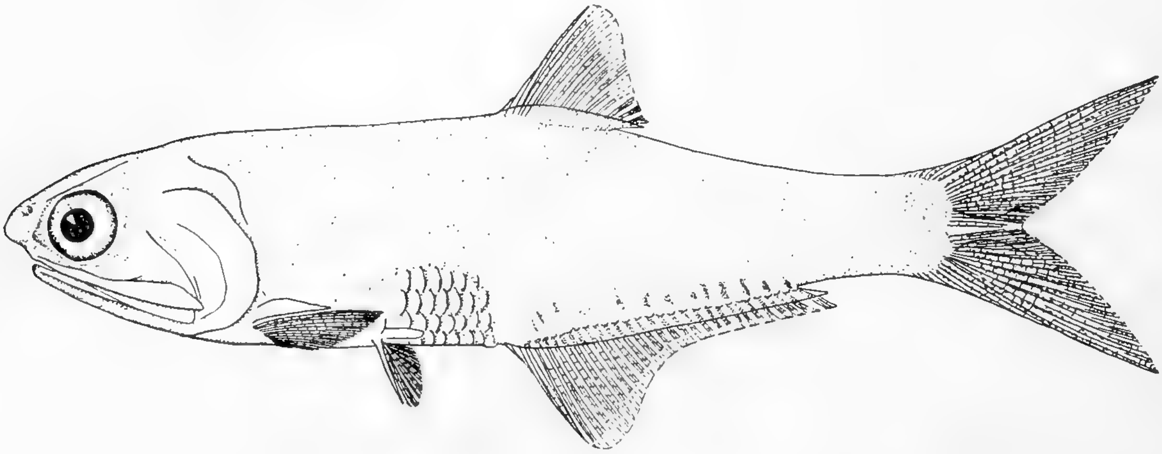

FIGURE 25. *Anchovia clupeoides*, 60 mm TL, 44 mm SL, from Gulf of Venezuela, USNM 127552. Drawn by Louella E. Cable.

Description. Proportional dimensions in per cent of standard length, and counts, based on study specimens 75–205 mm TL.

Body: depth 25–31.
Head: length 27.6–31.
Snout: length 3.1–4.3.
Eye: diameter 6.0–8.3.
Postorbital: distance 15.5–18.5.
Maxillary: length 19.5–22.
Mandible: length 19–20.5.
Anal fin: length of base 30–33.
Pectoral fin: length 15.4–17.3.
Scales: *ca.* 39–43.
Gill rakers: *ca.* 35–40 in younger specimens, 75–110 in those of 130 mm TL.
Fin rays: dorsal 13–15; anal 30–35; pectoral 13 or 14.
Vertebrae: 42 or 43 (6 specimens).

BODY strongly compressed, its depth increasing with age, about 3.2–4.0 in SL in specimens 75 mm TL and upward (*ca.* 4.5 at 50 mm). HEAD 3.2–3.6 in SL, its depth about equal to its length without snout in specimens 150–160 mm TL; less in smaller ones. SNOUT short, projecting about half of its length beyond mandible, 6.0–8.0 in head. EYE 3.5–4.5 in head. MAXILLARY abruptly pointed, reaching to or beyond joint of mandible, 1.3–1.5 in head. MANDIBLE 1.4–1.6 in head. CHEEK as long as snout and eye in large ones, proportionately shorter in small ones, its posterior angle about 35°. GILL RAKERS at angle fully as long as eye in large specimens, shorter in young.

DORSAL fin originating equidistant between caudal base and anterior half of eye, its longest rays often reaching beyond tip of last ray if deflexed. ANAL originating about under middle of dorsal base, its base 3.0–3.5 in SL. PELVIC small, reaching only a little more than halfway to origin of anal, inserted about equidistant between base of pectoral and origin of anal. PECTORAL fin reaching to or slightly beyond base of pelvic in small specimens, often not quite to pelvic in large examples, 1.7–1.9 in head. AXILLARY SCALE of pectoral broad, about half as long as fin, 3.0–3.9 in head.

Color. In alcohol, pale; side of head and lower 75% of body silvery. Young with a silvery lateral band, becoming diffuse in specimens about 100 mm long and disappearing entirely with age. Middle of back with dark streak (missing in some, probably due to fading). Fins unmarked.

Size. The largest specimen examined is 170 mm TL, but 300 mm has been reported (7: 413).

Relation to Man. Its commercial importance is not significant. It occurs occasionally in the Colón market (Panama) and, according to report, in the Havana market (Cuba).

Range. Its range extends from the West Indies to Panama and at least as far southward as Pernambuco (Recife), Brazil, probably to Rio de Janeiro and São Paulo. All specimens studied were apparently taken in salt or brackish water, with one exception; one specimen (CAS 9398) from Lake Rogagua, Bolivia, seems to be this species.

Synonyms and References:

Engraulis clupeoides Swainson, Nat. Hist. Fish. Amphib. Rept., *2*, 1839: 388 (orig. descr.; type local. Pernambuco, Brazil).

Engraulis productus Poey, Repert. Fisico-Nat. Cuba, *1*, 1866: 380 (orig. descr.; type local. Matanzas, Cuba; type MCZ 17961); Poey, Repert. Fisico-Nat. Cuba, *2*, 1868: 423 (Havana, Cuba); Günther, Cat. Fish. Brit. Mus., 7, 1868: 388 (descr., Cuba and Jamaica); Tortonese, Bull. Mus. Zool. Anat. comp. Torino, (3) *47*, 1929: 6 (diagn., Puerto Cabello, Venezuela).

Engraulis surinamensis Steindachner (not of Bleeker), Ichthyol. Beitr., *8*, 1879: 55 (descr., Bahia, Brazil).

Stolephorus clupeoides Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 447 (descr., range, *S. surinamensis* probably incorrectly put in synon.; see *Cetengraulis edentulus*, p. 245); Eigenmann, Rep. Princeton Exped. Patagonia, 1896–1899, *3* (4), 1910; 45 (Surinam to Rio Grande do Sul; *S. surinamensis* Bleeker apparently incorrectly put in synon.).

Stolephorus productus Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 447 (descr., Cuba and Jamaica); Jordan and Rutter, Proc. Acad. nat. Sci. Philad., 1897: 96 (descr., Jamaica); Evermann and Marsh, Bull. U. S. Fish Comm., *20* (1), 1900: 90 (descr., Palo Seco, and Ponce, Puerto Rico); Nichols, Bull. Amer. Mus. nat. Hist., *31*, 1912: 182 ("Havana market").

Anchovia clupeoides Fowler, Proc. Acad. nat. Sci. Philad., *63*, 1911: 211 (Santo Domingo and Rio Seco, Puerto Rico; *E. productus* Poey put in synon.); Starks, Stanf. Univ. Publ. Biol., 1913: 9 (notes, Lake Papary, Natal, Brazil); Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67*, 1926: 412 (descr., range, synon., partly incorrect); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), *2*, 1930: 50 (range, synon., partly incorrect); Fowler, Proc. Acad. nat. Sci. Philad., *83*, 1931: 393 (diagn., Quaima R., Trinidad); Howell-Rivero, Bull. Mus. comp. Zool. Harv., *82*, 1938: 172 (synon.; the larger of two specimens

[MCZ 17961, Poey's 36] stated to be holotype); Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 27, fig. 9 (descr., range, synon.); Schultz, Proc. U. S. nat. Mus., *99*, 1949: 39 (synon., locals. listed).

Anchovia producta Meek and Hildebrand, Field Mus. Publ., Zool., *15* (1), 1923: 210 (descr., Mindi Cut, Colón [market], and Porto Bello, Panama); Nichols, Ann. N. Y. Acad. Sci., *10* (2), 1929: 206 (diagn., range, "not uncommon about Puerto Rico").

Anchovia macrolepidota Fowler (not of Kner and Steindachner), Proc. Acad. nat. Sci. Philad., 1917: 130 (two from Colón, Panama, found by present writer to be *A. clupeoides*).

Anchoviella clupeoides Fowler, Arqu. Zool. estad. São Paulo, *3* (6), 1941: 134 (Brazilian rec.).

Doubtful References:

Stolephorus productus Schreiner and Ribeiro, Arch. Mus. nac., Rio de J., *12*, 1903: 93 (Rio de Janeiro, without comment).

Stolephorus clupeoides Eigenmann and Norris, Rev. Mus. paul., *4*, 1904: 360 (one from São Paulo, Brazil; proportions given indicate ident. probably not correct).

Anchovia nigra Schultz 1949[3]

La anchoa

Figure 26

Study Material. Many paratypes, 14–76 mm TL (12–60 mm SL), and the type, 125 mm TL (95 mm SL), from Lake Maracaibo and its tributary streams.

Distinctive Characters. See *Relationship and Variation*, p. 161.

Description. Proportional dimensions in per cent of standard length, not including small examples regarded as juveniles because they would distort the picture; dimensions and counts based on 11 or more specimens from *Study Material*, 50 mm TL and over.

Body: depth 21–28.9.
Head: length 23–31.3.
Snout: length 4.15–4.3.
Eye: diameter 6.1–8.3.
Postorbital: distance 15–19.
Maxillary: length 18.5–24.
Mandible: length 17–22.
Anal fin: length of base 26–31.
Pectoral fin: length 16–18.

Scales: *ca.* 40–48.
Gill rakers: *ca.* 70+140 in adults, fewer in young.
Fin rays: dorsal 12–14; anal 29–31; pectoral 12 or 13.
Vertebrae: 39–41 (18 specimens).

BODY strongly compressed, rather deep, its depth increasing with age, 3.5–4.75 in SL in specimens 60–125 mm TL, about 5.5 in specimens around 25 mm. HEAD 3.2–4.35, its depth scarcely as great as length of head without snout. SNOUT short, projecting 66% of its length beyond mandible, 6.5–7.1 in head. EYE 3.7–4.3. POSTORBITAL length 5.25–6.7. MAXILLARY abruptly pointed, reaching to or a little beyond joint of mandible, 1.25–1.4 in head. MANDIBLE 1.4–1.5. CHEEK moderately long and

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[3] Dr. Leonard P. Schultz has kindly placed his data on this species in my hands. The proportions and counts used in the *Description* are his and mine.

narrow, about equal to length of snout and eye in adults, its posterior angle approximately 30°. GILL RAKERS at angle fully as long as eye in adults, proportionately shorter in young.

DORSAL fin moderately high anteriorly, the longest rays reaching to or beyond tip of last ray if deflexed, its origin somewhat variable, generally a little nearer to base of caudal than the tip of snout. ANAL fin moderately long, its origin somewhat variable, sometimes nearly under middle of dorsal base, more frequently anterior to this point, its base generally about equal to length of head, 3.2–3.85 in SL. PELVIC fin small, reaching a little more than halfway to origin of anal, inserted a little nearer to base of pectoral than to origin of anal. PECTORAL fin rather large, reaching well beyond base of pelvic, 1.6–1.9 in head. AXILLARY SCALE of pectoral fin broad at base, variable in length, usually reaching to middle of fin or beyond, 3.4–4.1 in head.

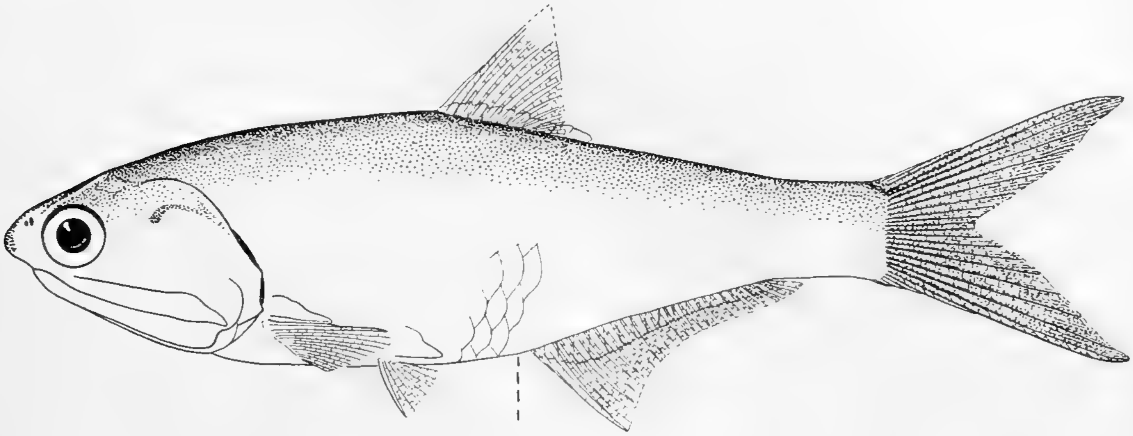

FIGURE 26. *Anchovia nigra*, type specimen, 125 mm TL, from Maracaibo Basin, Venezuela, USNM 121761. Drawn by A. M. Awl.

Color. In alcohol, back a pale straw color. Sides silvery. Silvery lateral band in specimens up to 75 mm TL, the band very narrow in 40-mm specimens, becoming proportionately broader and less well defined ventrally, diffused with silvery color on lower part of sides in largest example; dark streak present on middle of back in large examples but scarcely evident in small ones in which the dark punctulations that later form the band remain separate; scattered punctulations extending down to silvery lateral band. Dorsal and caudal fins with dark points; other fins plain translucent; small specimens, 75 mm TL and under, with dark dots along base of anal fin and on ventral surface of caudal peduncle.

Size. The largest specimen examined, the type (USNM 121761), is 125 mm (5 in.) TL or 95 mm SL. Since a length of 300 mm (12 in.) has been reported for its near relative, *clupeoides*, it may be assumed that larger examples of *nigra* will be found.

Development. The smallest specimen, only 14 mm, is very slender, its depth 9.15 and the head 4.0 times in SL. In this specimen the mouth is nearly terminal, the lower jaw is very thin, the gape ends under the eye, and the maxillary is imperfectly developed. The convoluted intestine, which is usual in larval herring and herring-like fishes, is externally visible. All fins, however, are sufficiently developed to have at least rudimentary rays. The body is pale, no doubt transparent in life, as general pigmentation has not taken place. The juvenile markings consist of dark dots, which, exclusive of a few spots at the nape, are on the lower part of the body; and a few less definite ones are on the side of the head. An elongate median streak extends backward from the isthmus; also there are spots along each side of the ventral edge of the abdomen that become darker and more concentrated along the base of the anal and are reduced to a single row on the midventral line of the caudal peduncle. A row of indefinite dark dots extends along the lateral side of the tail from above the anal base to the caudal base; there are a few more dark dots on the caudal fin.

The body of a fish 20 mm TL is proportionately much deeper than the 14-mm example, as its depth is contained 5.5 times in SL. The proportion of the head does not differ greatly from either the small or large ones described, being 3.75 in SL. Much progress in the development of the mouth parts has been made, however, for the snout is more pointed and it projects prominently beyond the lower jaw. The maxillary is definitely visible and extends well beyond the posterior margin of the eye, where it ends in a rather blunt point. The intestine is no longer visible externally. Pigmentation on the lower part of the body remains about the same as in the smaller example, but dorsally, especially on the median line of the back and on the head, the dark dots are more numerous.

The advances in development with growth between 20–30 mm are not great. The increase in proportionate depth has continued, with the depth now 5.0 times in SL. The snout has become more pointed and projects somewhat more strongly, about as in adults. Some of the gill rakers are developed, 10+20 having been counted in one specimen. Pigmentation has advanced somewhat, as dark dots on the back and on the head have become larger and more numerous. The dark line behind the isthmus has virtually disappeared. The dark spots on the side of the abdomen, along the base of the anal, and on the ventral side of the caudal peduncle have become less distinct. A few elongate dark markings at the base of the outer rays of both lobes of the caudal, already present in the 20-mm specimen, have become more distinct.

In a fish 40 mm long, the depth is contained 4.5 times in SL, and the head 3.5 times. The cheek and opercular bones are well outlined. And the maxillary, which now reaches the margin of the opercle, is provided with minute teeth along its free margin. The gill rakers on the first arch are so numerous and close-set that they are difficult to count; about 35–45 seem to be present. Pigmentation continues to advance; the dark dots on the back have become more numerous and those on the lower parts, exclusive of the ones along the anal base and on the peduncle behind the anal, have disappeared. The upper parts of the body are slightly straw-colored and the sides of the head are bright silvery; the lower part of the body shows a somewhat silvery sheen, and there is slight evidence of a silvery lateral band on the anterior half of the body.

A specimen 70 mm long is shaped essentially like the type, which is 125 mm TL; the body is proportionately about as deep in a 70-mm specimen as in the type; however, the gill rakers on the first arch are fewer, as 44 + 70 were counted, whereas about 70 + 140 seem to be present in the type. Furthermore, the smaller specimen retains the silvery lateral band which the larger specimen has lost; it also retains the juvenile dark markings along the base of the anal fin, which are missing in the larger one.

Relationship and Variation. This species is very close to *clupeoides*, from which it differs significantly in the number of vertebrae, the range in 17 specimens of *nigra* being 39–41 and in 22 specimens of *clupeoides* 42 or 43. The anal fin may begin under the middle of the dorsal base or well in advance of that point in *nigra*, consequently it overlaps with *clupeoides*, in which this fin begins about under the beginning of the second third of the dorsal base. Furthermore, *nigra* generally has fewer rays in the anal fin than *clupeoides*, 28–32 (av. around 30) in 38 specimens, and 30–35 (av. 33) in 58 specimens of *clupeoides*. The lower average number of rays in the anal of *nigra* is reflected in its somewhat shorter base, 3.2–3.85 in SL in 38 specimens of *nigra*, but 3.0–3.5 in 32 specimens of *clupeoides*. The pectoral fin of *nigra* extends well beyond the base of the pelvic fin in smaller specimens and only slightly beyond this point in the largest example, being variable with age in this respect; in *clupeoides* the pectoral generally does not extend quite so far back as the pelvic fin; nevertheless, enough overlapping occurs so that the character is not diagnostic. However, the place of insertion of the pelvic fin generally is diagnostic; in *nigra* it is nearly always inserted somewhat nearer to the base of the upper pectoral rays than to the origin of the anal, whereas in *clupeoides* its insertion generally is almost exactly equidistant between the two points mentioned. Finally, the snout projects about 66% of its length beyond the mandible in *nigra*, and only about half of its length beyond the mandible in *clupeoides*.

A. nigra is also closely related to *A. rastralis* of the Pacific coast of tropical America. But in *nigra* the pelvic fins are inserted somewhat nearer to the pectoral base than to the anal origin, whereas in *rastralis* they are inserted notably nearer to the anal origin than to the pectoral base. The anal in *nigra* begins at, or more usually in advance of, the vertical from the middle of the dorsal base, whereas in *rastralis* it generally begins at or behind this point; and *nigra* has 39–41 vertebrae, whereas *rostralis* (like *clupeoides*) has 42 or 43.

Habitat and Range. A. nigra is known only from the fresh or slightly brackish water of Lake Maracaibo, Venezuela, and from the lower sections of its tributary streams. Apparently it does not enter the salt water of the Gulf of Venezuela, where *clupeoides* has been taken.

Reference:

Anchovia nigra Schultz, Proc. U. S. nat. Mus., 99, 1949: 39, fig. 4 (orig. descr.; type local. Lake Maracaibo, Venezuela; type USNM 121761).

Genus *Anchoa* Jordan and Evermann 1927

Anchoa Jordan and Evermann, Proc. Calif. Acad. Sci., *4* (16), 1927: 501; type species by original designation, *Engraulis compressus* Girard 1858.

Characters. BODY usually quite elongate, moderately to strongly compressed. MAXILLARY long, reaching to, or more usually beyond, joint of mandible, frequently to or nearly to margin of opercle, always more or less pointed (except in very young). GILL RAKERS not numerous, seldom more than 22 on upper limb or more than 28 on lower limb except in *cubana* among Atlantic species, not increasing in number with age and growth. ANAL origin under base of dorsal, rarely wholly behind it. VERTEBRAE 38–44, rarely 45 (in Atlantic species).

Remarks. This genus differs from *Anchoviella* principally in its longer maxillary, which is somewhat sharply pointed rather than rounded or squared distally. From *Anchovia* it differs in the fewer gill rakers, the number of which does not increase with age. It differs principally from *Engraulis* (not represented in the western North Atlantic) in the more compressed body (also frequently deeper), and usually in the fewer vertebrae.

Species and Range. This genus contains many species that range the Atlantic from Massachusetts (rarely Nova Scotia) to Argentina, and the Pacific from California to Peru. Some of the species enter brackish or almost fresh water, but none is known to run far upstream.

Table I. Frequency Distribution of Anal Rays in *Anchoa*.

	Number of Rays																						
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
spinifer	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	3	13	6	2	2
argenteus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
duodecim	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
trinitatis	—	—	—	—	—	—	—	—	2	4	7	5	2	—	—	—	—	—	—	—	—	—	—
cayorum	—	—	—	—	—	—	—	3	22	22	12	4	—	—	—	—	—	—	—	—	—	—	—
pectoralis	—	—	—	—	—	—	—	6	8	2	1	—	—	—	—	—	—	—	—	—	—	—	—
mitchilli mitchilli	—	—	—	—	—	1	8	22	63	74	51	30	11	1	—	—	—	—	—	—	—	—	—
mitchilli diaphana	—	—	—	—	—	2	11	55	83	62	44	14	5	—	—	—	—	—	—	—	—	—	—
parva	—	—	1	8	18	18	3	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
januaria	—	—	—	1	3	12	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
choerostoma	—	—	—	5	14	16	9	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
tricolor	2	9	30	17	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
cubana	—	—	9	13	7	9	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
ginsburgi	3	3	2	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
lamprotaenia	—	1	10	31	43	81	56	14	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
hepsetus hepsetus	21	28	42	57	20	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
hepsetus colonensis	3	4	13	13	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
lyolepis	—	2	7	11	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
filifera	—	1	3	3	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Key to Species of the Western North Atlantic

1a. Anal fin with 25 rays or more (*m. mitchilli* rarely with 24); anal base 25–35.6% of SL (*pectoralis* sometimes only 23.4%).

2a. Origin of dorsal about an eye's diameter nearer to tip of snout than to base of caudal; anal with 30 rays or more.

3a. Origin of anal under or somewhat in advance of middle of dorsal base; 32 or more anal rays.

4a. Anal with 35–40 rays; pectoral fin generally reaching far beyond base of pelvic fin, 5.0–5.7 in SL; margin of caudal black.
spinifer (Cuvier and Valenciennes) 1848, p. 167.

4b. Anal with 32 rays; pectoral fin not reaching far beyond base of pelvic fin, 6.5 in SL; margin of caudal not black.
argenteus Schultz 1949, p. 169.

3b. Origin of anal behind dorsal base; 30 anal rays.
duodecim (Cope) 1869, p. 170.

2b. Origin of dorsal nearer to base of caudal than to tip of snout; anal usually with less than 30 rays (*mitchilli* and *trinitatis* sometimes with as many as 30).

5a. Origin of dorsal nearer to posterior margin of eye than to base of caudal; longest rays of dorsal reaching to or beyond tip of last ray when deflexed; pectoral usually with more than 12 rays (*cayorum* sometimes with only 12).

6a. Depth of body 22.2–25.5% of SL; gill rakers usually 16–19 + 19–22 (rarely only 15 on upper limb); anal base 29.4–33.4% of SL.
trinitatis (Fowler) 1915, p. 171.

6b. Depth of body 18.2–22.2% of SL; gill rakers 12–14 + 17–19 (*cayorum* rarely with 15 on upper limb, *pectoralis* occasionally with 20 on lower limb); anal base 23.5–29.4% of SL.

7a. Maxillary narrowly pointed, extending nearly or quite to margin of opercle, 19.2–22.5% of SL; origin of anal well in advance of middle of dorsal base; pectoral with 12 or 13 rays, generally failing to reach base of pelvic fin by about half of diameter of eye, 13.9–16.6% of SL. *cayorum* (Fowler) 1906, p. 173.

7b. Maxillary bluntly pointed, extending only slightly beyond joint of mandible, 17.7–19.0% of SL; origin of anal generally under middle of dorsal base; pectoral with 15–17 rays, reaching nearly to base of pelvic fin, 17.8–18.8% of SL.
pectoralis Hildebrand 1943, p. 174.

5b. Origin of dorsal nearer to base of caudal than to posterior margin of eye, very rarely equidistant; longest rays of dorsal usually failing to reach tip of last ray when deflexed; pectoral with 11 or 12 rays.
mitchilli (Cuvier and Valenciennes) 1848, p. 176.

8a. Greatest thickness of body usually exceeding depth of caudal peduncle; depth 15.8–25% of SL; pectoral often failing to reach base of pelvic by diameter of eye, 12–18% of SL; vertebrae 39–44, most frequently 42. *m. mitchilli* Hildebrand 1943, p. 176.

8b. Greatest thickness of body often less than depth of caudal peduncle; depth 18.2–26.5% of SL; pectoral often extending to or nearly to base of pelvic, 13–20% of SL; vertebrae 38–42, most frequently 40. *m. diaphana* Hildebrand 1943, p. 176.

1b. Anal fin with less than 25 rays (*lamprotaenia* occasionally with 25 or 26 rays, *choerostoma* rarely with 25); anal base 17.2–25% of SL (*januaria* sometimes 26).

9a. Pectoral without a long, filamentous ray (rarely with a slight filament in *lamprotaenia*); origin of dorsal fin usually nearer to base of caudal than to tip of snout, rarely equidistant.

10a. Origin of anal in advance of base of last dorsal ray; depth of head at joint of mandible exceeding postorbital length; snout much shorter than eye; cheek shorter than snout and eye combined; silvery lateral band much narrower than eye.

11a. Gill rakers on lower limb 23–33, on upper limb 18–23 (rarely only 17).

12a. Depth of body 18.2–22% of SL; pectoral fin 14–18.5% of SL; gill rakers rather robust, not closely crowded, not difficult to count.

13a. Origin of anal under or near middle of dorsal base; depth of body 20–22% of SL.

14a. Maxillary sharply pointed distally, extending nearly to margin of opercle, 1.2–1.35 in head; vertebrae 38–40 (rarely 41). *parva* (Meek and Hildebrand) 1923, p. 181.

14b. Maxillary bluntly pointed distally, extending only to or slightly beyond joint of mandible, 1.3–1.5 in head; vertebrae 41 or 42. *januaria* (Steindachner) 1879, p. 183.

13b. Origin of anal far behind middle of dorsal base; depth of body 18.2–21% of SL.

15a. Cheek as long as eye and fully 75% of snout length; pectoral fin 15.6–18.5% of SL; axillary scale of pectoral about half of length of fin, 3.0–4.0 in head; anal with 22–24 rays. *choerostoma* (Goode) 1874, p. 185.

15b. Cheek scarcely longer than eye; pectoral fin 14–14.8% of SL; axillary scale of pectoral fully 75% of length of fin, 1.9–2.75 in head; anal with 18–22 rays. *tricolor* (Agassiz) 1829, p. 186.

12b. Depth of body 15–18% of SL; pectoral fin 12.5–13.7% of SL; gill rakers very slender, close-set, often difficult to count. *cubana* (Poey) 1868, p. 188.

11b. Gill rakers on lower limb usually 16–22 (rarely 23 in *h. hepsetus*), on upper limb usually 14–20 (rarely 13 or 21).

16a. Depth of body 17.4–18.8% of SL; maxillary bluntly pointed distally, its upper margin rounded, extending to joint of mandible, 17.2–18.2% of SL; vertebrae 44 or 45. *ginsburgi* Hildebrand 1943, p. 190.

16b. Depth of body 18.5–23% of SL; maxillary usually sharply pointed distally, generally extending beyond joint of mandible, sometimes to or nearly to margin of opercle (moderately short, rather blunt distally, and rounded above in *lamprotaenia*), 19–24.5% of SL; vertebrae 39–43 (*h. hepsetus* sometimes with 44).

17a. Longest rays of dorsal fin usually reaching well beyond tip of last ray when deflexed; origin of anal about under beginning of posterior third of dorsal base; axillary scale of pectoral only a little more than half of length of fin, 3.0–3.6 in head; cheek fully as long as eye and half of snout. *lamprotaenia* Hildebrand 1943, p. 192.

17b. Longest rays of dorsal fin failing to reach tip of last ray when deflexed; origin of anal usually about under middle of dorsal base, sometimes posterior to middle; axillary scale of pectoral 2.0–2.5 in head; cheek usually not much longer than eye. *hepsetus* (Linnaeus) 1758, p. 194.

18a. Pectoral fin often failing to reach base of pelvic by diameter of eye; silvery lateral band usually 75% of width of eye. *h. hepsetus* Hildebrand 1943, p. 194.

18b. Pectoral fin frequently extending to or nearly to base of pelvic; silvery lateral band often scarcely wider than pupil. *h. colonensis* Hildebrand 1943, p. 194.

10b. Origin of anal under or behind base of last dorsal ray; depth of head at joint of mandible equal to postorbital length; snout scarcely shorter than eye, 4.3–5.5 in head; cheek about as long as snout and eye combined; silvery lateral band as broad as eye. *lyolepis* (Evermann and Marsh) 1902, p. 200.

9b. Pectoral with a long filamentous ray; origin of dorsal fin usually nearer to tip of snout than to base of caudal. *filifera* (Fowler) 1915, p. 202.

Table II. Frequency Distribution of Gill Rakers on Upper Limb of First Arch in *Anchoa*.*

	Number of Gill Rakers											
	12	13	14	15	16	17	18	19	20	21	22	23
spinifer	1	2	11	14	3	—	—	—	—	—	—	—
argenteus	—	—	—	1	—	—	—	—	—	—	—	—
duodecim	—	—	1	1	—	—	—	—	—	—	—	—
trinitatis	—	—	—	1	1	7	9	1	—	—	—	—
cayorum	1	12	24	3	—	—	—	—	—	—	—	—
pectoralis	1	12	2	—	—	—	—	—	—	—	—	—
mitchilli mitchilli	—	—	—	8	38	63	56	5	—	—	—	—
mitchilli diaphana	—	—	—	9	95	118	44	8	—	—	—	—
parva	—	—	—	—	—	—	3	25	10	—	—	—
januaria	—	—	—	—	—	—	—	—	2	1	2	2
choerostoma	—	—	—	—	—	1	9	9	4	—	—	—
tricolor	—	—	—	—	—	—	1	7	19	8	1	—
cubana	—	—	—	—	—	2	3	9	12	5	8	5
ginsburgi	—	—	—	—	1	2	1	—	—	—	—	—
lamprotaenia	—	7	56	47	13	6	4	—	—	—	—	—
hepsetus hepsetus	—	—	—	1	19	52	47	23	9	—	—	—
hepsetus colonensis	—	—	—	3	9	24	12	1	—	—	—	—
lyolepis	—	—	—	1	5	8	23	12	6	1	—	—
filifera	—	—	—	—	—	5	4	4	—	—	—	—

* When the counts exceed the number of specimens listed in the text, the rakers were counted on both anterior arches.

Table III. Frequency Distribution of Gill Rakers on Lower Limb of First Arch in *Anchoa*.*

	Number of Gill Rakers																		
	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
spinifer	4	11	24	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
argenteus	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
duodecim	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—
trinitatis	—	—	—	—	1	3	7	8	—	—	—	—	—	—	—	—	—	—	—
cayorum	18	40	22	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
pectoralis	—	—	3	13	4	2	—	—	—	—	—	—	—	—	—	—	—	—	—
mitchilli mitchilli	—	—	—	—	—	4	21	45	70	54	21	6	—	—	—	—	—	—	—
mitchilli diaphana	—	—	—	—	—	12	64	125	92	46	10	3	—	—	—	—	—	—	—
parva	—	—	—	—	—	—	—	—	7	10	14	13	1	—	—	—	—	—	—
januaria	—	—	—	—	—	—	—	—	2	4	4	5	—	—	—	—	—	—	—
choerostoma	—	—	—	—	—	—	—	—	10	12	9	6	—	—	—	—	—	—	—
tricolor	—	—	—	—	—	—	—	—	—	11	20	25	8	2	—	—	—	—	—
cubana	—	—	—	—	—	—	—	—	3	2	11	6	8	18	8	7	2	2	2
ginsburgi	—	—	—	—	—	2	3	8	—	—	—	—	—	—	—	—	—	—	—
lamprotaenia	—	2	26	94	82	31	8	5	—	—	—	—	—	—	—	—	—	—	—
hepsetus hepsetus	—	—	—	9	27	97	93	47	2	1	—	—	—	—	—	—	—	—	—
hepsetus colonensis	—	—	—	—	4	15	25	4	—	—	—	—	—	—	—	—	—	—	—
lyolepis	—	—	—	—	4	11	14	11	7	5	5	4	—	—	—	—	—	—	—
filifera	—	—	—	—	—	3	3	12	1	—	—	—	—	—	—	—	—	—	—

* When the counts exceed the number of specimens listed in the text, the rakers were counted on both anterior arches.

Anchoa spinifer (Cuvier and Valenciennes) 1848

Sardine

Figure 27

Study Material. Many specimens, 30–175 mm TL: from the Atlantic at the Gatun Locks, Canal Zone; Port-of-Spain, Trinidad; and Bahia, Cachoeira, and Santos, Brazil; from the Pacific at Pedro Miguel and Miraflores locks, Canal Zone; Panama Bay; and Guayaquil, Ecuador.

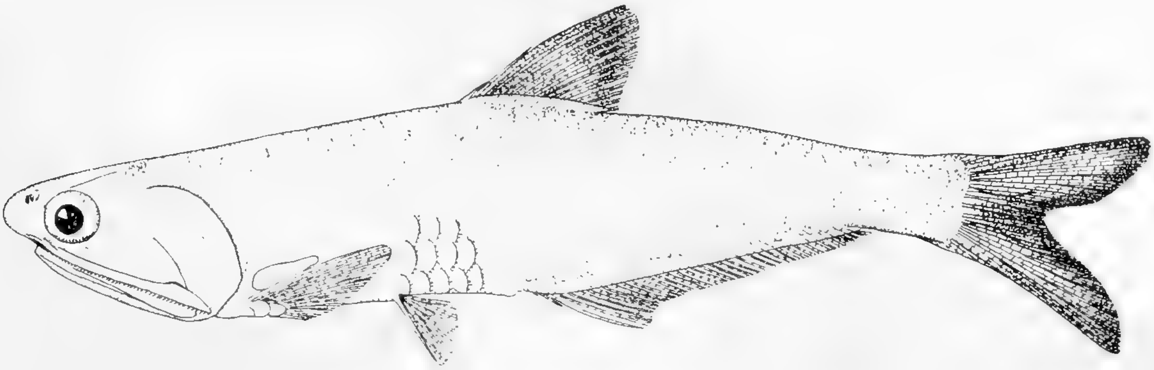

FIGURE 27. *Anchoa spinifer*, 90 mm TL, from Gatun Locks, Canal Zone, USNM 127560. Drawn by Louella E. Cable.

Distinctive Characters. The long anal fin, the dorsal's high rays in the anterior part, the dorsal's forward position, the long low head and especially its prolonged postorbital portion, the long narrow cheek, and the dark margin of the caudal fin distinguish this species from all of its relatives. Large examples generally are proportionally deeper than small ones, and generally Atlantic specimens are rather deeper than Pacific ones. However, there is so much overlapping that, with the material at hand, specimens from the opposite coasts cannot be separated by this character, nor seemingly by any other. The pectoral fin also varies greatly in proportional length, but this also seems to be an individual variation. Nevertheless, the comparison is not satisfactory because nearly all of the Atlantic specimens are old and faded, not in good condition.

Description. Proportional dimensions in per cent of standard length, and counts, based on 11 Atlantic specimens and 15 Pacific specimens, 66–175 mm TL.

Body: depth 19.2–25.
Head: length 25–27.8.
Snout: length 3.0–4.3.
Eye: diameter 4.5–6.25.
Postorbital: distance 14.9–16.6.
Maxillary: length 20.8–23.2.
Mandible: length 19.6–20.3.
Anal fin: length of base 33.1–36.6.
Pectoral fin: length 17.5–20.

Scales: *ca.* 45.
Gill rakers: 12–16+15–18.
Fin rays: dorsal 14–16; anal 35–40; pectoral 12–14.
Vertebrae: 43–45 (15 specimens).

Body quite elongate, rather strongly compressed, its depth 4.0–5.2 in SL, increasing somewhat with age and growth. Head 3.6–4.0 in SL, its depth scarcely exceeding its postorbital length. Snout projecting nearly its full length beyond mandible, 6.6–7.5 in head. Eye small, 4.2–5.0. Postorbital part of head long, 1.5–1.7 in head. Maxillary long and pointed, reaching to or nearly to margin of opercle, 1.1–1.25 in head. Mandible 1.22–1.4. Cheek in large specimens much longer than snout and eye, about equal to snout and eye in specimens about 80 mm TL; posterior angle sharp, about 30°.

Dorsal fin high anteriorly, its longest ray reaching far beyond tip of last ray if deflexed, its origin generally rather more than an eye's diameter nearer to tip of snout than to base of caudal. Anal 2.8–3.0 in SL, its origin generally somewhat in advance of middle of dorsal base. Pelvic reaching about 66% of distance to anal, inserted about equidistant between origin of anal and base of pectoral. Pectoral large, reaching to, and generally beyond, base of pelvic, 1.3–1.5 in head. Axillary scale of pectoral broad, reaching somewhat beyond midlength of fin, 2.4–2.9 in head.

Color. In alcohol, pale above. Lower half of side silvery. Young sometimes with a poorly defined silvery lateral band. Back with dusky punctulations. Fresh specimens 125 mm TL and upward (taken in Pedro Miguel and Miraflores locks, Canal Zone) bright orange, this color contrasting conspicuously with black margin of caudal fin.

Size. The largest specimen seen, about 175 mm TL or 7 inches (caudal fin damaged) and 138 mm SL, is probably near the maximum size attained.

Range and Habitat. The range in the Atlantic, so far as known, extends from Panama to Santos, Brazil. On the Pacific side it is known from Panama Bay to Guayaquil, Ecuador. The West Indies has been included in the general range (7: 410), but I have seen no specimens from that locality and have found no other record. In rather extensive collecting on the Atlantic coast of Panama (during the dry seasons), only a single small specimen was secured; but on the Pacific side it was exceedingly abundant in Pedro Miguel and Miraflores locks when these were drained in 1937; however, it was not seen elsewhere during four different seasons of collecting. The water ranges from near oceanic salinity in the lower flights of Miraflores Locks (at sea level) to fresh in Pedro Miguel Locks.

Synonyms and References:

Engraulis spinifer Cuvier and Valenciennes, Hist. Nat. Poiss., *21*, 1848: 39 (orig. descr.; type local. Cayenne, French Guiana); Günther, Cat. Fish. Brit. Mus., *7*, 1868: 394 (descr., type local.); Steindachner, Ichthyol. Beitr., 8, 1879: 58 (descr.; Guiana; Bahia and Cachoeira, Brazil; w. coast of Panama).

Stolephorus spinifer Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 448 (descr., range); Eigenmann, Mem. Carneg. Mus., *5*, 1912: 449 (synon., descr., Georgetown, British Guiana); Puyo, Bull. Soc. Hist. nat. Toulouse, *70*, 1936: 65, 163 (diagn., habitat French Guiana); Puyo, Bull. Soc. Hist. nat. Toulouse, *80*, 1945: 105, fig. 3 (descr., French Guiana); Puyo, Faune Emp. Franç., *12*, Poiss. Guyane Franç., 1949: 156, fig. 79 (descr., French Guiana).

Anchovia spinifera Gilbert and Starks, Mem. Cal. Acad. Sci., *4*, 1904: 46, pl. 8, fig. 15 (descr. based on two from Panama Bay); Meek and Hildebrand, Field Mus. Publ., Zool., *15* (1), 1923: 207 (synon., descr., range); von Ihering, Rev. Industr. Anim., Anno 1 (3), 1930: 233 (ref., diagn.); Hildebrand, Zoologica, N. Y., *24* (1), 1939: 25, 30, 36 (Panama Canal locks).

Anchoviella spinifera Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67*, 1926: 409 (descr., Cachoeira, Brazil; "Panama" presumably Pacific coast; "West Indies" in range); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 50 (range); Fowler, Arqu. Zool. estad. São Paulo, *3*, 1941: 134 (refs., Brazil).

Anchoa spinifer Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 38, fig. 10 (synon., descr., range, local abund.).

Anchoa argenteus Schultz 1949

Figure 28

Study Material. Known only from the type, *ca.* 115 mm TL (caudal fin damaged), 94 mm SL, from Lake Maracaibo, off Pueblo Viejo, Venezuela.

Distinctive Characters. This species is closely related to *A. spinifer*, with which it agrees in the shape and position of the dorsal fin, the long low head, the long narrow cheek, and in many other respects. But it differs significantly from that species (so far as can be determined from a single specimen) in having fewer anal rays, in a slightly greater number of gill rakers on the lower limb, in the longer mandible, in the shorter pectoral fins, and in the absence of a dark margin on the caudal fin.

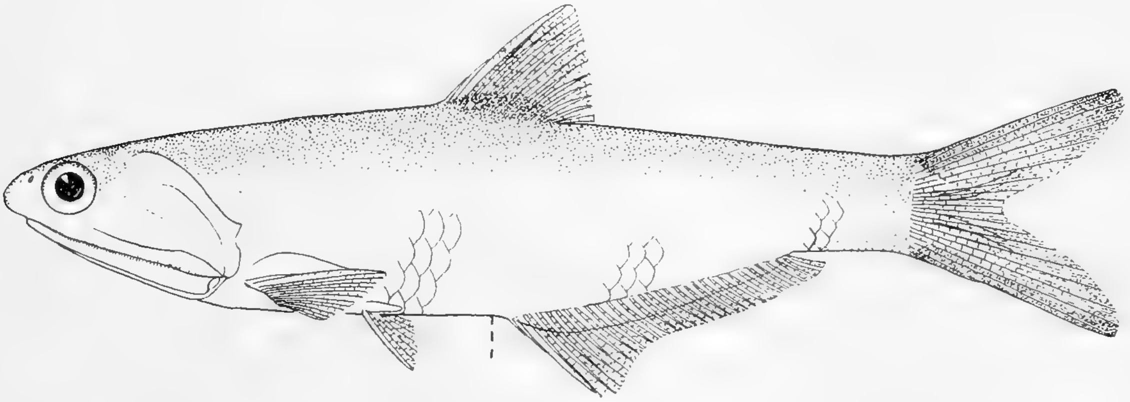

FIGURE 28. *Anchoa argenteus*, type specimen, 94 mm TL, from Maracaibo Basin, Venezuela, USNM 121777. Drawn by A. M. Awl.

Description. Proportional dimensions in per cent of standard length, and counts, based on the type specimen, 94 mm SL.

Body: depth 22.5.
Head: length 26.5.
Snout: length 4.25.
Eye: diameter 5.55.
Postorbital: distance 18.5.
Maxillary: length 23.5.
Mandible: length 20.6.

Anal fin: length of base 32.
Pectoral fin: length 15.5.

Scales: *ca.* 43.
Gill rakers: 14 + 19.
Fin rays: dorsal 16; anal 32; pectoral 13.

Body elongate, rather strongly compressed, its depth 4.5 in SL. Head 3.75, its depth a little greater than its postorbital length. Snout shorter than eye, projecting much more than half of its length beyond tip of mandible, 6.25 in head. Eye small, 4.8. Postorbital length 5.4. Maxillary moderately pointed, reaching margin of opercle, 1.15 in head. Mandible 1.3. Cheek narrow, much longer than snout and eye, its posterior angle about 30°. Gill rakers at angle of first arch about 66% of length of eye, with strong serrae on inner edge, somewhat expanded at tips.

Dorsal fin moderately elevated anteriorly, its margin nearly straight, its longest rays reaching well beyond the last ray if deflexed, its origin about an eye's diameter nearer to tip of snout than to base of caudal. Anal fin fairly long, its origin under middle of dorsal base, its base notably longer than head, 3.1 in SL. Pelvic fin reaching a little more than halfway to origin of anal, inserted a little nearer to base of pectoral than to origin of anal, 3.1 in head. Pectoral fin reaching beyond base of pelvic by about half of diameter of eye, 6.5 in SL, 1.7 in head. Axillary scale of pectoral extending to beginning of distal third of fin, 2.55 in head.

Color. In alcohol, somewhat straw-colored on back, changing rather abruptly to silvery on the side at level of upper margin of eye; back with dusky punctulations, these extending onto basal 66% or so of dorsal fin, and onto outer rays of caudal fin.

Range. Known only from Lake Maracaibo, off Pueblo Viejo, Venezuela.

Reference:

Anchoa argenteus Schultz, Proc. U. S. nat. Mus., *99*, 1949: 45, fig. 5 (orig. descr.; type local. Lake Maracaibo, off Pueblo Viejo, Venezuela; type USNM 121777).

Anchoa duodecim (Cope) 1869

New Jersey Anchovy

Study Material. Known only from the type, 97 mm long (77 mm SL), taken at Beesley's Point, New Jersey, ANSP 1363.

Distinctive Characters. This species has been considered identical with *A. mitchilli.* However, it differs strikingly from other local forms in its deep body, high dorsal fin, the positions of the dorsal and anal fins, and in several other respects. It is of interest that the species has never reappeared in collections.

Description. Proportional dimensions in per cent of standard length, and counts, based on the type specimen, 77 mm SL.

Body: depth 25.
Head: length 27.
Snout: length 4.7.
Eye: diameter 5.8.
Postorbital: distance 16.3.
Maxillary: length 22.
Mandible: length 21.

Anal fin: length of base 25.
Pectoral fin: length 18.2.

Scales: partly lost, *ca.* 38.
Gill rakers: 14 or 15+20.
Fin rays: dorsal 14; anal 30; pectoral 12.

Body rather short, deep, and well compressed; dorsal profile more strongly convex than ventral profile. Head short, deep, its depth equal to its postorbital length and half of eye. Snout rather short, projecting a little less than a third of its length beyond mandible, 5.8 in head. Eye small, 4.7. Postorbital 1.6 in head. Maxillary fairly short, reaching joint of mandible, broad and abruptly pointed, 1.25 in head. Mandible 1.3. Cheek as long as snout and eye, its posterior angle about 35°. Gill rakers at angle nearly as long as eye.

Dorsal fin high anteriorly, its longest rays reaching far beyond tip of last ray if deflexed, its origin an eye's diameter nearer to tip of snout than to base of caudal. Anal rather long and low, its origin half of an eye's diameter posterior to end of dorsal base, and about equidistant between base of caudal and base of pectoral, its base 4.0 in SL. Pelvic fin large, shorter than pectoral by diameter of pupil, extending about 66 % of the distance to origin of anal, inserted a little nearer to joint of mandible than to origin of anal. Pectoral reaching base of pelvic, 1.5 in head. Axillary scale of pectoral a little more than half of the fin length, 2.7 in head.

Color. Old preserved specimen grayish brown above. Lower two-thirds of side silvery; no lateral band and no punctulations visible.

Range. Known only from Beesley's Point, New Jersey.

Synonyms and References:

Engraulis duodecim Cope, Trans. Amer. philos. Soc., *13* (2), 1869: 405 (orig. descr.; type local. Beesley's Point, New Jersey; type ANSP 1363).

Anchovia duodecim Fowler, Rep. N. J. St. Mus. (1905), 1906: 111 (descr.); Fowler, Proc. Acad. nat. Sci. Philad., *63*, 1911: 219; Fowler, Proc. biol. Soc. Wash., *33*, 1920: 148.

Anchoa duodecim Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 46 (synon., descr. based on type).

Anchoa trinitatis (Fowler) 1915

Figure 29

Study Material. A total of 19 specimens, including the type, from Trinidad and Venezuela, ANSP, UMMZ, USNM.

Description. Proportional dimensions in per cent of standard length, and counts, based on 10 specimens from *Study Material*, 55–110 mm TL.

Body: depth 22–25.6.
Head: length 24.3–27.
Snout: length 3.9–4.35.
Eye: diameter 6.75–7.6.
Postorbital: distance 11.7–13.3.
Maxillary: length 16.6–22.
Mandible: length 16.4–19.

Anal fin: length of base 29.4–33.2.
Pectoral fin: length 16.6–19.

Scales: *ca.* 38–42.
Gill rakers: 15–19 + 18–22.
Fin rays: dorsal 13 or 14; anal 26–30; pectoral 13 or 14.
Vertebrae: 41 (1 specimen).

Body rather strongly compressed, its greatest thickness about equal to depth of caudal peduncle, its depth 3.9–4.5 in SL. Head short, 3.7–4.1 in SL, its depth equal to its postorbital length and about 66% of diameter of eye. Snout extending about 66% of its length beyond mandible, 5.7–6.6 in head. Eye 3.4–3.7. Postorbital 1.9–2.1 in head. Maxillary pointed, extending nearly to margin of opercle, 1.2–1.4 in head. Mandible 1.4–1.53. Cheek about as long as eye and half of snout, its posterior angle about 40°.

Dorsal fin moderately high anteriorly, its longest rays reaching beyond tip of last ray if deflexed, its origin equidistant between base of caudal and a point at anterior half of eye. Anal origin under, or somewhat in advance of, middle of dorsal base, its base 3.0–3.4 in SL. Pelvic reaching fully halfway to anal, inserted a little nearer to origin of anal than to base of pectoral. Pectoral sometimes not quite reaching to pelvic, 1.35–1.52 in head. Axillary scale of pectoral rather broad at base, scarcely extending to vertical at midlength of fin, 2.8–3.6 in head.

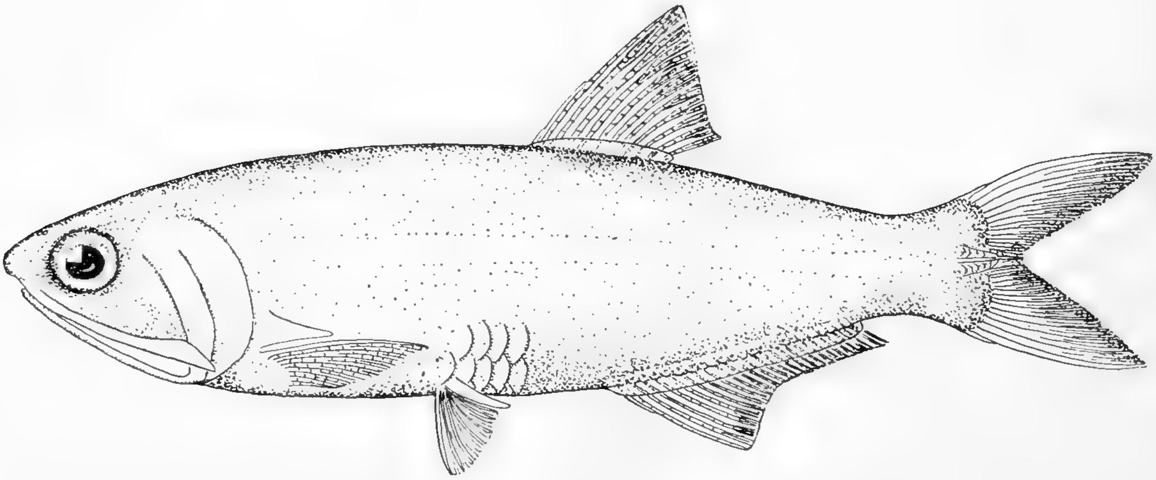

Figure 29. *Anchoa trinitatis*, type specimen, from Port-of-Spain, Trinidad, ANSP 45083, modified after Fowler (1915: 527, fig. 3). Drawn by Alice C. Mullen.

Color. In alcohol, pale above. Side of head and lower part of body silvery. Silvery lateral band faint, narrower than pupil, missing in specimens presumably preserved originally in formalin. Back and upper surface of head with dusky punctulations, sometimes forming two almost continuous lines posterior to dorsal fin.

Size. The largest individual seen is 110 mm TL.

Range. So far as known, this species is confined to four localities: Port-of-Spain and Vessigney, Trinidad; Laguna de Tacarigua (on coast 85 miles east of Caracas), and Rio Caño de Sagua, Sinamaica, Venezuela.

Synonyms and References:

Anchovia trinitatis Fowler, Proc. Acad. nat. Sci. Philad., 1915: 527, fig. 3 (orig. descr.; type local. Port-of-Spain, Trinidad; type ANSP 45083).

Anchoviella trinitatis Fowler, Proc. Acad. nat. Sci. Philad., *83*, 1931: 392 (Vessigney, Trinidad).

Anchoa trinitatis Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 96, fig. 40 (descr. cf. several related species, range); Schultz, Proc. U. S. nat. Mus., *99*, 1949: 44 (synon., specimens and local. listed; counts of rays, gill rakers, vert., and scales).

Anchoa cayorum (Fowler) 1906

Key Anchovy, Manjúa (Cuba)

Figure 30

Study Material. A total of 26 or more specimens, 50–85 mm TL, from Tortugas, Florida; Cabañas Bay, Cuba; Cozumel Island, off Yucatán, México; Belize, British Honduras; and Hailer's Rock, Florida Keys (type and paratype).

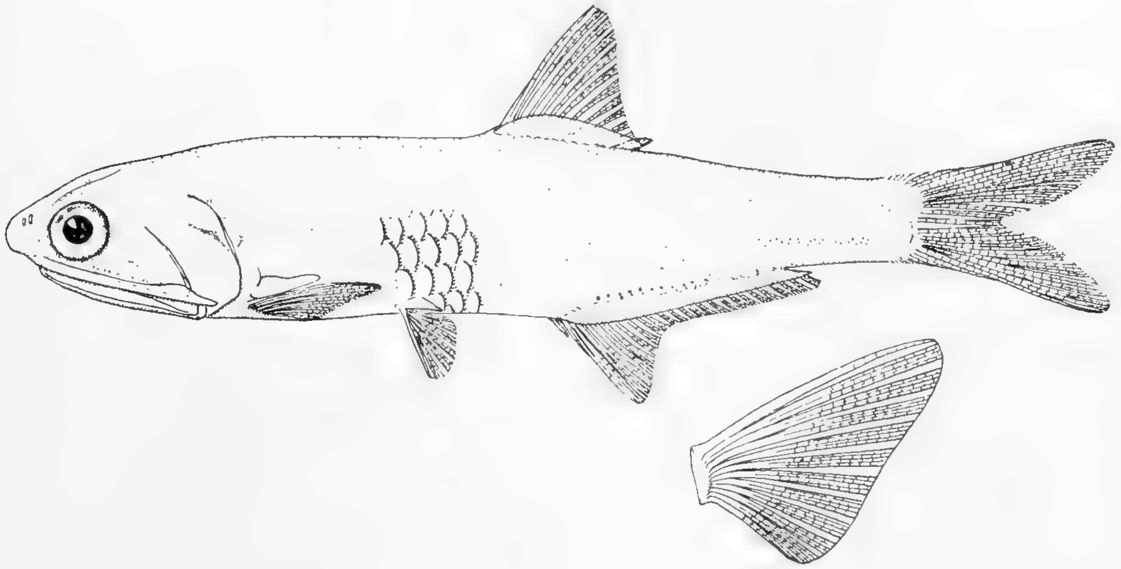

FIGURE 30. *Anchoa cayorum*, 85 mm TL, 68 mm SL, from Cabañas Bay, Cuba, USNM 82341, with pectoral fin enlarged. Drawn by Louella E. Cable.

Distinctive Characters. Museum specimens generally have been identified with *A. mitchilli*, presumably because of the long anal fin, but *cayorum* differs in the larger size it attains (largest seen 85 mm), in the notably fewer gill rakers, and in the much broader and more prominent silvery lateral band.

Description. Proportional dimensions in per cent of standard length, and counts, based on study specimens, 50–85 mm TL.

Body: depth 18–21.

Head: length 25–28.5.

Snout: length 4.3–5.0.

Eye: diameter 5.8–7.4.

Postorbital: distance 13.3–15.3.
Maxillary: length 19.2–22.5.
Mandible: length 18.5–20.
Anal fin: length of base 25–29.3.
Pectoral fin: length 13.9–16.6.
Scales: *ca.* 39–42.
Gill rakers: 13–15 + 15–17 (rarely 18).
Fin rays: dorsal 13–15; anal 26–28 (rarely 25 or 29); pectoral 12 or 13.
Vertebrae: 43 (3 specimens).

Body slender, moderately compressed, its depth 4.75–5.5 in SL. Head 3.5–4.0 in SL, its depth equal to its postorbital length and about half of eye. Snout projecting about 66% of its length beyond tip of mandible, 5.0–6.0 in head. Eye 3.5–4.25. Postorbital 1.65–2.0 in head. Maxillary long and pointed, its upper margin straight, reaching nearly or quite to margin of opercle, 1.1–1.35 in head. Mandible 1.2–1.4. Cheek equal to, or a little longer than, eye and 75% of snout, its posterior angle rather sharp, about 40°.

Dorsal fin with the longest rays reaching well beyond tip of last ray if deflexed, its origin about equidistant between base of caudal and anterior margin of eye. Anal fin with origin under beginning of second fourth of dorsal, its base 3.4–4.0 in SL. Pelvic inserted somewhat nearer to base of pectoral than to origin of anal. Pectoral falcate, sometimes failing to reach base of pelvic by diameter of pupil, occasionally reaching nearly to base of pelvic, the first (uppermost) ray generally as long as the second and about twice the last ray, 1.5–1.9 in head. Axillary scale of pectoral scarcely reaching beyond midlength of pectoral, 3.0–3.5 in head.

Color. In alcohol, pale. Side of head silvery. Silvery lateral band bright, about as wide as eye.

Range and Habitat. The range extends from the Florida Keys, where it is apparently rather rare, to Cuba, Yucatán, and British Honduras. The specimens examined were apparently taken in shallow water, near the shore.

Synonyms and References:

Stolephorus mitchilli Bean, Bull. U. S. Fish Comm. (1888), *8*, 1890: 206 (Cozumel I., off Yucatán, México; specimens re-exam. and found to be *A. cayorum*).

Anchovia choerostoma cayorum Fowler, Proc. Acad. nat. Sci. Philad., *58*, 1906: 85, fig. 4 (orig. descr.; type local. Hailer's Rock, Florida Keys; type ANSP 30613).

Anchovia cayorum Fowler, Proc. Acad. nat. Sci. Philad., *63*, 1911: 219 (types relisted).

Anchoviella cayorum Jordan, Evermann and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 49 (synon.).

Anchoa cayorum Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 50, fig. 17 (synon., descr., relation., range, type material re-exam.).

Anchoa pectoralis Hildebrand 1943

Study Material. Only the type material, 64 specimens, 43–65 mm TL, from Vigia, Brazil, MCZ 18004, listed for "Brazil, Louis Agassiz."

Distinctive Characters. This species is closely related to *A. mitchilli diaphana*, *A. parva*, and *A. januaria*, from all of which it differs in the more numerous pectoral rays. Other differences are evident in the descriptions and tables.

Description. Proportional dimensions in per cent of standard length based on 7 specimens, the counts based on many more. As the state of preservation is not very good, some of the proportions may not be entirely true.

Body: depth 19.5–23.0.
Head: length 23.8–26.2.
Snout: length 3.35–4.16.
Eye: diameter 6.7–8.0.
Postorbital: distance 12.9–13.7.
Maxillary: length 17.7–19.0.
Mandible: length 15.8–17.6.

Anal fin: length of base 23.4–25.6.
Pectoral fin: length 17.8–18.8.

Scales: *ca.* 35–40.
Gill rakers: 13 or 14 + 17–19.
Fin rays: dorsal 14–16; anal 25–27; pectoral 15–17 (most frequently 16).
Vertebrae: 42 (2 specimens).

BODY moderately slender, strongly compressed, its depth 4.35–5.1 in SL. HEAD 3.8–4.2 in SL, its depth nearly equal to its length without snout. SNOUT short, projecting about half of its length beyond mandible, 6.0–7.0 in head. EYE 3.2–3.7. POSTORBITAL 1.75–2.0 in head. MAXILLARY bluntly pointed, its upper margin rounded, reaching somewhat beyond joint of mandible, 1.2–1.4 in head. MANDIBLE 1.4–1.6. CHEEK about as long as eye, its posterior angle broad, about 50°.

DORSAL fin with longest rays reaching to, and occasionally beyond, tip of last ray if deflexed, its origin generally a little nearer to base of caudal than to middle of eye. ANAL with origin generally under middle of dorsal, its base 3.9–4.25 in SL. PELVIC reaching only about halfway to anal, inserted equidistant between origin of anal and base of pectoral, or slightly nearer the former. PECTORAL falcate, reaching nearly to base of pelvic, 1.3–1.4 in head. AXILLARY SCALE of pectoral pointed, about 66% of length of fin, 2.5 in head.

Color. Old specimens in alcohol, brownish silvery. A prominent silvery lateral band present, about as wide as eye. Back with dark dots, in more or less distinct longitudinal rows. Base of anal with black dots; caudal with dark dots and with a dark margin.

Range. Known only from the type material from Vigia, Brazil, collected in 1865 or 1866 by the Thayer Expedition of Harvard University. [Stieler's Atlas lists the name Vigia for two places in Brazil, one at the mouth of Rio Pará (Tocantins), the other well inland on Rio Jequitinhonha in the Province of Minas Gerais.–Y.H.O.].

Synonyms and References:

Anchoviella mitchilli Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67*, 1926: 405 (descr., distr., MCZ 18004).

Anchoa pectoralis Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 52, fig. 18 (orig. descr.; type local. Vigia, Brazil; type MCZ 35276).

Anchoa mitchilli (Cuvier and Valenciennes) 1848

Bay Anchovy

Figures 31, 32

Study Material. A total of 100 specimens, 52–102 mm TL; for characters considered important, such as body depth, pectoral length, number of vertebrae, gill rakers, and anal rays, many more were used; taken at many places from Woods Hole, Massachusetts, to Yucatán, México.

Distinctive Characters. The nearest relative is *A. parva*, a southern species that occurs in the West Indies and on the mainland coast from Panama to Venezuela. This relationship is discussed in the account dealing with *parva* (p. 181).

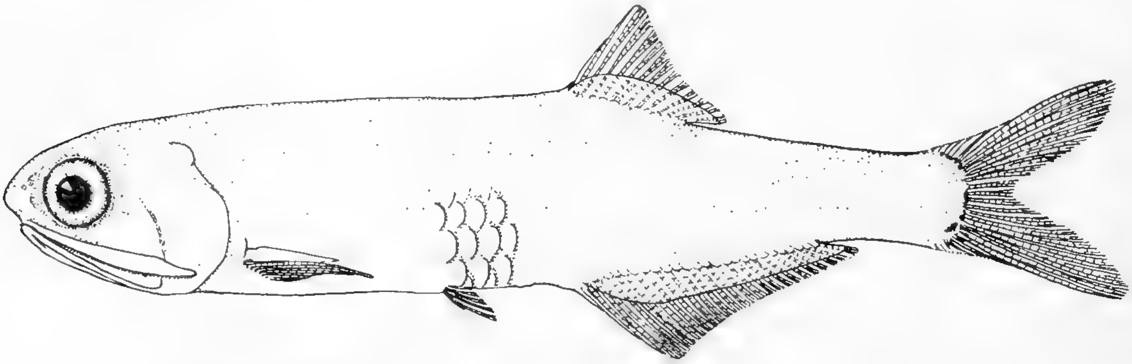

FIGURE 31. *Anchoa mitchilli mitchilli*, 85 mm TL, from Woods Hole, Massachusetts, USNM 125582. Drawn by Louella E. Cable.

Description. Proportional dimensions in per cent of standard length, and counts, based on *Study Material.*

Body: depth 16–27.
Head: length 22–26.5.
Snout: length 3.7–7.25.
Eye: diameter 5.8–8.2.
Postorbital: distance 11–13.5.
Maxillary: length 17.5–21.
Mandible: length 16.5–18.5.
Anal fin: length of base 25–30.

Pectoral fin: length 12–20.

Scales: (generally lost in preserved specimens) *ca.* 38–44.
Gill rakers: 15–19 + 20–26.
Fin rays: dorsal 14–16; anal 24–30; pectoral 11 or 12.
Vertebrae: 38–44 (1,233 specimens).

BODY rather slender, moderately compressed, its greatest thickness usually exceeding the depth of caudal peduncle, its depth 3.65–6.3 in SL. HEAD 3.75–4.5, its depth equal to its length without snout and fourth of eye. SNOUT short, projecting not more than a fourth of its length beyond tip of mandible, 5.0–7.0 in head. EYE 2.9–3.9. POSTORBITAL short, 1.8–2.1 in head. MAXILLARY pointed, extending nearly to margin of opercle, 1.1–1.3 in head. Cheek short and broad, about as long as eye, its posterior angle approximately 60°. Gill rakers somewhat shorter than eye.

Dorsal fin rather low, with nearly straight margin, its last ray scarcely longer than the one immediately before it, its longest rays failing to reach its tip if depressed, the origin varying between a little nearer to caudal base than to upper anterior angle of gill opening and equidistant between caudal base and posterior margin of eye. Anal usually originating somewhat posterior to dorsal origin, its base 3.3–4.0 in SL. Pelvic fin very small, not quite reaching halfway to origin of anal, inserted nearer to anal origin than to pectoral base by diameter of pupil. Pectoral variable, failing to reach base of pelvic by a distance equal to, or even greater than, diameter of eye in northern specimens, sometimes reaching pelvic base in southern fish, 1.4–1.85 in head. Axillary scale of pectoral rather narrow, 2.3–3.0 in head.

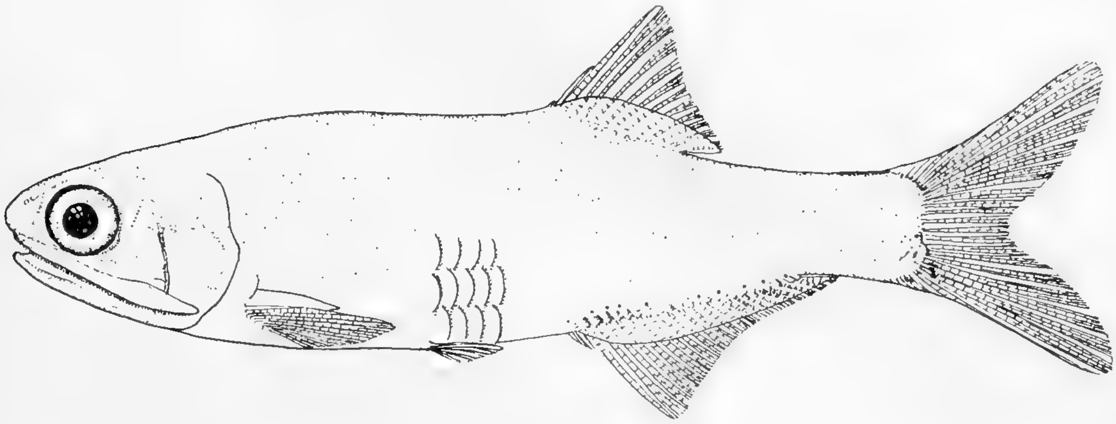

Figure 32. *Anchoa mitchilli diaphana,* 72 mm TL, from Grand Isle, Louisiana, USNM 119790. Drawn by Louella E. Cable.

Color. Preserved specimens, straw-colored above. Lower parts pale silvery. Sides of head bright silvery. Middle of side with a silvery band, often nearly as wide as eye in northern specimens, generally narrower in southern ones. Back with dusky punctulations, arranged in two more or less definite rows posterior to dorsal fin; base of anal with dark spots continued as a single unbroken median ventral line on caudal peduncle; caudal with many dark points. Color in life, greenish with bluish reflections above; lower parts pale; abdominal walls translucent.

Size. A total length of 100 mm (4 in.) is seldom exceeded, the usual length being around 75 mm (3 in.). The largest examples measured were taken in New York, where this species evidently grows larger than in the southern part of its range, for the largest specimen among thousands from the Gulf of Mexico was only 75 mm long.

Development and Growth. The egg generally is slightly oblong, but occasionally round; the major axis is about 0.75 mm and the minor one about 0.62 mm. It is transparent and has no oil globule. The yolk consists of separate masses that appear as large cells under the microscope, a character that seems to be common to all species of Engraulidae whose eggs have been studied. The egg floats at or near the surface and hatches in about 24 hours at room temperature, at least at Beaufort, North Carolina, during early summer.[4]

The newly hatched fish, 1.8–2.0 mm long, is rather slender, perfectly transparent, and has no pigment spots. The yolksac is absorbed within about two days, and the large mouth, which is terminal at this stage, then seems to be functional. The projecting snout is not developed until the young fish reaches a length of about 20–25 mm. But the fins are sufficiently developed at a length of about 15 mm to permit a fairly accurate enumeration of the rays. The number of anal rays and the relative positions of the dorsal and anal fins are very useful in identifying the postlarvae with the adults.

The early young of the season seem to become sexually mature during their first summer, for specimens 45–60 mm long that remained quite transparent, taken late in July and during the first half of August at Beaufort, N. C., contained well developed roe.

Spawning. In the vicinity of Beaufort, N. C., spawning takes place at least from early spring to midsummer. The eggs were taken in tows there as early as April 21 (in 1930) and as late as July 15 (in 1929), while gravid fish were seen as late as August 12 (from my unpublished notes).

Food. The food apparently consists mostly of *Mysis* and copepods, the latter being the sole food of the young. Other items taken are small fish, gastropods, and isopods (5: 110).

Enemies. This fish, which is exceedingly numerous in a large part of its range, is preyed upon extensively by predatory fish and water birds.

Variation. The variation within this species is so great that I recognized a northern subspecies, *A. mitchilli mitchilli*, and a southern one, *A. mitchilli diaphana* (3: 87–94). The specimens from the southern part of the range have rather consistently deeper and more strongly compressed bodies, fewer gill rakers, fewer vertebrae, a longer pectoral fin, and a narrower silvery lateral band. These differences are shown by comparing the characters of a small lot of specimens from Woods Hole, Massachusetts, with another lot from Grand Isle, Louisiana, which show the widest divergence (Table IV). Complete intergradation of the two subspecies occurs in the midsection of their range, as in North and South Carolina.

Commercial Importance. This Anchovy is used as bait and to a limited extent in the preparation of anchovy paste. However, it is important chiefly as forage for many important foodfishes. As this fish usually occurs in schools and is a rather sluggish swimmer, it is an easy prey of many predators.

Range and Habitat. Cape Cod, Massachusetts (rarely northward into the Gulf of Maine), and southward to Yucatán, México. Brazilian records probably are referable either to *A. parva* or *A. januaria*. While *A. mitchilli* occurs along the outer and exposed

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[4] The information as to the eggs and young fish is in part from Kuntz (9: 13–19) and in part from my field notes.

Table IV. Comparison of Divergent Specimens of *A. mitchilli.*

Woods Hole, Massachusetts	Grand Isle, Louisiana
Eight specimens, 62–85 mm TL	Sixteen specimens, 48–76 mm TL.
Depth, 19–21 % of SL.	*Depth,* 23–26 % of SL.
Greatest thickness of body, usually exceeding depth of caudal peduncle.	*Greatest thickness of body,* less than depth of caudal peduncle.
Pectoral fin, 13–13.5 % of SL.	*Pectoral fin,* 16.5–17.5 % of SL.
Gill rakers, 24–28 on lower limb.	*Gill rakers,* 21–23 on lower limb.
Vertebrae, 43 or 44 in four specimens.	*Vertebrae,* 39–41 in nine specimens.
Silvery lateral band about as broad as eye.	Silvery lateral band scarcely broader than pupil.

beaches at Beaufort, N. C., at least to a depth of 15–20 fms., it is found more often in inside waters, especially in areas with muddy bottoms and brackish water. The distribution is so general that the fish may be expected also in "grassy" areas and along sandy beaches.

Migrations. It was formerly thought that this species, as well as several other anchovies, migrated northward and southward with the seasons. This theory was based on the fact that in the northern part of the range, as at Woods Hole, Massachusetts, the fish is present only during the summer. However, it has been shown (*3*: 87–94) that virtually every section of the coast within the range of *mitchilli* has a distinctive population, which suggests that whatever migration takes place is an inshore and offshore movement.

Details of Occurrence. The most northern records are for Casco Bay, Maine, and for Provincetown at the tip of Cape Cod, Massachusetts; these have been based on stray specimens only. But it is described as abundant in the Woods Hole region and in Rhode Island waters (both adults and larvae), common in New York waters, exceedingly abundant (often in large schools) at many New Jersey localities, and second in abundance (if not the most abundant) in Chesapeake Bay. It has been recorded for North Carolina, South Carolina,[5] and Georgia, and it is at least tolerably plentiful in the Indian River on the eastern coast of Florida. No certain evidence has been found of its presence among the Florida Keys, but it has long been known to be plentiful in the inlets and passes all along the western coast of Florida. It has been recorded for so many localities in Mississippi, Louisiana (Cameron, Grand Isle, and Lake Ponchartrain), Texas (Galveston, Corpus Christi, Dickinson Bayou), and México (Vera Cruz, Rio Pánuco, Tampico) as to prove it practically universal in suitable situations all around the coastline of the Gulf of Mexico to Yucatán. But present indications are that Yucatán marks the southern boundary of its range, there being no reliable record of its presence anywhere to the southward around the Central or South American shores of the Caribbean.

Reports of it for Cuba (*20*: 57; *17*: 421; *7*: 405) on the strength of two specimens from Poey in the Museum of Comparative Zoology seem to have been based on a misinterpretation of what Poey wrote about this Anchovy. Actually the

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[5] The Museum of Comparative Zoology has a specimen from Charleston, collected by Louis Agassiz.

locality given in the Museum catalogue for these specimens is "United States," to which a label in the bottle in my handwriting adds "Sent to Poey by Gill for comparison."

Synonyms and References:

Engraulis mitchilli Cuvier and Valenciennes, Hist. Nat. Poiss., *21*, 1848: 50 (orig. descr.; type local. New York; mentions *Engraulis louisiana*[6]); Günther, Cat. Fish. Brit. Mus., 7, 1868: 391 (synon., descr., range).

Stolephorus mitchilli Jordan and Gilbert, Proc. U. S. nat. Mus. (1882), *5*, 1883: 248 (descr., synon., includ. *Engraulis duodecim* Cope, a valid species; Galveston, Texas; Pensacola, Florida; Woods Hole, Massachusetts); Swain, Bull. U. S. Fish Comm. (1882), *2*, 1883: 57 (range; Princetown and Woods Hole, Massachusetts; Pensacola, Florida; Lake Ponchartrain, Louisiana; Galveston, Texas; and Cuba, which is probably *A. parva*; includ. *Engraulis duodecim* Cope); Bean, Bull. U. S. Fish Comm. (1887), *7*, 1888: 149 (Ocean City, Beesley's Pt., and Longport, New Jersey; local abund.); Henshall, Bull. U. S. Fish Comm. (1889), *9*, 1891: 373 (very abund. in most inlets and passes of Florida west coast); Smith, Bull. U. S. Fish Comm. (1892), *12*, 1894: 361 (abund. in New Jersey; relation. to commerc. fishes); Evermann and Kendall, Bull. U. S. Fish Comm. (1892), *12*, 1894: 105 (Galveston, Corpus Christi, Dickinson Bayou, Texas); Moore, Bull. U. S. Fish Comm. (1892), *12*, 1894: 359 (near Sea Isle City, New Jersey); Lönnberg, Oefvers. Svensk. Vet. Akad. Forh., *51*, 1894: 115 (St. Petersburg, Florida); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 446 (descr., range, synon., includ. *Engraulis duodecim* Cope); Evermann and Bean, Rep. U. S. Comm. Fish. (1896), 1897: 241 (many at Cocoa and St. Lucia on Indian R., Florida); Smith, Bull. U. S. Fish Comm. (1897), *17*, 1898: 92 (Woods Hole, Massachusetts); Smith and Bean, Bull. U. S. Fish Comm. (1898), *18*, 1899: 184 (Potomac R. at Bryants Pt., Maryland); Evermann, Rep. U. S. Comm. Fish. (1898), 1899: 309 (Baldwin Lodge, Mississippi; Lake Lapourde, Louisiana); and (1899), 1900: 56 (Florida); Bean, Rep. Forest Comm. N. Y. (1901), 1902: 311 (refs., range, New York, econ. import.); Bean, Bull. N. Y. St. Mus., 60, Zool. 9, 1903: 218 (descr., range, a forage fish; New York); Latham, Copeia, 1917 (Orient, Long Island, New York); Breder, Zoologica, N. Y., *2*, 1922: 338 (Sandy Hook Bay, New Jersey).

Anchovia mitchilli Fowler, Rep. N. J. St. Mus. (1905), 1906: 110, fig. (descr., Delaware R. off Ft. Delaware, Delaware; Beesley's Pt. and Ocean City, New Jersey); and (1906), 1907: 267 (Sea Isle City, New Jersey; taken for bait); Smith, N. C. geol. econ. Surv., *2*, 1907: 134 (synon., descr., range, Morehead City, North Carolina); Jordan and Dickerson, Proc. U. S. nat. Mus., *34*, 1908: 12 (diagn., mouth of Rio Pánuco, Tampico, México); Kendall, Occ. Pap. Boston Soc. nat. Hist., *7*, 1908: 42 (Casco Bay, Maine; Provincetown and Woods Hole, Massachusetts; Rhode Island); Weymouth, Proc. U. S. nat. Mus., *38*, 1910: 136 (Cameron, Louisiana); Fowler, Proc. Acad. nat. Sci. Philad., *63*, 1911: 219 (Woods Hole, Massachusetts; Seaside Park, Beesley's Pt., Carson's Inlet, New Jersey; Ft. Delaware, Delaware; Tolchester Beach, Maryland); Sumner, Osburn, and Cole, Bull. U. S. Bur. Fish. (1911), *31* (2), 1913: 743 (Woods Hole, Massachusetts); Kuntz, Bull. U. S. Bur. Fish. (1913), *33*, 1914: 13–19, figs. 25–46 (spawn., Beaufort, North Carolina; develop. of eggs and larvae); Bigelow and Welsh, Bull. U. S. Bur. Fish. (1924), *40* (1), 1925: 124 (descr., size, range, Gulf of Maine); Nichols and Breder, Zoologica, N. Y., *9*, 1927: 44 (diagn., range, Orient, New York; life hist. notes).

Anchoviella mitchilli Jordan and Seale (in part; not of Cuvier and Valenciennes), Bull. Mus. comp. Zool. Harv., *67* (11), 1926: 405 (synon., includ. *Engraulis duodecim* Cope; descr., range; Brazilian and West Indian specimens not this species); Hildebrand and Schroeder, Bull. U. S. Bur. Fish. (1927), *43* (1), 1928: 109 (synon., descr., food, spawn., eggs descr., size, abund., habitat, Chesapeake Bay); Breder, Field Bk. Mar. Fish. Atl. Cst., 1929: 71 (genl.); Jordan, Manual Vert. Anim. NE U. S., ed. 13, 1929: 43 (descr., range); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 48 (synon., includ. *Engraulis duodecim* Cope; range); Hildebrand and Cable, Bull. U. S. Bur. Fish., *46*, 1930: 388 (econ. import., spawn., Beaufort, North Carolina; develop. of eggs and young cf. *A. hepsetus*; distinguish. characters this species and *A. hepsetus*; growth rate); Perlmutter, 28th Rep. N. Y. Conserv. Dept.

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6. Said to have been described and figured by LeSueur, but since no reference to *E. louisiana* LeSueur is given and since none can now be found, the name presumably was taken from a manuscript, and Hildebrand, in his review of the American Engraulidae regarded it as having no standing in modern nomenclature (*3*).

(1938), Suppl., 15 (2), 1939: 18 (around Long Island, New York; spawn.); Greeley, 28th Rep. N. Y. Conserv. Dept. (1938), Suppl., 15 (2), 1939: 83 (Long Island, New York; a forage fish).

Anchoa mitchilli mitchilli Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 87, fig. 37 (synon., descr., cf. *A. mitchilli diaphana*, range).

Anchoa mitchilli diaphana Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 91, fig. 38 (orig. descr. of subspecies *A. m. diaphana*; relation., range); Gunter, Publ. Inst. mar. Sci. Texas, *1* (1), 1945: 33 (depth, temp., salinity, season, spawn., growth, Texas coast).

Negative References:

Stolephorus mitchilli Bean, Bull. U. S. Fish Comm. (1888), *12*, 1890: 206 (many at Cozumel Island, Yucatán; USNM 37053, 37105 are *A. cayorum*); Schreiner and Miranda-Ribeiro, Arch. Mus. nac., Rio de J., *12*, 1903: 93 (Rio de Janeiro, where this species does not occur).

Anchoviella mitchilli Fowler, Arqu. Zool. estad. São Paulo, *3* (6), 1941: 135 (refs. Brazilian recs., where this species does not occur).

Anchovia mitchilli von Ihering, Rev. Industr. Anim., Anno 1 (3), 1930: 232 (Brazil, where the species does not occur).

Anchoa parva (Meek and Hildebrand) 1923

Manjúa (Cuba)

Figure 33

Study Material. At least 34 specimens, 35–60 mm TL, and many more used for some measurements and counts, from the following localities: many from Jamaica; two from Cuba; many from Colón and Porto Bello, Panama, and from Gatun Locks, Canal Zone; one from Laguna de Tacarigua, Venezuela; and one from Trinidad; in USNM, MCZ, UMMZ, BOC, Museo Poey collections.

Distinctive Characters. A. parva is rather close to both subspecies of *mitchilli*, differing principally in having fewer anal rays and more numerous gill rakers, though there is slight overlapping in each instance (see Tables I, II, and III), in the smaller anal fin (see *Description*), in the origin of the anal, which is somewhat farther back under the base of the dorsal, and in the more strongly projecting snout (Figs. 31–33). For the relationship of *parva* to *januaria*, see p. 183. Its closest relative is *curta* of the Pacific coast of Central and South America, from which it is scarcely more than subspecifically distinct (*3*: 84).

Description. Proportional dimensions in per cent of standard length, and counts, based on at least 34 specimens in *Study Material*, 35–60 mm TL.

Body: depth 20–22.
Head: length 23.3–27.8.
Snout: length 4.0–5.5.
Eye: diameter 6.9–9.5.
Postorbital: distance 11.1–14.3.
Maxillary: length 17.3–21.7.
Mandible: length 15–19.
Anal fin: length of base 21–25.
Pectoral fin: length 14.3–17.4.

Scales: *ca.* 38–42.
Gill rakers: 18–20 + 23–27.
Fin rays: dorsal 13–16; anal 21–23 (rarely as many as 25); pectoral 12 or 13.
Vertebrae: 38–40, rarely 41 (61 specimens).

Body moderately deep, strongly compressed, its depth 4.5–5.0 in SL. Head 3.6–4.3, its depth usually equal to its length without snout. Snout 4.5–6.0 in head, extending about half of its length beyond mandible. Eye 3.0–3.5. Postorbital 1.8–2.3 in head. Maxillary pointed, reaching to margin of opercle, 1.2–1.6 in head. Mandible 1.4–1.75. Cheek scarcely longer than eye, its posterior angle about 60°.

Dorsal fin with the longest rays failing to reach tip of last ray if deflexed, its origin generally equidistant between base of caudal and about middle of eye. Anal with origin under, or more frequently slightly anterior to, middle of dorsal base, its base 4.0–4.8 in SL. Pelvic reaching scarcely halfway to anal, inserted about equidistant between origin of anal and base of pectoral. Pectoral rather variable in length, usually failing to reach pelvic by diameter of pupil, 1.5–1.7 in head. Axillary scale of pectoral generally reaching to beginning of distal third of fin, 2.3–3.0 in head.

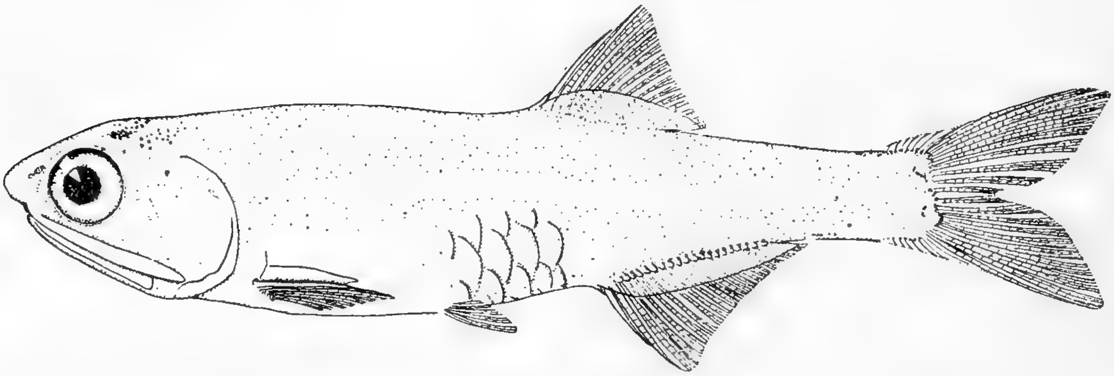

Figure 33. *Anchoa parva*, paratype, 59 mm TL, from Fox Bay, Colón, Panama, USNM 79554. Drawn by Louella E. Cable.

Color. In alcohol, very pale (presumably preserved originally in formalin). Silvery lateral band scarcely as wide as pupil (indistinct or missing in some specimens). Back with dusky punctulations, at least posterior to dorsal fin and extending onto base of upper rays of caudal; larger dark dots usually present at base of anal and continued as a single row onto median line of caudal peduncle.

Size. It is apparently small, as the largest specimen seen is only 60 mm (2.4 in.) TL.

Range and Habitat. Known from the West Indies and the Atlantic coast of Panama and Venezuela. Records of *A. mitchilli* for the West Indies, in part at least, are referable to this species. This fish inhabits salt and brackish water, and fresh water at least to a limited extent. It was very numerous in all three flights of Gatun Locks, Canal Zone, in 1935. The water in the lowermost flight was quite salty, that in the middle one brackish, and that in the uppermost flight, fresh. It has been reported also as occurring in fresh water in Venezuela.

Synonyms and References:

Anchovia parva Meek and Hildebrand, Field Mus. Publ., Zool., *15* (1), 1923: 202, pl. 10, fig. 2 (orig. descr.; type local. Porto Bello, Panama; type USNM 81767; also recorded from Colón); Hildebrand, Zoologica,

N. Y., *24* (1), 1939: 25, 35 (numerous in Gatun Locks, Canal Zone; erroneously reported from Miraflores Locks, Canal Zone, which is *A. curta*).

Anchoviella mitchilli Jordan and Seale (in part; not of Cuvier and Valenciennes), Bull. Mus. comp. Zool. Harv., *67*, 1926: 405 (part of Cuban specimens, *A. parva*).

Anchoviella parva Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 49 (ref. to orig. descr.).

Anchoa parva Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 83, fig. 35 (refs., descr., relation., range); Schultz, Proc. U. S. nat. Mus., *99*, 1949: 43 (synon.; Venezuela; notes, counts).

Doubtful Reference:

Anchoviella parva Fowler, Proc. Acad. nat. Sci. Philad., *83*, 1931: 392 (98-mm specimen from Trinidad much larger than any seen by me; also anal rays more numerous).

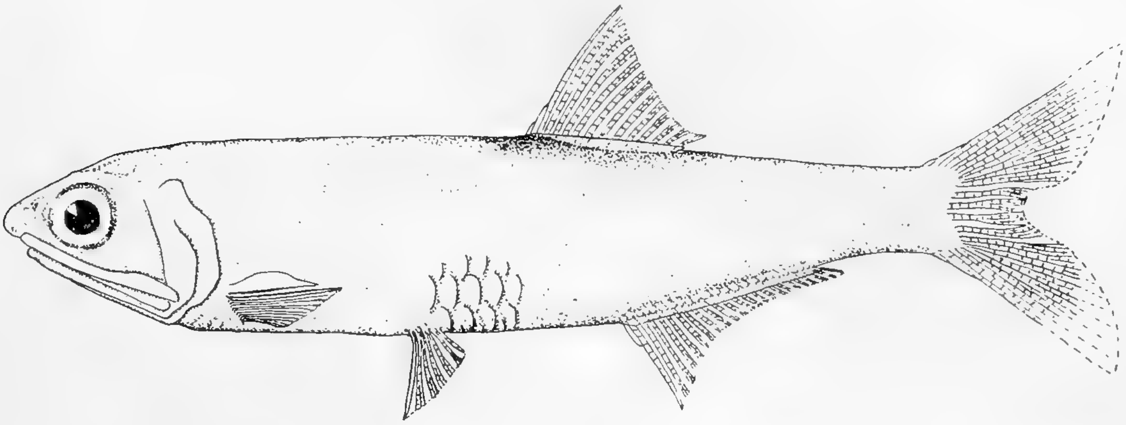

FIGURE 34. *Anchoa januaria*, 75 mm TL, from Pernambuco, Brazil, MCZ 18012. Drawn by Alice C. Mullen.

Anchoa januaria (Steindachner) 1879

Figure 34

Study Material. A total of 28 specimens, 30–75 mm TL, from Amuay[7] and Salinas bays, Gulf of Venezuela; Pernambuco (Recife), Natal, and Rio de Janeiro, Brazil; in USNM and MCZ collections.

Distinctive Characters. From both subspecies of *mitchilli*, *januaria* differs in a somewhat greater number of gill rakers, fewer anal rays, the more posterior position of the anal fin, and the more strongly projecting snout. Compared to both *mitchilli* and *parva*, it has a shorter and blunter maxillary; and from *parva* it differs further in having more numerous gill rakers on the upper limb and in the slightly more posterior position of the anal fin. It differs from *pectoralis* in having fewer pectoral and anal rays and in the more numerous gill rakers.

[7] Schultz (*19*: 44) has claimed that the somewhat mutilated specimens from Amuay Bay, Gulf of Venezuela, identified by me as this species, are *A. blackburni*.

Description. Proportional dimensions in per cent of standard length, and counts, based on 15 or more specimens from 33 mm SL upward.

Body: depth 18–20.
Head: length 22–26.2.
Snout: length 4.15–5.7.
Eye: diameter 6.9–8.0.
Postorbital: distance 10.5–14.2.
Maxillary: length 16.4–19.3.
Mandible: length 15.3–17.
Anal fin: length of base 22–26.
Pectoral fin: length 15.6–17.5.

Scales: *ca.* 36–40.
Gill rakers: 20–23+23–26.
Fin rays: dorsal 14 or 15; anal 21–24; pectoral 12 or 13.
Vertebrae: 41 or 42 (3 specimens).

Body strongly compressed, its depth 4.3–5.0 in SL. Head short, 3.8–4.5 in SL, its depth equal to its length without snout. Snout 5.0–6.0 in head, projecting fully half of its length beyond mandible. Eye 2.9–3.6 in head. Postorbital 2.0–2.3 in head. Maxillary rather bluntly pointed, its upper margin somewhat rounded, reaching to, or slightly beyond, joint of mandible, 1.3–1.5 in head. Mandible 1.4–1.55. Cheek about as long as eye, its posterior angle about 50°.

Dorsal fin with its longest rays failing to reach tip of last ray if deflexed, its origin equidistant between base of caudal and about middle of eye. Anal low, its origin under or slightly posterior to middle of dorsal base, its base scarcely shorter than head, 3.8–4.5 in SL. Pelvic very small, reaching much less than halfway to anal, inserted about equidistant between origin of anal and base of pectoral. Pectoral small, failing to reach ventral by more than half of diameter of eye, 1.4–2.0 in head. Axillary scale of pectoral about 75% of length of fin, 2.4 in head.

Color. In alcohol, pale silvery. Silvery lateral band distinct, about 0.5–0.66 of width of eye. Back with dark punctulations, arranged in two rows in some specimens, probably faded in others.

Size. So far as known, this Anchovy reaches a length of only about 75 mm (3 in.).

Range. It apparently ranges from the Gulf of Venezuela to Rio de Janeiro, Brazil.

Synonyms and References:

Engraulis januarius Steindachner, Ichthyol. Beitr., 8, 1879: 58 (orig. descr.; type local. Rio de Janeiro, Brazil; cf. *E. mitchilli*).

Anchovia januaria Starks, Stanf. Univ. Publ., Univ. Ser., 1913: 9 (Natal, Brazil).

Anchoviella januaria Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67*, 1926: 206 (descr., Rio de Janeiro, Brazil, and "Brazil"); Fowler, Arqu. Zool. estad. São Paulo, *3* (6), 1941: 134 (refs. to Brazilian recs.).

Anchoviella mitchilli Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67*, 1926: 405 (Pernambuco, Brazil; MCZ 18012 are *A. januaria*).

Anchoa januaria Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 81, fig. 34 (synon., descr., range; cf. *mitchilli*, *parva*, and *pectoralis*).

Anchoa choerostoma (Goode) 1874

Figure 35

Study Material. Many specimens in nine collections from Bermuda.

Description. Proportional dimensions in per cent of standard length, and counts, based on at least 22 specimens, 55–75 mm TL.

Body: depth 18.2–20.8.
Head: length 27.8–30.2.
Snout: length 5.1–6.4.
Eye: diameter 6.5–8.4.
Postorbital: distance 13.3–15.9.
Maxillary: length 21.2–24.3.
Mandible: length 19.2–22.

Anal fin: length of base 20–22.6.
Pectoral fin: length 15.6–18.5.

Scales: *ca.* 38–40.
Gill rakers: 17–20+23–26.
Fin rays: dorsal 13–15; anal 22–24 (rarely 21 or 25); pectoral 12–14.
Vertebrae: 41 or 42 (2 specimens).

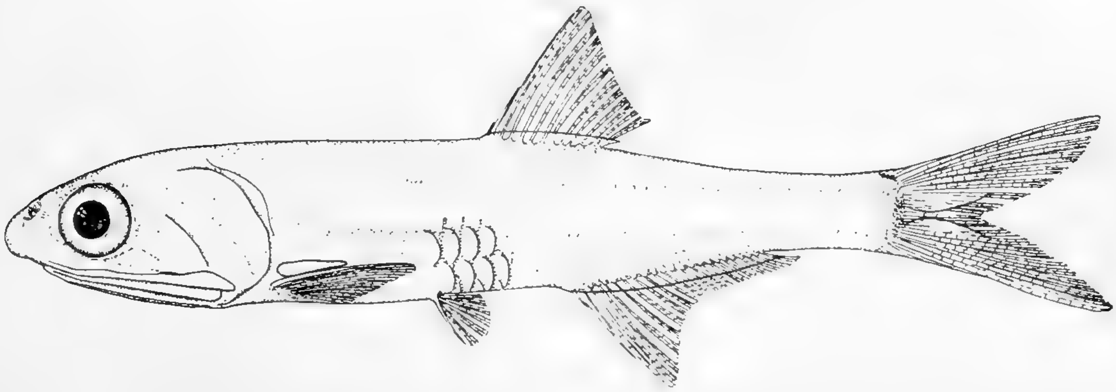

FIGURE 35. *Anchoa choerostoma,* 68 mm TL, from Bermuda, USNM 21976. Drawn by Louella E. Cable.

BODY strongly compressed, moderately deep, its depth 4.8–5.8 in SL. HEAD 3.3–3.6 in SL, its depth equal to postorbital and about half of eye. SNOUT short, projecting rather more than half of its length beyond mandible, 4.7–5.8 in head. EYE 3.3–4.2. POSTORBITAL 1.85–2.1 in head. MAXILLARY reaching nearly to gill opening, not sharply pointed, its upper margin rounded, 1.2–1.3 in head. MANDIBLE 1.3–1.5 in head. CHEEK length equal to eye and fully 75% of snout, its posterior angle about 30°.

DORSAL fin rather high anteriorly, its longest rays reaching to or beyond tip of last ray if deflexed, its origin about equidistant between base of caudal and anterior margin of eye. ANAL with origin somewhere under posterior half of dorsal, but well in advance of the base of last ray, its base 4.4–5.0 in SL. PELVIC failing to reach anal by nearly an eye's diameter, inserted a little nearer to origin of anal than to pectoral base. PECTORAL moderately long, reaching nearly or quite to pelvic, 1.5–1.9 in head.

Axillary scale of pectoral reaching somewhat beyond midlength of fin, 3.0–4.0 in head.

Color. In alcohol, generally pale. Side with a silvery band (often missing in specimens preserved a long time in formalin), about 75 % of width of eye. Upper surface of head and back with dusky dots, usually arranged in two longitudinal series posterior to dorsal fin.

Size. The largest seen is 75 mm (3 in.) TL, which may be near the maximum size attained.

Reproduction. Specimens taken on June 24, 1927 at Nonsuch, Bermuda contain well developed eggs, indicating that at least some reproduction takes place there during the early part of summer.

Range and Habitat. The range seems to be limited to Bermuda, where no other species of anchovy has been found. West Indian and Panamanian (Atlantic) records are mostly referable to *A. lyolepis*. The collections studied, according to the information furnished, were either seined near shore or taken at night under an electric light. This species has been reported as fairly common about Bermuda (numerous in Hamilton Harbor). Although it has been reported as not at all common during July, it was abundant in August when seined for bait in Bailey's Bay and Flatts Inlet.

Synonyms and References:

Engraulis choerostoma Goode, Amer. J. Sci., *8*, 1874: 125 (orig. descr.; type local. Bermuda; types lost); Ann. Mag. nat. Hist., (4) *14*, 1874: 380 (as in Goode, 1874).

Stolephorus choerostoma Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 444 (descr. after Goode; ref.); Barbour, Bull. Mus. comp. Zool. Harv., *46*, 1905: 113 (abund. in Bermuda; distrib., includ. Puerto Rico, where it apparently does not occur; refs.); Bean, T. H., Field Mus. Publ., Zool., 7, 1906: 34 (several locals in Bermuda).

Anchoviella choerostoma Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 48 (ref., Hamilton Harbor, Bermuda); Fowler, Proc. biol. Soc. Wash., *43*, 1930: 146 (72 from Bermuda).

Anchoa choerostoma Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 71, fig. 28 (refs., descr., distrib.).

Negative References:

Anchoviella choerostoma Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67*, 1926: 404 (not *A. choerostoma* [Goode]; descr. evidently based on *A. lyolepis* [Evermann and Marsh]; those from Puerto Rico and e. coast of Panama are *lyolepis*); Beebe and Tee-Van, Field Bk. Shore Fish. Bermuda, 1933: 38, fig. (not *A. choerostoma* [Goode]; fig. and descr. at least in part from Beebe and Tee-Van [1928: 47]; distrib. includ. West Indies, where this species apparently does not occur); Beebe and Tee-Van, Zoologica, N. Y., *13* (7), 1933: 136 (*A. choerostoma* var. *atlantica* Borodin [1928: 7] from e. coast of Panama put in synon., but *A. choerostoma* [Goode] apparently does not occur there. Borodin's fish not ident. from his descr.).

Anchoa tricolor (Agassiz) 1829

Piquitinga

Figure 36

Study Material. Many specimens, from: Gulf of Venezuela (1); Natal (8), Rio de Janeiro (52), São Francisco (5), and Sambara River (20), Brazil; Montevideo, Uruguay

(1); and Puerto de (or Rio) Quequen, Mar del Plata, Argentina (2), in USNM, MCZ, CNHM, MHNBA, UMMZ, SU collections.

Distinctive Characters. This species generally has been identified in museum collections with *brownii* = *hepsetus*, which it resembles in size and general appearance, but it differs sharply from it in the shorter and differently shaped maxillary and in the more numerous gill rakers (Tables II and III).

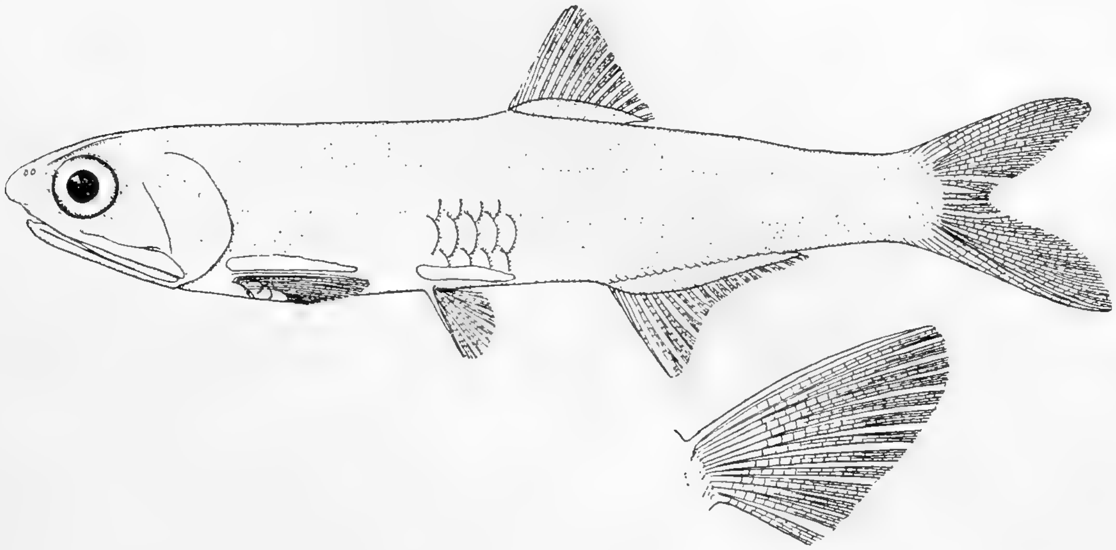

FIGURE 36. *Anchoa tricolor*, 110 mm TL, 91 mm SL, from Rio de Janeiro, Brazil, USNM 87721, with pectoral fin enlarged. Drawn by Louella E. Cable.

Description. Proportional dimensions in per cent of standard length, and counts, based on at least 41 specimens, 63–118 mm TL.

Body: depth 18.2–21.
Head: length 23.8–26.7.
Snout: length 4.15–5.9.
Eye: diameter 6.7–8.1.
Postorbital: distance 12.5–13.5.
Maxillary: length 18.2–21.5.
Mandible: length 15.6–18.3.

Anal fin: length of base 17.2–20.
Pectoral fin: length 14–14.8.

Scales: *ca.* 42–45.
Gill rakers: 18–22 + 24–28.
Fin rays: dorsal 14–16; anal 18–22; pectoral 13–15.
Vertebrae: 40–42 (5 specimens).

Body quite slender, moderately compressed, its depth 4.75–5.5 in SL. Head 3.75–4.2 in SL, its depth equal to its postorbital length and fully half of eye. Snout projecting about half of its length beyond mandible, 4.75–5.8 in head. Eye 3.25–3.75. Postorbital 1.85–2.15 in head. Maxillary not sharply pointed, its upper margin rounded, reaching to, or a little beyond, joint of mandible, 1.3–1.4 in head. Mandible 1.3–1.5. Cheek rather broad, scarcely longer than eye, its posterior angle about 55°.

Dorsal fin with longest rays failing to reach tip of last ray if deflexed, its origin about equidistant between base of caudal and middle of eye. Anal with origin somewhere under posterior fourth of dorsal, its base 5.0–5.8 in SL. Pelvic reaching scarcely halfway to anal, inserted about equidistant between origin of anal and pectoral base. Pectoral scarcely falcate, failing to reach pelvic by diameter of pupil to 75% of diameter of eye, 1.75–2.0 in head. Axillary scale of pectoral often shorter than fin by diameter of pupil, 1.9–2.75 in head.

Color. In alcohol, generally rather pale. Side of head silvery. Lateral band bright silvery, about 75% of width of eye.

Size. The largest measured is 118 mm (4.7 in.) TL, which may be near the maximum length attained.

Commercial Importance. Most of the specimens examined were obtained in markets, indicating that this Anchovy has at least some direct economic value to man.

Range. The range, so far as known, extends from the Gulf of Venezuela to Mar del Plata, Argentina, but it apparently does not include streams. This Anchovy's frequent appearance in the Rio de Janeiro market (Brazil) seems to indicate that it is common locally.

Synonyms and References:

Engraulis tricolor Agassiz, in Spix and Agassiz, Pisc. Brasil., 1829: 51, tab. 23, fig. 1 (orig. descr.; type local. Bahia, Brazil; plate labeled *Engraulis piquitinga*); Goeldi, Boll. Museu Paraense, *2* (3), 1898: 466 (names; from type local.).

Stolephorus brownii Jordan and Evermann, Bull. U. S. nat. Mus., *47* (1), 1896: 443 (descr., range, synon., includ. *E. tricolor* Agassiz).

Anchovia brownii Starks, Stanf. Univ. Publ., Univ. Ser., 1913: 10 (Natal, Brazil; local abund.; descr. *tricolor* by my exam.).

Anchoviella salvatoris Fowler and Bean, Proc. U. S. nat. Mus., *63* (19), 1923: 6 (orig. descr.; type local. Rio de Janeiro, Brazil; type USNM 83165, in bad condition, apparently *tricolor*); Fowler, Arqu. Zool. estad. São Paulo, *3* (6), 1941: 134 (refs.).

Anchoviella epsetus Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67*, 1926: 396 (Rio de J. and "Sambaia" [probably Sambara R.], Brazil; Montevideo, Uruguay; all exam. and are *tricolor*); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 48 (includ. *tricolor*); Fowler, Arqu. Zool. estad. São Paulo, *3* (6), 1941: 134 (refs. to Brazilian recs., in part *tricolor*).

Anchoviella bonaiensis Marini, Physis, Rev. Soc. Argent. Cienc. nat., *11*, 1935: 446 (NOMEN NUDUM; type local. Mar del Plata, Argentina; type in MHNBA; exam. by me and found to be *tricolor*).

Anchoa tricolor Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 74, fig. 30 (synon., descr., relation., distrib.); Schultz, Proc. U. S. nat. Mus., *99*, 1949: 43 (synon.).

Anchoa cubana (Poey) 1868

Cuban Anchovy, Bocón, Manjúa (Cuba)

Figure 37

Study Material. A total of 39 specimens, 45–70 mm TL, including two from Poey's type material, MCZ 17958, and two paratypes of *Stolephorus astilbe* Jordan and Rutter, MCZ 31392; many more for the gill raker counts; from Melbourne Beach and Marco, Florida; Mobile Bay, Alabama; off Grand Isle, Louisiana; Progreso, Yucatán, México; Puerto Barrios, Guatemala; Cuba; Jamaica; and St. Thomas.

Distinctive Characters. This species differs from *A. hepsetus* and from nearly all other local forms in a very slender body and more numerous gill rakers.

Description. Proportional dimensions in per cent of standard length, and counts, based on 39 specimens, 45–70 mm TL.

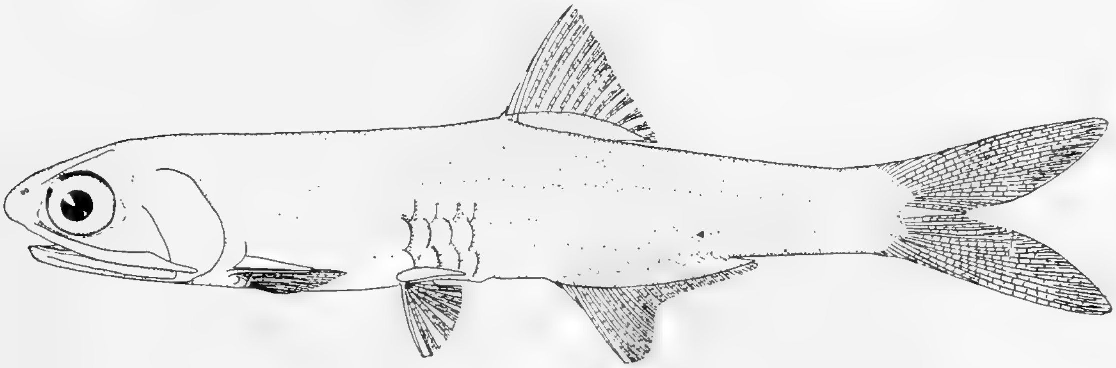

Figure 37. *Anchoa cubana*, 63 mm TL, 53 mm SL, from St. Thomas, West Indies, USNM 83802. Drawn by Louella E. Cable.

Body: depth 15–18.
Head: length 22.7–27.8.
Snout: length 3.85–4.7.
Eye: diameter 6.1–7.75.
Postorbital: distance 10.5–12.5.
Maxillary: length 18.7–22.2.
Mandible: length 15.6–18.8.
Anal fin: length of base 18.5–22.2.

Pectoral fin: length 12.5–13.7.

Scales: *ca.* 40–43.
Gill rakers: 17–23 + 23–33, usually 19–22 + 25–28 (Tables II, III).
Fin rays: dorsal 14–16; anal 20–24; pectoral 13 or 14.
Vertebrae: 42 or 43 (14 specimens).

Body slender, rather strongly compressed, with a rather sharp edge on chest and abdomen, its depth 5.5–6.7 in SL. Head small, 3.6–4.3 in SL, its depth equal to its postorbital length and about a third of eye. Snout short, extending about 66% of its length beyond tip of mandible, 4.8–6.5 in head. Eye small, 3.5–4.0. Postorbital short, 1.9–2.3 in head. Maxillary bluntly pointed, its upper margin nearly straight, usually extending nearly to margin of opercle, 1.1–1.25 in head. Mandible 1.4–1.75. Cheek somewhat longer than eye, its posterior angle rather broad, about 45°. Gill rakers slender, close-set, often difficult to count (probably accounting for wide range given).

Dorsal fin with the longest rays failing to reach tip of last ray if deflexed, its origin about equidistant between base of caudal and some point over posterior half of eye. Anal with origin under or slightly in advance of middle of dorsal base, its base 4.5–5.4 in SL. Pelvic reaching somewhat less than halfway to origin of anal, inserted a little nearer to origin of anal than to pectoral base. PECTORAL failing to reach base of pelvic by nearly an eye's diameter, 1.75–1.9 in head. AXILLARY SCALE of pectoral about 75% of length of fin, 2.4–3.0 in head.

Color. In alcohol, rather pale. Side of head silvery. Lateral band bright silvery, about as wide as pupil (often missing in specimens preserved in formalin). Back usually with dusky punctulations not arranged in definite longitudinal series.

Size. The largest fish seen was only 70 mm (2.8 in.) long, and most of the numerous specimens examined were under 65 mm TL.

Range and Habitat. A. cubana ranges from both coasts of Florida, along Alabama and Louisiana, and through the West Indies, to Yucatán, México, and Puerto Barrios, Guatemala. It is also recorded for Puerto Rico (*18*: 344) and Grenada (*1*: 269). It seems to be common around Jamaica, probably also around Cuba, but apparently it is rather rare on our southern coast. The specimens from the West Indies, in part at least, were taken in shallow water, whereas those from the United States were taken with trawls hauled at depths as great as 30 fms.

Synonyms and References:

Engraulis cubanus Poey, Repert. Fisico-Nat. Cuba, *2*, 1868: 420 (orig. descr.; type local. Cuba; MCZ 17958); Poey *in* Gundlach, An. Soc. esp. Hist. Nat., *10* (4), 1881: 344 (Puerto Rico).

Stolephorus cubanus Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 442 (descr. from orig., range); Evermann and Marsh, Bull. U. S. Fish Comm. (1900), *20* (1), 1902: 88 (after Jordan and Evermann, 1896).

Stolephorus astilbe Jordan and Rutter, Proc. Acad. nat. Sci. Philad., 1897: 95 (orig. descr.; type local. Kingston, Jamaica; type SU 4854; paratypes MCZ 31392); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (3), 1898: 2815 (descr. from orig., synon.).

Anchoviella cubana Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67*, 1926: 399 (synon., descr., Cuba, includ. type material, MCZ 17958); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 48 (synon., range); Fowler, Proc. Acad. nat. Sci. Philad., *82*, 1930: 269 (Grenada, B.W.I.); Howell-Rivero, Bull. Mus. comp. Zool. Harv., *82*, 1938: 172 (4 specimens in type material, the largest said to be type, MCZ 17958).

Anchoviella astilbe Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67*, 1926: 402 (synon., descr., paratypes MCZ 31392); Jordan, Evermann, and Clark, Rept. U. S. Comm. Fish. (1928), 2, 1930: 49 ("West Indies"); Fowler, Proc. Acad. nat. Sci. Philad., *82*, 1930: 269 (Grenada, B.W.I.).

Anchovia cubana Nichols, N. Y. Acad. Sci., *10* (2), 1929: 204 (synon., diagn., Cuba and Puerto Rico).

Anchoa cubana Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 76, fig. 31 (synon., descr., extension of range; cf. paratypes of *cubana* and *astilbe*).

Anchoa ginsburgi Hildebrand 1943

Figure 38

Study Material. Type material, 16 specimens, from juveniles 28 mm long to adults or near adults 63 mm TL, from Gulf of Venezuela.

Distinctive Characters. This species differs from *hepsetus* chiefly in the shorter and blunter maxillary and in the more numerous vertebrae when compared with *hepsetus* from southern localities, especially from Yucatán and Panama (*3*: 56, tab. 7). Among specimens of equal size, this species seems to be more slender.

Description. Proportional dimensions in per cent of standard length, and counts, based on 13 specimens, 43–63 mm TL.

Body: depth 17.4–18.8.
Head: length 25–28.5.
Snout: length 4.9–5.9.
Eye: diameter 6.6–9.1.
Postorbital: distance 14.5–15.8.
Maxillary: length 17.2–18.2.
Mandible: length 15.5–17.8.

Anal fin: length of base 19.2–22.
Pectoral fin: length 13.7–15.3.

Scales: *ca.* 42–45.
Gill rakers: 16–18 + 20–22.
Fin rays: dorsal 14 or 15; anal 18–20; pectoral 13–15.
Vertebrae: 44 or 45 (2 specimens).

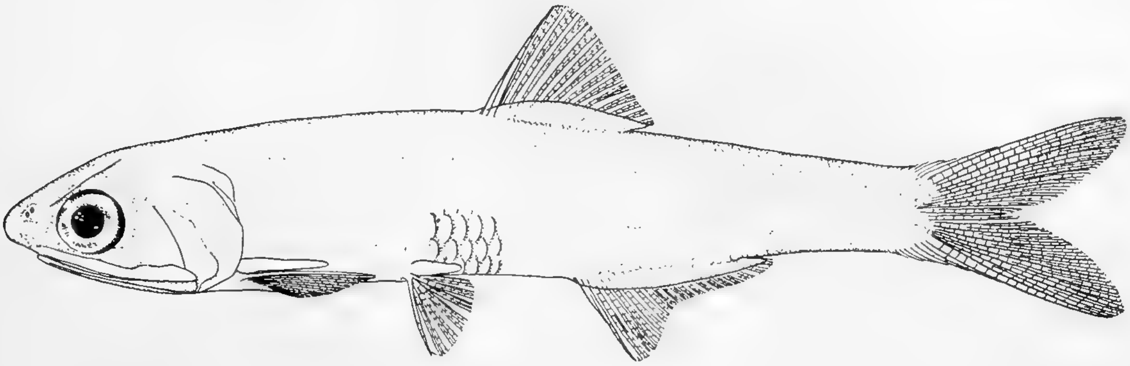

FIGURE 38. *Anchoa ginsburgi*, paratype, 60 mm TL, 52 mm SL, from Gulf of Venezuela, USNM 119789. Drawn by Louella E. Cable.

BODY slender, moderately compressed, its depth 5.3–5.75 in SL. HEAD 3.5–4.0 in SL, its depth equal to its postorbital length and about half of eye. SNOUT short, projecting a little more than half of its length beyond mandible, 4.5–5.25 in head. EYE 3.25–4.0. POSTORBITAL moderately long, 1.3–1.9 in head. MAXILLARY short, its upper margin rounded, reaching joint of mandible, 1.3–1.5 in head. MANDIBLE 1.5–1.65. CHEEK broad, a little longer than eye, its posterior angle about 45°.

DORSAL fin low, the longest rays failing to reach tip of last ray if deflexed, its origin usually somewhat nearer to base of caudal than to anterior margin of eye. ANAL short, with origin commonly slightly posterior to middle of dorsal, its base 4.5–5.2 in SL. PELVIC small, inserted equidistant between origin of anal and base of pectoral, or a little nearer to the latter. PECTORAL scarcely falcate, failing to reach pelvic by about half of diameter of eye, 1.7–2.0 in head. AXILLARY SCALE of pectoral moderately pointed, failing to reach tip of fin by about 75% of diameter of eye, 2.8–3.1 in head.

Color. In alcohol pale (originally preserved in formalin). Side of head silvery. Lateral band bright silvery, about 75% of width of eye.

Range. Known only from the holotype and 15 paratypes, all from the Gulf of Venezuela, partly from Estauques Bay and partly from Salinas Bay.

References:

Anchoa ginsburgi Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 55, fig. 20 (orig. descr.; type local. Estauques Bay, Gulf of Venezuela; type USNM 119788); Schultz, Proc. U. S. nat. Mus., *99*, 1949: 43 (ref., types, locals.).

Anchoa lamprotaenia Hildebrand 1943

Longnose Anchovy, Manjúa (Cuba)

Figure 39

Study Material. A total of 80 specimens, 46–92 mm TL, collected at Palm Beach, Miami, Key West, and Tortugas, Florida; Progreso, Yucatán, México; Cuba; Puerto Rico; British Honduras; and the Atlantic coast of Panama.

Distinctive Characters. This species until recently has been consistently identified with *A. hepsetus* in museum collections. Since these species are not easily separated by any one character, a combination of characters is sometimes necessary. Generally *A. lamprotaenia* is distinguished by its longer and more falcate pectoral fin, higher dorsal fin, shorter and broader axillary scale of the pectoral, and by the shorter and more bluntly pointed maxillary with its upper rounded margin. The average number of anal rays is greater and the average number of pectoral rays, gill rakers, and vertebrae is fewer (see *Description* and Tables I–III).

Description. Proportional dimensions in per cent of standard length, and counts, based on study specimens, 46–92 mm TL.

Body: depth 19–23.
Head: length 25–30.
Snout: length 8.1–9.5.
Eye: diameter 7.5–8.3.
Postorbital: distance 14.3–16.
Maxillary: length 21.5–24.5.
Mandible: length 18.5–22.
Anal fin: length of base 20.5–23.5.
Pectoral fin: length 14.3–18.

Scales: *ca.* 38–41.
Gill rakers: 13–18 + 16–20 (usually 14 or 15 + 18 or 19).
Fin rays: dorsal 13–15; anal 19–26 (usually 21–24); pectoral 11–15 (most frequently 12 or 13).
Vertebrae: 39–42 (98 specimens).

BODY strongly compressed, its greatest thickness about equal to depth of caudal peduncle, its depth 4.3–5.25 in SL. HEAD 3.3–4.0, its depth about equal to its postorbital length and half of eye. SNOUT pointed, projecting about 66% of its length beyond tip of mandible, 4.5–5.75 in head. EYE 3.5–4.0 in head. POSTORBITAL 1.75–2.0 in head. MAXILLARY not sharply pointed, usually distinctly rounded above, reaching to, or more usually somewhat beyond, joint of mandible, 1.2–1.4 in head. MANDIBLE 1.35–1.6 in head. CHEEK as long as eye and fully half of snout, its posterior angle about 35°. GILL RAKERS about 75% of length of eye.

DORSAL fin rather high anteriorly, its longest rays usually reaching beyond tip of last ray if deflexed, its origin equidistant between some point over snout or anterior half of eye and base of caudal. ANAL fin with origin under or near beginning of posterior third of dorsal base, its base 4.25–4.9 in SL. PELVIC usually inserted slightly nearer to origin of anal than to base of pectoral. PECTORAL long, falcate, usually failing to reach pelvic by only diameter of pupil, its longest ray in a few specimens with a slight filament, the rays decreasing rapidly in length after the third one, the shortest ray scarcely reaching past midlength of first (uppermost) one, 1.5–1.9 in head. AXILLARY SCALE of pectoral broad at base, scarcely reaching beyond midlength of fin, 3.0–3.6 in head.

FIGURE 39. *Anchoa lamprotaenia*, paratype, 60 mm TL, 48 mm SL, from Key West, Florida, USNM 35000, with pectoral fin enlarged. Drawn by Louella E. Cable.

Color. Preserved specimens pale. Side of head bright silvery. Silvery lateral band prominent, not quite as wide as eye. Punctulations on back not prominent; a few dark dots at base of anal; dorsal and caudal with a few dusky points; other fins unmarked.

Size. A. lamprotaenia apparently attains a smaller size than *A. hepsetus*, the largest seen being only 92 mm (3.7 in.) TL.

Reproduction. Specimens taken at Key West, Florida, June 11, 1936, and at Bush Key (Tortugas), Florida, July 23, 1937, contained well-developed roe, showing that at least some spawning takes place in southern Florida during midsummer.

Range and Habitat. From southern Florida through the West Indies to Panama, and probably to northern Brazil as shown by an imperfect specimen. The collections studied were apparently taken in shallow water near shore. The species is common in the Florida Keys, where *A. hepsetus* seems to be very rare.

Synonyms and References:

Stolephorus brownii Jordan, Proc. U. S. nat. Mus., 7, 1885: 106 (abund. at Key West, Florida; specimens USNM 35000 are *A. lamprotaenia*); Evermann and Marsh, Bull. U. S. Fish Comm. (1900), *20* (1), 1902: 88 (descr., range, distr. in Puerto Rico; synon.; specimens from Fajardo [USNM 73755], at least, are *A. lamprotaenia*).

Anchovia brownii Meek and Hildebrand, Field Mus. Publ., Zool., *15* (1), 1923: 204, pl. 14, fig. 1 (synon., descr., range, specimens from Colón [CNHM 8217] and Porto Bello [CNHM 8216], Panama, in part are *A. lamprotaenia*).

Anchoviella epsetus Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67*, 1926: 396 (synon., descr., range; specimens from Tortugas [MCZ 17944] and Key West [MCZ 18035], Florida, are *A. lamprotaenia*); Pierce, Copeia, 1936: 123 (sample of specimens used in feed. experiments are *A. lamprotaenia*); Longley and Hildebrand, Publ. Carneg. Instn. Wash., 535, 1941: 12 (notes on structure; distr. at Tortugas, Florida; specimens preserved are *A. lamprotaenia*).

Anchoa lamprotaenia Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 62, fig. 23 (orig. descr.; type local. Key West, Florida; type USNM 117661; range cf. *A. hepsetus*).

Doubtful References:

Anchovia brownii Jordan and Thompson, Bull. U. S. Bur. Fish. (1904), 24, 1905: 233 (Garden Key [Tortugas], Florida; probably part, if not all, are *lamprotaenia*); Fowler, Proc. Acad. nat. Sci. Philad., *58*, 1906: 84; and *63*, 1911: 216 (from several Florida Keys; probably part, if not all, are *lamprotaenia*).

Anchoa hepsetus (Linnaeus) 1758

Striped Anchovy (U.S.), Manjúa (Cuba)

Figures 40, 41

Study Material. At least 83 specimens, 55–140 mm TL, and many more, taken at various places from New Jersey southward to Uruguay.

Distinctive Characters. A. hepsetus is related closely enough to *A. lamprotaenia* so that they are not always separable by any one character, a combination of characters sometimes being necessary. In general, *hepsetus* has a shorter and less falcate pectoral fin, a lower dorsal fin, a longer and narrower axillary scale on the pectoral, and a rather longer and more sharply pointed maxillary. Also, its average number of anal rays is lower, and its average number of pectoral rays, gill rakers, and vertebrae is higher. It is related also to *A. ginsburgi*, from which it differs especially in the longer and more sharply pointed maxillary, and generally in having fewer vertebrae.

Description. Proportional dimensions in per cent of standard length, and counts, based on at least 83 specimens, 55–140 mm TL.

Body: depth 18.5–22.
Head: length 25–30.
Snout: length 4.4–6.3.
Eye: diameter 7.15–8.7.
Postorbital: distance 13.5–15.5.
Maxillary: length 19–24.5.
Mandible: length 16.5–20.
Anal fin: length of base 19–22.5.
Pectoral fin: length 14.5–17.5.
Scales: *ca.* 37–43.
Gill rakers: 15–20+18–24 (usually 16–19+19–22).
Fin rays: dorsal 13–16; anal 18–23; pectoral 13–15 (most frequently 14 or 15).
Vertebrae: 40–44 (399 specimens), decreasing somewhat in number southward at least to Panama.

Body slender, moderately compressed, its greatest thickness generally exceeding the depth of caudal peduncle, its depth 4.5–5.4 in SL. Head 3.3–4.0 in SL, its depth equal to postorbital and about a fourth of eye. Snout projecting about 66% of its length beyond tip of mandible, 4.5–6.0 in head. Eye 3.25–4.0 in head. Postorbital 1.8–2.1 in head. Maxillary quite pointed, its upper free margin generally straight, reaching nearly to margin of opercle, 1.2–1.3 in head. Mandible 1.4–1.6 in head. Cheek a little longer than eye, its posterior angle rather broad, about 45°. Gill rakers at angle of first arch about 75% of length of eye.

Dorsal fin low, its margin somewhat concave, its longest rays failing to reach tip of last ray if deflexed, its origin usually about equidistant between base of caudal and middle of eye. Anal fin with origin under middle to posterior fourth of dorsal base, its base 4.4–5.2 in SL. Pelvic reaching about halfway to origin of anal, inserted nearly equidistant between origin of anal and pectoral base. Pectoral not strongly falcate, its four uppermost rays usually of about equal length, its first or uppermost one sometimes a little shorter than the second one, its last or shortest ray usually reaching well past midlength of the first one, the fin often failing to reach base of pelvic by diameter of eye, though sometimes nearly reaching it, its length 1.7–2.0 in head. Axillary scale of pectoral slender, usually failing to reach tip of fin by less than diameter of pupil, 2.0–2.5 in head.

Color. Preserved specimens, pale above. Lower parts pale silvery. Side of head silvery. Middle of side with a bright silvery band, variable in width, often about 75% of width of eye above base of anal, sometimes scarcely wider than pupil.

Size. The largest specimen seen, from Beaufort, North Carolina, is 153 mm (6.1 in.) TL, which probably is near the maximum size attained. A specimen 150 mm long, weighing one ounce, has been reported for Chesapeake Bay. The usual size ranges between about 100–125 mm TL.

Development and Growth. The egg is elliptical, with a major axis of about 1.4–1.6 mm and a minor one of about 0.7–0.85 mm. It is transparent and has no oil globule. The yolk, as in other anchovies studied, is separated into masses having the appearance of large cells under magnification. The egg floats at or near the surface and hatches within about 48 hours at a water temperature of about 66°–70° F.

The newly hatched fish, very slender and thread-like, is about 3.6–4.0 mm long. It is transparent, has a slight greenish shade on the head, and has no definite chromatophores; the head is slightly concave. The myomeres are very distinct. It is quite active. The yolksac generally is absorbed within 24 hours after hatching at 65°–70° F. The fish is then about 4.0–4.5 mm long, at which stage the mouth is open and apparently functional. The fish is still transparent.

The first chromatophores, situated in the midventral line of the chest, appear when the fish is about 5.0 mm long, and at this stage the mouth is large, terminal, and oblique. The dorsal and anal fins become more or less definitely differentiated at a length of 5.0–6.0 mm, but the rays cannot be counted accurately until the fish is about 10 mm, at which length it has become considerably more robust, the notochord is definitely bent upward in the base of the caudal fin, and the caudal has indefinite rays.

At a length of 15 mm the caudal fin is well developed and forked, the notochord is no longer visible, and the mouth remains terminal and oblique. Some additional chromatophores have appeared along the ventral surface, and dark pigment has appeared along the upper margin of the eye.

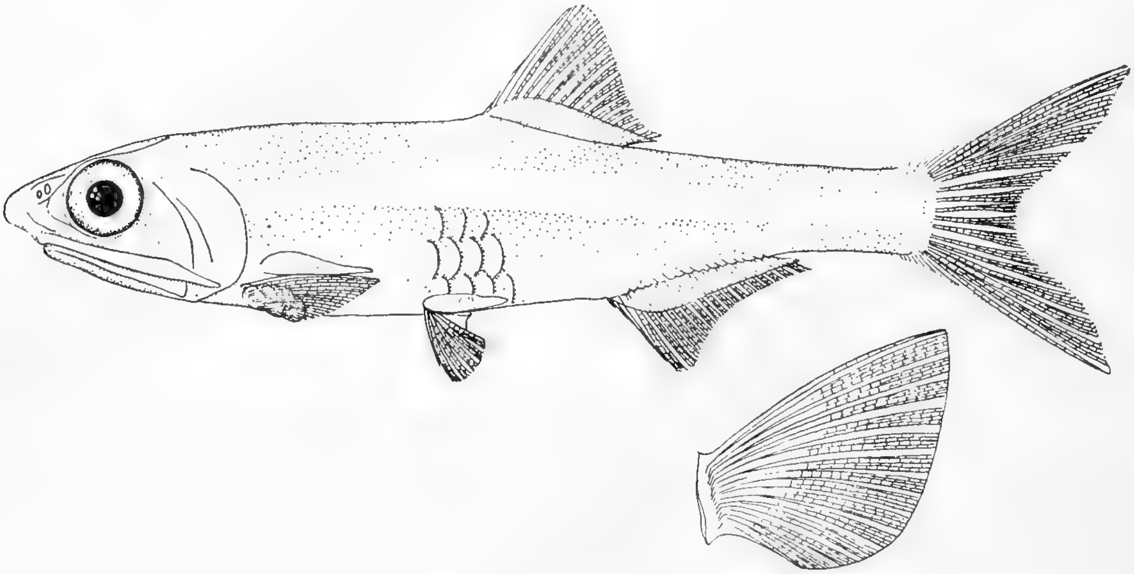

FIGURE 40. *Anchoa hepsetus hepsetus*, 114 mm TL, from Atlantic City, New Jersey, USNM 127525, with pectoral fin enlarged. Drawn by Louella E. Cable.

Little external development takes place while the fish grows from a length of 15 to 25 mm. However, when the fish reaches 35 mm, the mouth has become almost horizontal, as in adults, and the conical snout projects prominently. Pigmentation has increased and the silvery lateral band of the adult, though narrow and indistinct at this point, has appeared. Although the body has now become fairly robust, it remains more slender than in adults, its depth being contained in the length about 6.0 times.

When it reaches a length of about 40–45 mm it may be definitely considered a young adult. Although it remains somewhat more slender than larger fish, it is fully pigmented, has the characteristic silvery lateral band well developed, is fully scaled, and is easily identified with the adult (*4*: 389–393; also unpublished field notes of the writer).

Spawning. In the vicinity of Beaufort, North Carolina, spawning begins early in the spring. April 16 is the earliest date on which eggs have been taken. Toward the middle of June, eggs diminished in number in the tows, though a few were taken throughout July. The young, 22 mm and less, were collected in Beaufort Inlet as early as April 11. (*4*: 388; also unpublished data of the writer).

Food. When the fish is about 20 mm the food consists largely of copepods. As the fish grows, this diet is supplemented by gastropods, foraminifera, an occasional ostracod, and annelid worms. The diet of the adult is essentially the same (Linton, *11*: 440; *12*: 353; *4*: 395).

Parasites. The principal parasites are nematodes, cestodes (*Scolex polymorphus* and *Rhynchobothrium* sp.), and trematodes (*Distomum appendiculatum* and *Distomum* sp.) (*11*: 440; *12*: 353).

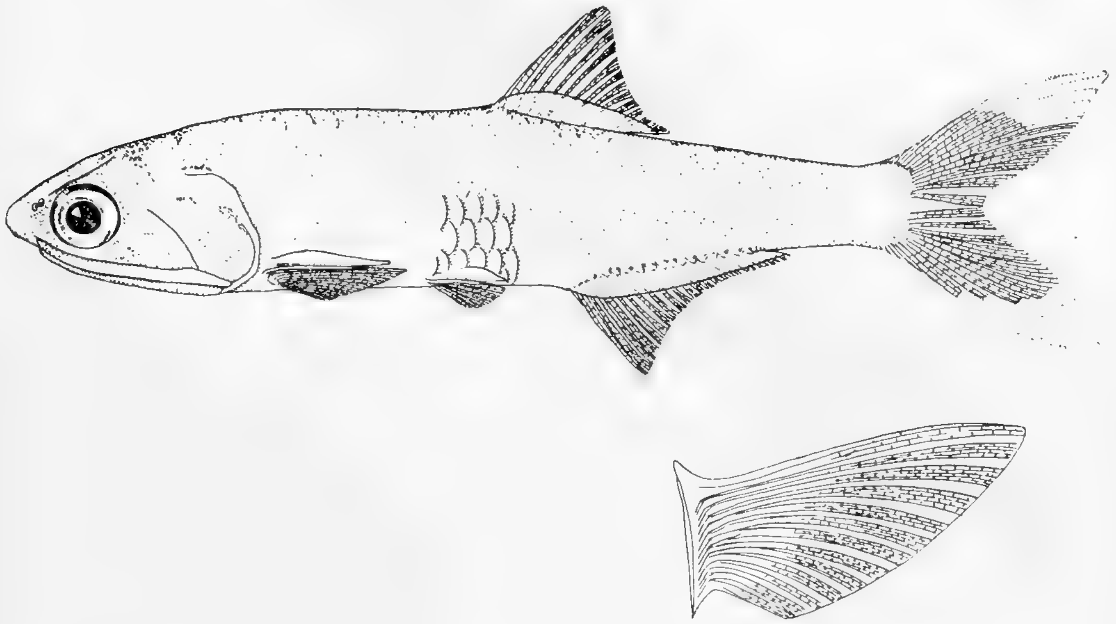

FIGURE 41. *Anchoa hepsetus colonensis*, 70 mm TL, 56 mm SL, from Colón, Panama, USNM 117664, with pectoral fin enlarged. Drawn by Louella E. Cable.

Variation. So great is the variation in this species that certain specimens from Colón, Panama, and northward to the Gulf of Mexico were recognized (*3*: 60, fig. 22) as a subspecies, *A. hepsetus colonensis.* The greatest divergence is apparent in specimens from Colón, Panama, with complete intergradation in specimens on the Gulf coast of the United States. As typical *hepsetus* occurs through the range of *h. colonensis*, the latter is not a geographical variant but one that occurs within the range of the typical species.

The variant, or subspecies *colonensis*, differs from typical *hepsetus* in having a somewhat deeper and more strongly compressed body, its greatest thickness scarcely exceeding the depth of the caudal peduncle. Its pectoral fin is longer and more pointed, generally extending nearly or quite to the base of the pelvic fin. Its silvery lateral band is narrower, often scarcely exceeding the width of the pupil.

Commercial Importance. Each year large quantities are marketed as food for man. In 1939 about 21,000 pounds and in 1940 about 29,000 pounds were handled in the New York City markets. It is economically important, however, chiefly as a forage fish.

It is preyed upon by several commercially important fishes, especially the seatrouts (*Cynoscion*). Water birds also feed on it extensively.

Range. Plentiful from Chesapeake Bay to the West Indies; north irregularly to southern New England and as a stray to Maine and the outer coast of Nova Scotia; south at least as far as Montevideo, Uruguay. It has also been recorded for Cape Verde, Africa, but that record is in need of verification.

In some years it is numerous at Beaufort, North Carolina, appearing in large schools, but in other years less abundant. At Beaufort and in Chesapeake Bay it was taken chiefly with seines near the shore and rarely with trawls in somewhat deeper water; however, in the Gulf of Mexico it was taken in deeper water more commonly. Collections made with otter trawls, some of them in water as much as 30–40 fms. deep, are at hand from off Corpus Christi, Texas, off Grand Isle, Louisiana, and off St. Vincent Island and Apalachicola Bay, Florida.

Details of Occurrence.[8] Stray specimens of this Anchovy were reported for Halifax, Nova Scotia, in 1931 (*21*: 3), and for the mouth of the Penobscot River, Maine, in 1930, when many others were reported as seen (*8*). The next most northerly locality of record is the vicinity of Woods Hole, southern Massachusetts, where it has been reported as abundant, at least in some years. But only one specimen of this particular Anchovy has been reported for Rhode Island. It is less common in New York waters than its relative *mitchilli* (p. 179), but it has been reported as being locally abundant there; this applies equally to New Jersey waters and to Chesapeake Bay as a whole.

Farther to the south, *hepsetus* appears in large schools in some years along the coast of North Carolina (see above), where *mitchilli* has been reported only once (p. 179). It is known from Georgia, the Florida Keys region, various localities along the western coast of Florida from Cape Sable to Pensacola, the coast of Mississippi, Grand Isle and Cameron, Louisiana, Galveston and Mustang Island, Texas, on the Mexican coast off Tampico, Vera Cruz, and Yucatán, and the Atlantic coast of Panama. It is widespread throughout the West Indies also, where it has been recorded for the northern coast of Cuba, St. Thomas, Puerto Rico, Haiti, Santo Domingo, Jamaica, Curaçao, St. Kitts, Martinique, and Barbados. On the coast of Brazil it is known at Mamanguape (near Pernambuco), Bahia, and Rio de Janeiro.

Synonyms and References:

Esox hepsetus Linnaeus, Syst. Nat., ed. 10, 1758: 314 (diagn.; type local. "America"; refs. to 'Piquitinga' Marcgrave, Brazil, and Menidia Browne, Jamaica, nonbinomials).

Atherina epsetus Bonnaterre, Tabl. Encyc. Meth. Ichthyol., 1788: 175 (descr., same fin ray counts as Linnaeus; ref. to Linnaeus, but apparently not ed. 10).

Atherina brownii Gmelin, Syst. Nat., *1*, 1788: 1397 (based on Menidia Browne, pre-Linnaean).

Clupea vittata Mitchill, Trans. Lit. philos. Soc. N. Y., *1*, 1815: 456 (orig. descr.; type local. New York; type lost); De Kay, New York Fauna, Pt. 4: Fishes, 1842: 254 (descr.); Storer, Mem. Amer. Acad. Arts Sci., 1846: 205, in separate (brief descr., New York).

Engraulis brownii Cuvier and Valenciennes, Hist. Nat. Poiss., *21*, 1848: 41 (descr., New York, West Indian

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[8] Added by H. B. Bigelow.

locals., Vera Cruz, Rio de Janeiro; also several Indian O. locals. where this species does not occur); Günther, Cat. Fish. Brit. Mus., *7*, 1868: 389 (descr., West Indies, Gulf of Mexico, and Bahia; also from "Libertad," Pacific Central America, and Ceylon where the species does not occur; synon. includ. *E. tricolor*, which is a valid species); Poey, Repert. Fisico-Nat. Cuba, *2*, 1868: 419 (descr., Cuba); Poey, Enumerat., Pisc. Cubana, 1875: 149 (relations., Cuba, Jamaica, and San Domingo); Yarrow, Proc. Acad. nat. Sci. Philad., 1877: 215 (Ft. Macon, North Carolina; "not common").

Argentina menidia Gronow, Cat. Fish., 1754: 141 (based on Menidia Browne, pre-Linnaean).

Engraulis vittatus Jordan and Gilbert, Proc. U. S. nat. Mus., *1*, 1879: 385 (common, Beaufort Harbor, North Carolina).

Engraulis hiulcus Goode and Bean, Proc. U. S. nat. Mus., *2*, 1880: 343 (orig. descr.; type local. Clearwater Harbor, Florida; USNM 23632; in bad condition, about 57 mm long, not 47 mm as stated by Goode and Bean).

Stolephorus perthecata Goode and Bean, Proc. U. S. nat. Mus., *5*, 1883: 434 (orig. descr.; type local. Pensacola, Florida; type USNM 30483); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 442 (descr.).

Stolephorus browni Jordan and Gilbert, Bull. U. S. nat. Mus., 16, 1883: 273 (descr., range, synon.); Swain, Bull. U. S. Fish Comm. (1882), *2*, 1883: 56 (descr., several locals. between New York and Brazil; synon., includ. *tricolor*); Jordan and Swain, Proc. U. S. nat. Mus., *7*, 1885: 230 (Cedar Keys, Florida); Bean, T. H., Bull. U. S. Fish Comm. (1887), *7*, 1888: 149 (common around Great Egg Harbor, New Jersey; eaten by weakfish); Henshall, Bull. U. S. Fish Comm. (1889), *9*, 1891: 373 (Cape Sable Cr., Cape Romano, and Big Gasparilla, Florida); Bean, B. A., Proc. U. S. nat. Mus., *14*, 1892: 93 (abund., Cape Charles City, Virginia); Evermann and Kendall, Bull. U. S. Fish Comm. (1892), *12*, 1894: 105 (Galveston, Texas); Moore, Bull. U. S. Fish Comm. (1892), *12*; 1894: 359 (abund., size, Sea Isle City, New Jersey); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 443 (descr., range, synon.); Smith, Bull. U. S. Fish Comm. (1897), *17*, 1898: 92 (abund., season, Woods Hole, Massachusetts); Evermann and Kendall, Rep. U. S. Comm. Fish. (1899), 1900: 56 (Florida locals.); Gilbert, Proc. Wash. Acad. Sci., *2*, 1900: 163 (Mamanguape, Brazil); Linton, Bull. U. S. Fish Comm. (1899), *19*, 1901: 440 (food, parasites); Bean, T. H., 7th Rep. Forest Comm. N. Y. (1901), 1902: 310 (synon., forage fish); Evermann and Marsh, Bull. U. S. Fish Comm. (1900), *20*, 1902: 88 (descr., range, Puerto Rico; synon.); Schreiner and Miranda-Ribeiro, Arch. Mus. nac., Rio de J., *12*, 1903: 93 (Rio de Janeiro); Bean, T. H., Bull. N. Y. St. Mus., 60, Zool. 9, 1903: 214 (descr., synon., New York); Linton, Bull. U. S. Bur. Fish. (1904), *24*, 1905: 353 (food, parasites); Barbour and Cole, Bull. Mus. comp. Zool. Harv., *50*, 1906: 156 (Progreso, México); Breder, Zoologica, N. Y., *2* (15), 1922: 338 (Sandy Hook, New Jersey); Metzelaar, Bijdr. Dierk. Amst., 1922: 134 (Curaçao).

Anchovia brownii Fowler, Rep. N. J. St. Mus. (1905), 1906: 109 (descr., New Jersey); Fowler, Rep. N. J. St. Mus. (1906), 1907: 267, pl. 85 (ill.); Smith, N. C. geol. econ. Surv., *2*, 1907: 133 (descr., range, abund., forage fish); Jordan and Dickerson, Proc. U. S. nat. Mus., *34*, 1908: 12 (Tampico, México); Weymouth, Proc. U. S. nat. Mus., *38*, 1910: 136 (Cameron, Louisiana); Fowler, Proc. Acad. nat. Sci. Philad., *63*, 1911: 216 (New Jersey, North Carolina, Florida Keys, San Domingo, Puerto Rico, Rio de Janeiro); Sumner, Osburn, and Cole, Bull. U. S. Bur. Fish. (1911), *31*, 1913: 742 (habitat, spawn. time, food, parasites, Woods Hole, Massachusetts); Fowler, Copeia, 1915: 50 (San Domingo); Latham, Copeia, 1919: 55 (Orient, Long Island, New York); Meek and Hildebrand, Field Mus. Publ., Zool., *15* (1), 1923: 204, pl. 14, fig. 1 (synon., descr., range, Colón and Porto Bello, Panama); Breder, Zoologica, N. Y., *4* (4), 1925: 152 (large schools, Caledonia Bay, Panama); Nichols and Breder, Zoologica, N. Y., *9* (1), 1927: 43 (descr., range, abund. New York to Woods Hole, Massachusetts; size); Nichols, N. Y. Acad. Sci., *10* (2), 1929: 205, fig. 38 (diagn., range, abund., Puerto Rico).

Anchoviella epsetus Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67* (11), 1926: 396 (synon., descr., range; Rio de Janeiro, "Sambaia" [probably Sambara], Brazil, and Montevideo, Uruguay, specimens are *tricolor*; specimens from Key West and Tortugas, Florida, are *lamprotaenia*); Hildebrand and Schroeder, Bull. U. S. Bur. Fish. (1927), *43* (1), 1928: 110 (descr., food, spawn. season, size, range, Chesapeake Bay); Beebe and Tee-Van, Zoologica, N. Y., *10* (1), 1928: 46 (descr., range, Port-au-Prince, Haiti); Breder, Field Bk. Mar. Fish. Atl. Cst., 1929: 71, text fig. (range, spawn., food, abund.); Jordan, Manual Vert. Anim. NE U. S., ed. 13, 1929: 43 (descr., range); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 48 (synon., range); Hildebrand and Cable, Bull. U. S. Bur. Fish., *46*, 1930: 388 (econ. import., spawn., develop. of eggs and young, growth rate, food); Kendall, Bull. Boston Soc. nat. Hist., *58*, 1931: 11 (Portland, Maine); Vladykov, Proc. N. S. Inst. Sci., *19* (1), 1935: 3, 55, fig. 31

(Halifax Harbor, Nova Scotia); Hubbs, Publ. Carneg. Instn. Wash., 457, 1936: 175 (discus. ident., Rio Champoton and Campeche, Yucatán); Bigelow and Schroeder, Bull. U. S. Bur. Fish., *48* (20), 1936: 328 (Portland, Maine; Halifax Harbor, Nova Scotia); Howell-Rivero, Handbk. Jamaica, 1936: 1, in reprint (Port Antonio, Jamaica); Gunter, Ecol. Monogr., *8*, 1938: 337 (spawn., abund., Louisiana); Gunter, Amer. Nat., *72*, 1938: 78, 79; Gunter, Ecology, *22* (2), 1941: 203–208 (killed by freeze, Texas); Fowler (in part, not of Linnaeus), Arqu. Zool. estad. São Paulo, *3* (6), 1941: 134 (Brazilian recs., in part *tricolor*).

Anchoa hepsetus hepsetus Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 57, fig. 21 (synon., descr., range).

Anchoa hepsetus colonensis Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 60, fig. 22 (orig. descr.; type local. Colón, Panama; type USNM 117664; cf. typical *hepsetus*; range).

Anchoa hepsetus Gunter, Publ. Inst. mar. Sci. Texas, *1* (1), 1945: 32 (shallow water, temp., salinity, length frequencies by months, sex. develop. in spring, Texas).

Doubtful References:

Anchovia brownii Jordan and Thompson, Bull. U. S. Bur. Fish. (1904), *24*, 1905: 233 (Garden Key, Florida; some, if not all, were *lamprotaenia*); Fowler, Proc. Acad. nat. Sci. Philad., *58*, 1906: 84 (Florida Keys; in part, if not all, *lamprotaenia*).

Engraulis brownii Lampe, Fisch. Dtsch. Südpolar Exped., 1901–1903, III, Die Hochsee und Küsten Fische, *15*, Zool. 7, 1914: 216 (Cape Verde, So. Africa; ident. needs verification).

Engraulis hepsetus Fowler, Bull. Amer. Mus. nat. Hist., *70* (1), 1936: 183 (descr. based on New Jersey specimens; rec. for Cape Verde after Lampe).

Negative References:

Stolephorus brownii Jordan, Proc. U. S. nat. Mus., *7*, 1885: 106 (abund. Key West, Florida; USNM 35000 listed; these exam. and found to be *lamprotaenia*); Puyo, Bull. Soc. Hist. nat. Toulouse, *80*, 1945: 100, fig. 1 (descr., French Guiana; descr. and ill. appear to be unnamed new species of *Anchoviella*); Puyo, Faune Emp. Franc., 12, Poiss. Guiane Franç., 1949: 154 (see Puyo, 1945).

Anchovia brownii Starks, Stanf. Univ. Publ., Univ. ser., 1913: 10 (Natal, Brazil; specimens are *tricolor*).

Anchoa lyolepis (Evermann and Marsh) 1902

Dusky Anchovy, Manjúa (Cuba)

Figure 42

Study Material. At least 22 specimens, 45–70 mm TL; juveniles, including the type material, also at hand for comparison; from off St. Vincent Island, Florida; Mobile Bay, Alabama; Mississippi Sound, Mississippi; Grand Isle, Louisiana; Galveston and Aransas Pass, Texas; several places in Puerto Rico, Cuba, and St. Martin, West Indies.

Distinctive Characters. This species is quite distinctive. It is probably nearest to *lamprotaenia*, from which it differs rather prominently in the lower head, the longer snout, longer and narrower cheek, and in the more posteriorly placed anal fin.

Description. Proportional dimensions in per cent of standard length, and counts, based on *Study Material*, 45–70 mm TL.

Body: depth 16.6–20.
Head: length 27–32.2.
Snout: length 5.9–6.6.

Eye: diameter 5.5–7.0.
Postorbital: distance 15.4–16.7.
Maxillary: length 21–27.

Mandible: length 20–22.2.
Anal fin: length of base 19–22.5.
Pectoral fin: length 14–15.4.

Scales: *ca.* 40–44.

Gill rakers: 15–21 + 19–26 (most frequently 18 or 19 + 20–22).
Fin rays: dorsal 12–15; anal 19–23; pectoral 12–14.
Vertebrae: 41–43 (9 specimens).

Body very slender, rather strongly compressed, its depth 5.0–6.0 in SL. Head 3.1–3.7 in SL, its depth about equal to its postorbital length. Snout extending nearly its full length beyond tip of mandible, 4.3–5.5 in head. Eye scarcely longer than snout in large specimens, 4.25–5.0 in head. Postorbital part of head slightly longer than snout and eye, 1.7–2.0 in head. Maxillary rather bluntly pointed, its upper margin gently rounded, not quite reaching margin of opercle, 1.15–1.3 in head. Mandible 1.25–1.55. Cheek narrow, about as long as snout and eye, its posterior angle acute, about 25°.

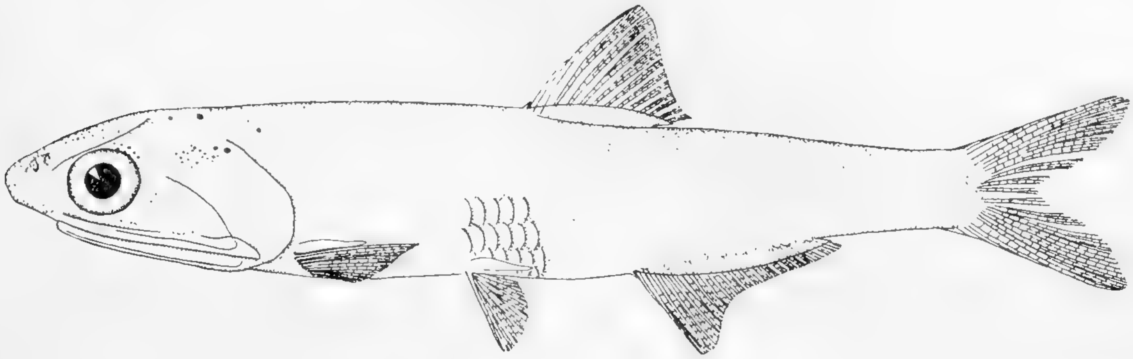

Figure 42. *Anchoa lyolepis*, 63 mm TL, from Hucares, Puerto Rico, USNM 125580. Drawn by Louella E. Cable.

Dorsal fin moderately high anteriorly, its longest rays reaching nearly to tip of last ray if deflexed, its origin usually a little nearer to base of caudal than to tip of snout. Anal with origin under or slightly behind base of last dorsal ray, its base 4.45–5.3 in SL. Pelvic inserted equidistant between origin of anal and pectoral base, sometimes a little nearer to the latter. Pectoral rather falcate, failing to reach pelvic by 50–75% of diameter of eye, the last ray only about half as long as the first or uppermost ray, 1.75–2.1 in head. Axillary scale of pectoral rather short and broad, about 50–75% of length of pectoral, 2.9–3.5 in head.

Color. In alcohol pale. Side of head silvery. Lateral band bright silvery, fully as wide as eye (often dusky in specimens preserved in formalin); back and both dorsal and caudal fins with dusky dots, these frequently present at base of anal also.

Size. The 70-mm (2.8 in.) specimen measured is the largest one seen, and it is probably near the maximum size attained.

Reproduction. Specimens of two different lots taken during February in Puerto Rico contain well-developed roe.

Variation. Specimens from the Gulf of Mexico have more numerous gill rakers than those from farther south, but they seem to agree in other respects.

Commercial Importance. So far as known, this Anchovy is not used directly as food by man. However, where it is common, as in Puerto Rico, it no doubt furnishes considerable forage for larger predatory fishes that are used as food by man.

Range and Habitat. The range extends from the Gulf coast of the United States through the West Indies to the Gulf of Venezuela. Although some of the specimens examined were taken with trawls hauled at depths down to 30 fms., most of them were seined along the shore.

Synonyms and References:

Stolephorus lyolepis Evermann and Marsh, Bull. U. S. Fish Comm. (1900), *20* (1), 1902: 89, fig. 13 (orig. descr. based on juveniles, 30–37 mm long; type local. Culebra, Puerto Rico; type USNM 49528).

Stolephorus choerostoma Evermann and Marsh, Bull. U. S. Fish Comm. (1900), *20* (1), 1902: 88 (descr., synon., specimens in part re-exam., not *E. choerostoma* Goode).

Anchovia platyargyrea Fowler, Proc. Acad. nat. Sci. Philad., *63*, 1911: 216, fig. 4 (orig. descr.; type local. St. Martin, West Indies; type ANSP 1416; cf. *E. choerostoma* Goode; type material, exam. by me, is *S. lyolepis* E. and M.).

Anchoviella choerostoma Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67*, 1926: 404 (specimens from e. coast of Panama and Puerto Rico probably this species); Beebe and Tee-Van, Zoologica, N. Y., 10 (1), 1928: 47, fig. (refs., descr., distr., abund. Port-au-Price, Haiti; descr. and fig. show it to be *S. lyolepis* E. and M., not *E. choerostoma* Goode).

Anchoviella lyolepis Beebe and Tee-Van, Zoologica, N. Y., *10* (1), 1928: 47, fig. (refs., descr., Port-au-Prince, Haiti; descr. based on juveniles); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 49 (synon., Puerto Rico only).

Engraulis platyargyreus Fowler, Proc. Acad. nat. Sci. Philad., *80*, 1928: 468 (St. Lucia, B.W.I.).

Anchovia choerostoma Nichols, N. Y. Acad. Sci., *10* (2), 1929: 205, fig. 39 (refs., diagn., Puerto Rico; *S. lyolepis* E. and M., not *E. choerostoma* Goode).

Anchoviella platyargyrea Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 49 (ref. to orig. descr.); Beebe and Hollister, Zoologica, N. Y., *19* (6), 1935: 211 (Union I., Grenadines, West Indies).

Anchoa lyolepis Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 65, fig. 25 (synon., descr., relation., range); Schultz, Proc. U. S. nat. Mus., *99*, 1949: 43 (synon.).

Doubtful Reference:

Engraulis (*Stolephorus*) *argentivittatus* Regan, Ann. Mag. nat. Hist., (7) *13*, 1904: 257 (orig. descr.; type local. Pas Penas, Jalisco, México; type in BMNH).

Anchoa filifera (Fowler) 1915

Figure 43

Study Material. At least 11 specimens, ranging between 55–75 mm TL. In addition to the three types from Port-of-Spain, Trinidad, 16 additional specimens from Kingston, Jamaica, were examined.

Distinctive Characters. This species in general resembles *A. lyolepis*, from which it differs: in the produced ray of the pectoral, the fin itself being longer; the more anterior position of the dorsal and anal fins; and the slightly fewer vertebrae. It differs from

A. howelli Hildebrand (*3*: 105), known only from Santos and Rio de Janeiro, Brazil, in having fewer anal rays, gill rakers, and vertebrae, longer pectoral and pelvic fins, and a slightly more posteriorly inserted pelvic fin. For details, compare the descriptions of the two species.

Description. Proportional dimensions in per cent of standard length, and counts, based on study specimens, 55–75 mm TL.

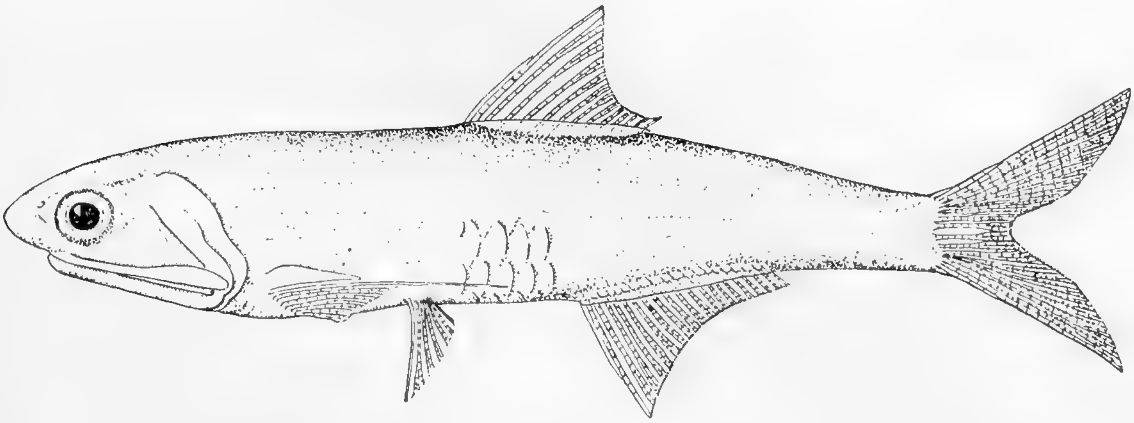

FIGURE 43. *Anchoa filifera*, 70 mm TL, from Kingston, Jamaica, USNM 127611. Drawn by Alice C. Mullen.

Body: depth 17.8–20.
Head: length 28–29.3.
Snout: length 5.17–5.85.
Eye: diameter 5.9–7.0.
Postorbital: distance 14.7–16.
Maxillary: length 20.5–23.
Mandible: length 18–21.
Anal fin: length of base 18.5–21.
Pectoral fin: length (without filament) 15.5–16.6.

Scales: *ca.* 39 or 40.
Gill rakers: 17–19+20–23.
Fin rays: dorsal 13–15; anal 19–23; pectoral 13 or 14.
Vertebrae: 39 or 40 (3 specimens).

BODY strongly compressed, its depth 5.0–5.6 in SL. HEAD 3.4–3.6, its depth slightly exceeding the postorbital length. SNOUT long, projecting nearly its full length beyond mandible, only a little shorter than eye, 5.0–5.5 in head. EYE small, 4.2–4.8. POSTORBITAL part of head 1.6–1.8 in head. MAXILLARY not sharply pointed, its upper margin rounded, reaching nearly to margin of opercle, 1.25–1.3 in head. MANDIBLE 1.4–1.5. CHEEK narrow, equal to eye and snout, its posterior angle sharp, about 30°.

DORSAL fin rather high anteriorly, its longest rays reaching nearly to tip of last ray if deflexed, its origin slightly nearer to tip of snout than to base of caudal. ANAL with origin nearly under the beginning of the last third of dorsal base, the base 4.8–5.4 in SL. PELVIC reaching much more than halfway to anal, inserted a little nearer to pectoral base than to anal origin. PECTORAL with upper ray produced, its filament (often broken) extending to, and possibly beyond, tip of pelvic in perfect specimens, the fin, without filament (second ray), reaching base of pelvic, 1.6–1.8 in head.

AXILLARY SCALE of pectoral about 66% of length of fin (without filament), 2.8–3.5 in head.

Color. In alcohol pale. Side of head and lower part of side silvery. Silvery lateral band as wide as eye (often dusky in specimens preserved in formalin). Upper parts of head and back with numerous punctulations not arranged in longitudinal series.

Size. The longest specimen seen (type) is 75 mm (3 in., 61 mm SL).

Range. This species, as here understood, is known from Puerto Rico, Jamaica, Haiti, and Trinidad.

Synonyms and References:

Anchovia filifera Fowler, Proc. Acad. nat. Sci. Philad., 1915: 524, fig. 2 (orig. descr.; type local. Port-of-Spain, Trinidad; type ANSP 45080; cf. *A. platyargyrea* = *A. lyolepis* and *A. choerostoma*. Gill rakers given as 25 + 22, total anal rays 25, depth 4.75. My counts and measurements give gill rakers 18 + 22, anal rays 23, depth 5.0. Orig. fig. shows mandible projecting too far in advance of vertical from anterior margin of eye; anal fin rather too far back, its origin actually well in advance of vertical from base of last dorsal ray).

Anchoviella filifera Fowler, Proc. biol. Soc. Wash., *43*, 1930: 146 (Jamaica); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish (1928), 2, 1930: 50 (ref.).

Anchoviella longipinna Beebe and Tee-Van, Zoologica, N. Y., *10* (1), 1928: 48, fig. (orig. descr.; type local. Bizoton, Haiti; type NYZS 7460; also Port-au-Prince, Haiti; type material not seen; descr. and fig. agree well with *A. filifera* from Jamaica and Trinidad).

Anchoa filifera Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 105, fig. 45 (synon., descr., range).

Genus *Anchoviella* Fowler 1911

Anchoviella Fowler, Proc. Acad. nat. Sci. Philad., *43*, 1911: 211; genotype by original designation, *Engraulis perfasciatus* Poey 1861.

Amplova Jordan and Seale, Copeia, 1925: 31; type species *Anchovia brevirostris* Meek and Hildebrand 1923 equals *Amplova balboae* Jordan and Seale 1925.

Characters. BODY usually slender, its depth less than 25% of SL (except in *pallida*, 26–28.5%). GILL RAKERS usually fewer than 35 on lower limb (except in *pallida*, which may have as many as 45), not known to increase in number with age. ANAL fin rather short, with fewer than 30 rays, its origin usually under or posterior to middle of dorsal base (somewhat in advance of middle of dorsal in *blackburni* and *jamesi*). VERTEBRAE 39–45.

Size. Although a maximum length of 155 mm has been reported for *eurystole*, the largest in the collections studied is only 130 mm TL, and the other species are smaller.

Remarks. Anchoviella obviously is closely related to *Anchoa*, from which it differs in the shorter and distally square-to-round maxillary. This structure, variable in length in both genera, may reach only a little beyond the vertical from the posterior margin of the eye, as in *Anchoviella jamesi*, or it may reach to the joint of the mandible, as in *Anchoviella eurystole*. Indeed, Jordan and Seale (6: 31) erected a new genus, *Amplova*, on the basis of the very short maxillary in *A. balboae*, a species common on the Pacific

Table V. Frequency Distribution of Anal Rays in *Anchoviella*.*

Species	Number of Anal Rays												
	15	16	17	18	19	20	21	22	23	24	25	26	27
eurystole	6	8	17	7	1	—	—	—	—	—	—	—	—
estauquae	1	1	2	—	—	—	—	—	—	—	—	—	—
perfasciata	6	9	22	9	2	—	—	—	—	—	—	—	—
brevirostris	—	2	1	1	1	—	—	—	—	—	—	—	—
guianensis	—	—	—	1	1	—	—	—	—	—	—	—	—
alleni	—	—	—	4	4	—	—	—	—	—	—	—	—
pallida	—	—	—	—	—	—	—	—	—	1	1	1	—
elongata	—	—	—	—	—	—	—	4	5	5	—	—	—
lepidentostole	—	—	—	—	—	—	—	—	1	—	1	—	—
blackburni	—	—	—	—	—	—	—	—	—	—	2	2	3
jamesi	—	—	—	—	1	—	1	—	—	—	—	—	—

* Anal rays given as 9–11 for *cayennensis*, see p. 212.

Table VI. Frequency Distribution of Gill Rakers on Upper Limb in *Anchoviella*.*

Species	Number of Gill Rakers on Upper Limb of First Arch																								
	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
eurystole	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	11	12	7	4	—	—	—	—	—	—
estauquae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—
perfasciata	—	—	—	—	—	—	—	—	1	12	20	16	5	3	—	—	—	—	—	—	—	—	—	—	—
brevirostris	—	—	—	4	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
guianensis	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
alleni	—	—	—	—	—	—	1	7	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
pallida	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	2	1
elongata	—	—		—	—	—	—	7	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
lepidentostole	—	—	—	—	—	—	—	3	1	—		—	—	—	—	—	—	—	—	—	—	—	—	—	—
blackburni	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
jamesi	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

* When the number of counts exceeds the number of specimens listed in the text, the gill rakers on both anterior arches in at least some of the specimens were counted.

Table VII. Frequency Distribution of Gill Rakers on Lower Limb in *Anchoviella*.*

Species	Number of Gill Rakers on Lower Limb of First Arch																														
	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
eurystole	—	—	—	—	—	—	—	—	—	—	—	—	2	10	13	10	3	5	2	—	—	—	—	—	—	—	—	—	—	—	—
estauquae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—
perfasciata	—	—	—	—	—	—	—	—	—	—	6	19	17	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
brevirostris	—	—	—	2	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
guianensis	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
alleni	—	—	—	—	—	—	—	—	1	5	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
pallida	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	1	—	1	—	—	1
elongata	—	—	—	—	—	—	—	2	10	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
lepidentostole	—	—	—	—	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
blackburni	1	4	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
jamesi	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

* When the number of enumerations exceeds the number of specimens listed in the text, the gill rakers have been counted on both anterior arches in at least some of the fish.

coast of Panama. However, there are species quite intermediate between the type species of *Amplova* (*balboae*) and that of *Anchoviella* (*perfasciata*). For that reason *Amplova* was reduced to subgeneric rank (*3*: 108).

The very short maxillary in some species of *Anchoviella* furnishes a near transition from the Engraulidae to the Clupeidae; but other family characters, such as the projecting snout and the anteriorly more-or-less embedded and widely separated premaxillaries, remain as in other Engraulidae.

Range and Habitat. The genus seems to be restricted to the two coasts of America, ranging in the Atlantic from Woods Hole, Massachusetts, at least to southern Brazil, and in the Pacific from southern California to northern Peru. Most of the species enter fresh water. In fact, several of the South American species from the Atlantic drainage are known only from freshwater lakes and streams, a few of them having been taken a great distance from the sea.

Key to Species of the Western Atlantic

1a. Maxillary usually extending beyond posterior rim of orbit by a distance equal to or greater than diameter of pupil. Subgenus *Anchoviella.*

2a. Origin of anal posterior to middle of dorsal base, sometimes entirely behind dorsal; not more than 20 anal rays.

3a. Origin of anal clearly posterior to dorsal base, generally under or behind tips of dorsal rays if deflexed; gill rakers 24–28 + 27–33.

4a. Longest rays of dorsal failing to reach tip of last ray if deflexed; eye 3.75–4.5 in head, 2.1–2.5 in postorbital; maxillary 15.8–17.8% of SL; postorbital 13.8–15.5% of SL.
eurystole (Swain and Meek) 1884, p. 208.

4b. Longest rays of dorsal reaching beyond tip of last ray if deflexed; eye 4.4–4.8 in head, 2.5–2.75 in postorbital; maxillary 17.5–18.7% of SL; postorbital 15.5–15.8% of SL.
estauquae Hildebrand 1943, p. 211.

3b. Origin of anal under or slightly behind base of last 2 or 3 rays of dorsal; gill rakers usually 13–23 + 19–28.

5a. Only 9–11 anal rays; depth of body less than 14% of SL.
cayennensis (Puyo) 1945, p. 212.

5b. 15 anal rays or more; depth of body more than 15% of SL.

6a. Pectoral with 14–16 rays; gill rakers 19–23 + 24–28.
perfasciata (Poey) 1860, p. 213.

6b. Pectoral with 11–13 rays; gill rakers 18 or fewer on upper limb, generally fewer than 25 on lower limb.

7a. Gill rakers 13 or 14 + 18 or 19; pectoral failing to reach base of pelvic by diameter of eye, 11.2–13.8% of SL, 1.7–2.0 in head. *brevirostris* (Günther) 1868, p. 216.

7b. Gill rakers 16–18 + 22–26; pectoral failing to reach pelvic by a distance considerably less than eye, 14.7–16.8% of SL, 1.4–1.6 in head.

8a. Eye 7.0–7.5% of SL, 3.2–3.5 in head; cheek fully as long as eye, with a definite posterior angle of about 60°; axillary scale of pectoral about 50% of fin, 2.4 in head; a median dark line posterior to anal fin.
guianensis (Eigenmann) 1912, p. 217.

8b. Eye 5.5–6.25% of SL, 3.7–4.1 in head; cheek scarcely as long as eye, without a definite posterior angle; axillary scale of pectoral about 75% of length of fin, 2.0–2.2 in head; no median dark line posterior to anal fin.
alleni (Myers) 1940, p. 219.

2b. Origin of anal under, or in advance of, middle of dorsal base; 22–29 anal rays.

9a. Anal with 28 or 29 rays; pectoral extending to midlength of pelvic.
nattereri (Steindachner) 1879, p. 220.

9b. Anal with fewer than 28 rays; pectoral usually failing to reach base of pelvic.

10a. Gill rakers 28–34 + 36–45; depth about 26–28.5% of SL; pectoral extending slightly beyond base of pelvic, 19–20% of SL.
pallida (Starks) 1913, p. 221.

10b. Gill rakers 18 or fewer on upper limb, 24 or fewer on lower limb; depth 25% of SL or less; pectoral failing to reach base of pelvic, 16.7% of SL.

11a. Maxillary extending beyond orbit a distance about equal to diameter of eye, 15–20% of SL; mandible 15.8–18.8; gill rakers 17 or 18 + 19–24; origin of anal under or slightly behind middle of dorsal base.

12a. Depth of body 17.5–20% of SL; head 25.5–28%; postorbital part of head 12–13.3%; mandible 17.8–18.8%; silvery lateral band poorly defined, narrower than eye. *elongata* (Meek and Hildebrand) 1923, p. 223.

12b. Depth of body 22–25% of SL; head 22.7–23.7%; postorbital 10.7–11%; mandible 15.8–16.3%; silvery lateral band well defined, broader than eye.
lepidentostole (Fowler) 1911, p. 224.

11b. Maxillary extending beyond orbit a distance equal to only half of diameter of eye, 12–15% of SL; mandible 12.3–14.8; gill rakers 10–12 + 15–17; origin of anal well in advance of middle of dorsal base. *blackburni* Hildebrand 1943, p. 226.

1b. Maxillary extending a little less than diameter of pupil beyond orbit.
Subgenus *Amplova*.
jamesi (Jordan and Seale) 1926, p. 227.

Anchoviella eurystole (Swain and Meek) 1884

Silver Anchovy

Figure 44

Study Material. At least 29 specimens, 55–130 mm, from: Woods Hole and Menemsha Bight, Massachusetts; Noank, Connecticut; Long Island, New York; Brigantine Bay, New Jersey; and Beaufort, North Carolina.

Distinctive Characters. A. estauquae is the nearest relative of this species. The relationship is shown in the account of that species (p. 211).

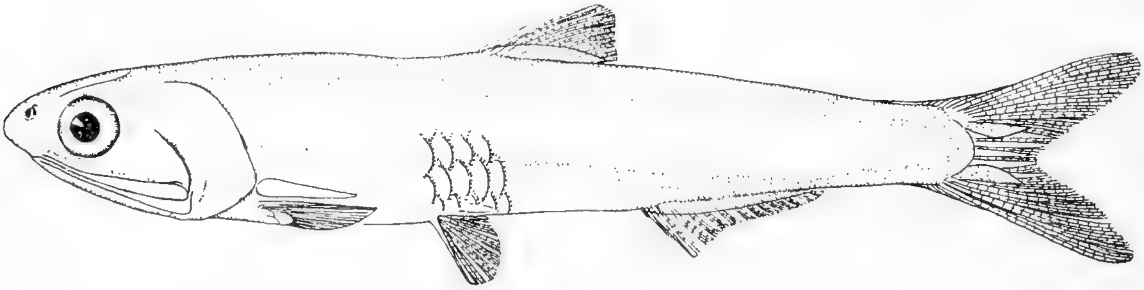

FIGURE 44. *Anchoviella eurystole*, 75 mm TL, from Woods Hole, Massachusetts, USNM 77778. Drawn by Louella E. Cable.

Description. Proportional dimensions in per cent of standard length, and counts, based on *Study Material*, specimens 55–130 mm.

Body: depth 15.4–19.
Head: length 25–28.5.
Snout: length 3.85–5.0.
Eye: diameter 5.7–7.0.
Postorbital: distance 13.8–15.5.
Maxillary: length 15.8–17.8.
Mandible: length 15–18.5.
Anal fin: length of base 12.5–16.
Pectoral fin: length 12.5–13.7.

Scales: *ca.* 40–45.
Gill rakers: 24–28 + 27–33 (most frequently 25 or 26 + 28–30).
Fin rays: dorsal 13–16; anal 15–18 (rarely 19); pectoral 15 or 16.
Vertebrae: 43–45 (3 specimens).

BODY slender, not strongly compressed, its depth 5.25–6.5 in SL. HEAD 3.5–4.0, its depth equal to length of postorbital part of head. SNOUT projecting about half of its length beyond mandible, only a little shorter than eye in large examples, 4.75–6.5 in head. EYE 3.75–4.5 in head, 2.1–2.5 in postorbital length of head. POSTORBITAL part of head 1.6–1.8 in head. MAXILLARY rather narrow, rounded distally, extending beyond orbit by a distance equal to about 1.3 diameter of eye, failing to reach joint of mandible by about half of diameter of pupil, 1.5–1.7 in head. MANDIBLE 1.45–1.75. CHEEK only a little shorter than snout and eye, its posterior angle about 45°. GILL RAKERS about 75% of length of eye, not broad or close-set, with moderate serrations on inner edge.

DORSAL fin low anteriorly, the longest rays failing to reach tip of last ray if deflexed, its origin usually somewhat nearer to tip of snout than to base of caudal. ANAL small, its origin wholly behind dorsal base, most frequently about under tips of longest deflexed rays, its base 6.25–8.0 in SL. PELVIC inserted nearly an eye's diameter in advance of dorsal and usually somewhat nearer to pectoral base than to anal origin, reaching much less than halfway to anal. PECTORAL usually failing to reach pelvic by more than diameter of eye, 1.8–2.2 in head. AXILLARY SCALE of pectoral long and narrow, generally failing to reach tip of fin by about half of diameter of pupil, 2.25–3.0 in head.

Color. In alcohol, some rather pale above, others bluish. Side of head and lower part of side on some silvery. Silvery lateral band about as broad as eye in small specimens, broader and less distinctly outlined ventrally in large ones.

Size. Although a maximum total length of 155 mm (6.2 in.) has been reported, the largest example in the collections examined in this study is only 130 mm TL.

Development. The information on the development of the eggs and larvae that follows is based mostly on the work of Kuntz and Radcliffe (*10*: 116), who took the eggs in tows during August 1915 off Gay Head, Massachusetts.

The egg is buoyant, highly transparent, and ellipsoidal, having a long axis of 1.15–1.25 mm, a short axis of 0.55–0.8 mm. The yolk, as usual among anchovies, has a network of lines on its surface, giving the appearance of large cells. In this anchovy, as in other species studied, the blastodisc forms at one end of the elongated egg. The egg is similar to that of *Anchoa hepsetus* but seems to be slightly shorter though scarcely narrower. The development, so far as known, is identical in the two species.

The newly hatched fish is about 3.0 mm long, being slightly shorter than the newly hatched larva of *A. hepsetus*, in keeping with the rather smaller egg. The body is very slender, and the vent as usual in the larvae of anchovies is situated very far back, in this species about at the beginning of the distal fourth of the body. Black chromatophores occur in a series along the intestine posterior to the yolksac and at the base of the ventral finfold behind the vent. A day or so after hatching, the yolk is virtually all absorbed and the fish has grown to a length of about 4.0 mm. The young fish, when 5.2 mm long, has developed a large oblique, terminal mouth, the fins are becoming differentiated, and the convoluted intestine, incompletely invaginated, is conspicuous. The chromatophores have become less conspicuous than in the earlier stages. The development in older stages apparently remains unknown.

Spawning. Although the duration of spawning has not been determined, it is at its height during July and August (*15*: 44).

Range and Habitat. This anchovy ranges from Woods Hole, Massachusetts, at least as far south as Beaufort, North Carolina. The southern limit of its range remains undetermined, for no specimens of the genus are at hand or seem to be reported for the coast between Beaufort, North Carolina, and Melbourne Beach, Florida; those from the last mentioned locality are *A. perfasciata*. During some summers this anchovy is common at Woods Hole; during other summers it seems to be missing. Off Connecticut, New York, and New Jersey it appears only occasionally. It is not recorded for

Chesapeake Bay; and for North Carolina it is known by only one specimen taken during the summer of 1913 in inside waters at Beaufort, where intensive collecting was carried on during many years. It has been stated often that the home of the Silver Anchovy is in the Gulf Stream. The basis for this statement is unknown and certainly stands in need of verification, especially as it has been rather definitely established that the specimens known from North Carolina northward represent a species distinct from the examples from the West Indies northward to Melbourne Beach, Florida. All records of *argyrophana* based on northern specimens apparently apply to *eurystole* as herein understood.

Synonyms and References:

Stolephorus perfasciatus Swain (not of Poey), Bull. U. S. Fish Comm. (1882), *2*, 1883: 55 (descr. of one from Woods Hole, Massachusetts; indicated as orig. descr. of *S. eurystole* by Swain and Meek); Jordan and Gilbert (not of Poey), Bull. U. S. nat. Mus., 16, 1883: 273 (descr. of one from Woods Hole, Mass., apparently the same one used by Swain; West Indies includ. in the range where *eurystole* does not occur); Bean, T. H. (not of Poey), Bull. N. Y. St. Mus., 60, Zool. 9, 1903: 217 (descr., Noank, Connecticut, and Gravesend Bay, Long Island, New York; in part exam. by me and found to be *A. eurystole*).

Stolephorus eurystole Swain and Meek, Proc. Acad. nat. Sci. Philad., 1885: 35 (descr. by Swain and by Jordan and Gilbert above referred to as orig.; type local. Woods Hole, Mass.; type destroyed by fire. This species was said to differ from *Engraulis perfasciatus* Poey chiefly in the greater number of anal rays, a broader lateral band, and a larger size; this northern species apparently reaches a somewhat larger size, but at most there is only a small average difference in the number of anal rays, and the width of the lateral band varies with age. For diagn. char., see Key); Bean, T. H., Bull. U. S. Fish Comm. (1887), *7*, 1888: 150, pl. 3, fig. 19 (Ocean City and Longport, New Jersey).

Stolephorus argyrophanus Jordan and Evermann (not of Cuvier and Valenciennes), Bull. U. S. nat. Mus., 47 (1), 1896: 444 (descr. apparently based on type of *E. eurystole*; range "Gulf Stream, occasionally northward"); Smith (not of C. and V.), Bull. U. S. Fish Comm. (1897), *17*, 1898: 92 (occur. assoc. with other species round Woods Hole, Massachusetts); Bean, T. H. (not of C. and V.), Bull. N. Y. St. Mus., 60, Zool. 9, 1903: 216 (descr., Ocean City, New Jersey, and Fire Island, New York).

Anchovia eurystole Fowler, Rep. N. J. St. Mus. (1905), 2, 1906; 109 (descr., Ocean City and Longport, New Jersey; ident. of this species and *Engraulis argyrophanus* C. and V. questioned); Fowler, Rep. N. J. St. Mus. (1906), 1907: 267, fig. (name); Fowler, Proc. Acad. nat. Sci. Philad., *63*, 1911: 219 (Corson Inlet, New Jersey); Fowler, Proc. Acad. nat. Sci. Philad., *64*, 1912: 34 (Long Beach, New York).

Anchovia argyrophana Sumner, Osburn, and Cole (not of C. and V.), Bull. U. S. Bur. Fish (1911), *31* (2), 1913: 743 (abund., where and how taken, Woods Hole, Massachusetts; parasites); Kuntz and Radcliffe (not of C. and V.), Bull. U. S. Bur. Fish., *35*, 1917: 116 (embryol., larval develop.); Nichols and Breder (not of C. and V.), Zoologica, N. Y., *9* (1), 1927: 43, fig. (diagn., distr., life hist., size); Hildebrand (not of C. and V.), Copeia, 1941: 224 (Beaufort, North Carolina).

Anchoviella argyrophana Jordan and Seale (not of C. and V.), Bull. Mus. comp. Zool. Harv., *67*, 1926: 402 (descr. of one from Provincetown, Mass.; *argyrophana* and *eurystole* regarded ident. by Jordan from exam. of type of former in Paris, which had 19 anal rays instead of 17, as stated in orig. descr. But number of anal rays does not distinguish this species from *perfasciata*); Breder (not of C. and V.), Field Bk. Mar. Fish. Atl. Cst., 1929: 70, 71 (defined in key; range; "Gulf Stream species"; eggs, size); Jordan (not of C. and V.), Manual Vert. Anim. NE U. S., ed. 13, 1929: 43 (descr., range); Jordan, Evermann, and Clark (not of C. and V.), Rep. U. S. Comm. Fish. (1928), 2, 1930: 48 (range; *eurystole* in synon.).

Anchoviella eurystole Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 112, fig. 47 (descr., cf. *perfasciata*, range).

Doubtful References:

Anchovia perfasciata Nichols and Breder (probably not of Poey), Zoologica, N. Y., *9* (1), 1927: 42, fig. (diagn., N. Y. City area; distingu. char. of this species and one rec. as *argyrophana* not stated correctly; fig.

looks like *perfasciata*; as it is the same one used by Nichols [1929: 204], it may have been based on a West Indian specimen).

Anchoviella perfasciata Greeley, 28th Rep. N. Y. Conserv. Dept., Suppl., 15 (2), 1939: 83 (rare at Long Island; prabably *A. eurystole*).

Anchoviella estauquae Hildebrand 1943

Figure 45

Study Material. Holotype and 3 paratypes, about 77–92 mm TL (caudal fins damaged), 65–77 mm SL, collected on a sandy beach in Estauques Bay, Gulf of Venezuela, by the U. S. S. Niagara, on February 20, 1925.

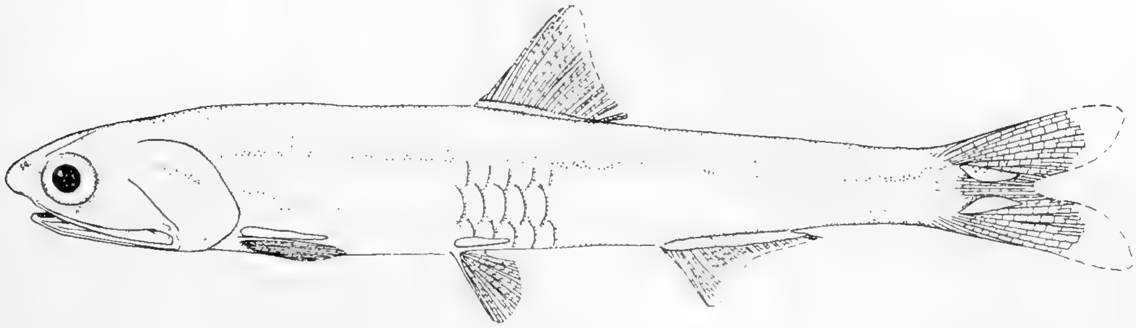

Figure 45. *Anchoviella estauque,* type specimen, 82 mm TL, 72 mm SL, from Gulf of Venezuela, USNM 119795. Drawn by Louella E. Cable.

Distinctive Characters. This species is very close to *A. eurystole*, from which it is difficult to separate it with the meager material at hand. The number of gill rakers is within the range of *eurystole*, but the rakers seem to be a little longer, certainly broader, apparently closer together, and the serrations on their inner edges are slightly smaller. The eye appears to be a little smaller and the postorbital part of the head is slightly longer. The dorsal fin is higher anteriorly and somewhat different in shape; the anal fin is placed farther back.

Description. Proportional dimensions in per cent of standard length, and counts, based on type material, 65–76 mm SL.

Body: depth 15.3–19.2.
Head: length 26–27.7.
Snout: length 5.0–5.55.
Eye: diameter 5.7–6.16.
Postorbital: distance 15.5–15.8.
Maxillary: length 17.5–18.7.
Mandible: length 17.3–18.5.

Anal fin: length of base 13.3–15.3.
Pectoral fin: length 12.8–14.3.

Scales: *ca.* 44–46.
Gill rakers: 26–28 + 30–32.
Fin rays: dorsal 13–15; anal 15–17; pectoral 15 or 16.
Vertebrae: 45 (1 specimen).

Body not strongly compressed, its depth 5.2–6.5 in SL. Head 3.6–3.7, its depth scarcely equal to its postorbital length. Snout projecting rather more than half of its length beyond mandible, only a little shorter than eye, 5.0–5.3 in head. Eye 4.4–4.8 in head, 2.5–2.75 in postorbital length of head. Postorbital part of head long, 1.73–1.77 in head. Maxillary rather narrow, rounded distally, extending beyond orbit a distance equal to about 1.3 diameter of eye, not quite to joint of mandible, 1.5–1.6 in head. Mandible 1.48–1.53. Cheek nearly as long as snout and eye, its posterior angle about 40°. Gill rakers scarcely as long as eye, broad and close-set, with minute serrations on inner edge.

Dorsal fin with longest rays reaching beyond tip of last ray if deflexed, its origin about equidistant between tip of snout and base of caudal. Anal with origin well behind tips of longest deflexed rays of dorsal, its base 6.5–7.5 in SL. Pelvic inserted about half of diameter of eye in advance of dorsal and nearly equidistant between base of pectoral and anal origin, reaching rather less than halfway to anal. Pectoral usually failing to reach pelvic by rather more than diameter of eye, 1.9–2.5 in head. Axillary scale of pectoral long, narrow, failing to reach tip of fin by a distance equal to or less than diameter of pupil, 2.3–2.7 in head.

Color. In alcohol, pale (originally in formalin). Sides of head bright silvery. Lateral band bright silvery, fully as broad as eye.

Range. This species is known only from the Gulf of Venezuela.

References:

Anchoviella estauquae Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 115, fig. 48 (orig. descr.; type local. Estauques Bay, Gulf of Venezuela; type USNM 119795; cf. *A. eurystole* and *A. perfasciata*); Schultz, Proc. U. S. nat. Mus., *99*, 1949: 47 (ref., type and paratypes listed).

Anchoviella cayennensis (Puyo) 1945

Jamais-gouté

Study Material. None.

Distinctive Characters. The short maxillary, extending about a pupil's diameter posterior to a vertical at end of eye, the elongate body, with the depth more than 7 times in SL, and the very short anal, with 9–11 rays and with its origin below that of the last dorsal ray, show that this species is a very distinctive one, if Puyo's descriptions are reliable.

Description. Based on published accounts and figures by Puyo (see References below). Body very elongate, lightly compressed anteriorly and progressively more rounded posteriorly (in transverse section); depth a little more than 7 times in total body length (SL). Head a little more than 5 times in same; a sort of transverse keel present on superior surface of head. Snout somewhat rounded. Eye equal to snout (pupil shown as abnormally large in most of Puyo's drawings, probably in error). Maxillary rounded at the end, extending about a normal pupil's diameter posterior to vertical at posterior border of eye (in Puyo's published figure). LOWER JAW slightly shorter than the upper.

DORSAL fin origin midway between tip of snout and caudal base. ANAL fin origin under base of last dorsal ray. FIN RAYS: dorsal 12, anal 9–11. PECTORAL fin slightly less than twice the length of ventral, extending somewhat more than half of the distance from its origin to that of the pelvic.

Color (from Puyo). On the whole, body clear blackish (apparently in formalin); opercular bones iridescent. A black longitudinal band on each side; band towards posterior part of body giving off irregular transverse projections from its lower border; lateral band merging gradually into an irregular streak on middle caudal rays; dark band on body bordered below by a silvery band wider than eye diameter. Dorsal and anal pale. Pectoral and pelvic hyaline. Caudal lighter than the body, its border lightly tinted with brown.

Size. Puyo's two type specimens, the only examples so far recorded, were 130 and 135 mm SL.

Habits. Said to be confined to estuaries and river mouths.

Range. Known only from the coast of French Guiana. The types were taken in the Cayenne River, as far up as Macouria,[9] but fishermen told Puyo they found this species also in the Mahury River and at the mouth of the Kourou.

References:

Stolephorus cayennensis Puyo, Bull. Soc. Hist. nat. Toulouse, *80*, 1945: 101, fig. 1 (descr., Cayenne R., French Guiana); Puyo, Faune Emp. Franç., 12, Poiss. Guyane Franç., 1949: 157, fig. 80 (descr.).

Anchoviella perfasciata (Poey) 1860

Flat Anchovy, Manjúa (Cuba)

Figure 46

Study Material. At least 41 specimens, 60–105 mm TL, from Puerto Rico, Jamaica, Cuba, and St. Lucia; also some poorly preserved specimens from off Melbourne Beach, Key West, Tortugas, and Pensacola, Florida, and from Mississippi Sound, probably belonging to this species.

Distinctive Characters. This species differs from *A. eurystole* principally in having a larger eye, a higher dorsal fin, a more anteriorly placed anal fin, a longer pectoral fin, and fewer gill rakers.

Description. Proportional dimensions in per cent of standard length, and counts, based on at least 41 specimens, 60–105 mm TL.

Body: depth 15.4–18.2.
Head: length 23.3–25.6.
Snout: length 4.0–5.25.
Eye: diameter 6.6–7.7.

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[9] Stieler's *Atlas* shows Macouria to be on the coast, as is Kourou.—Y. H. O.

Postorbital: distance 11.7–13.3.
Maxillary: length 15.2–17.3.
Mandible: length 15–17.2.
Anal fin: length of base 13.7–15.3.
Pectoral fin: length 12.2–14.2.
Scales: *ca.* 40–44.
Gill rakers: 19–23+24–28 (most frequently 19–21+26 or 27).
Fin rays: dorsal 12–15; anal 15–18; pectoral 14–16.
Vertebrae: 42–44 (7 specimens).

Body not strongly compressed, its depth 5.5–6.5 in SL. Head 3.9–4.3 in SL, its depth slightly exceeding its postorbital length. Snout much shorter than eye, extending about half of its length beyond mandible, 4.2–5.75 in head. Eye 3.25–4.0 in head, 1.6–2.0 in postorbital length of head. Postorbital 1.9–2.1 in head. Maxillary slightly expanded and rounded distally, generally extending about an eye's diameter beyond rim of orbit, failing to reach joint of mandible by nearly diameter of pupil, 1.4–1.55 in head. Mandible 1.4–1.66. Cheek slightly longer than eye, its posterior angle about 60°. Gill rakers shorter than eye, broad, not close-set, with short coarse serrations on inner edge.

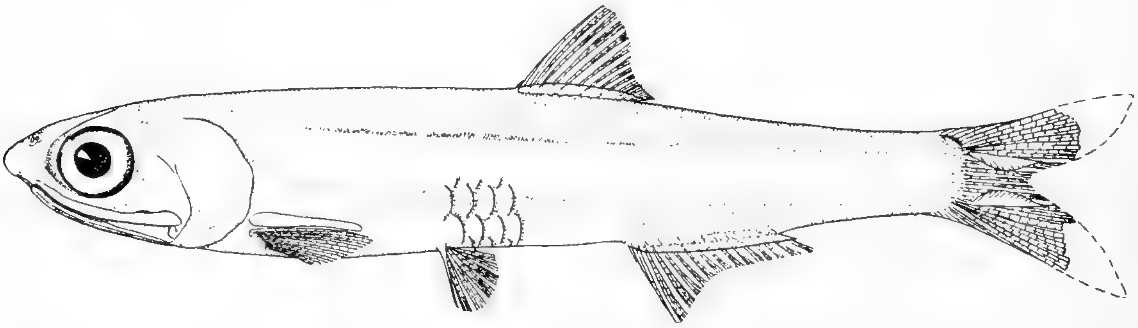

Figure 46. *Anchoviella perfasciata,* 100 mm TL, 83 mm SL, from Cuba, USNM 37472. Drawn by Louella E. Cable.

Dorsal fin with longest rays reaching to, or more usually beyond, tip of last ray if deflexed, its origin variable, most frequently equidistant between caudal base and tip of snout. Anal originating under or slightly behind base of last dorsal ray, its base 6.5–7.25 in SL. Pelvic inserted nearly an eye's diameter in advance of dorsal and about equidistant between base of pectoral and anal origin, reaching much less than halfway to anal. Pectoral failing to reach pelvic base by about an eye's diameter, 1.7–2.0 in head. Axillary scale of pectoral narrow, failing to reach tip of fin by less than diameter of pupil, 1.9–2.3 in head.

Color. In alcohol, pale. Sides of head silvery. Silvery lateral band distinct, generally nearly as broad as eye; some specimens with dusky punctulations on back extending onto caudal fin.

Size. A total length of about 105 mm (4.2 in.) is attained.

Variation. Certain poorly preserved specimens from Melbourne Beach, Key West, Tortugas, and Pensacola, Florida, in the *Study Material* above, appear to be more or less intermediate between this species and *eurystole.* The gill rakers, which are difficult to count because of the rather small size and poor condition of the specimens, seem to be rather more numerous than in West Indian specimens. The shape of the dorsal, the length of the pectoral, and the size of the eye all agree with specimens from the West Indies, but the position of the anal is rather intermediate.

Range and Habitat. This Anchovy apparently ranges from the West Indies to Florida and the Gulf Coast, and probably to North Carolina. It has been reported for New York (*15*: 42), but none from New York and neighboring states has been available for study. This fish seems to be common, though probably not numerous, in the West Indies. Northward it is apparently only a stray. Most of the specimens studied were taken in shallow water. A few, one from off Melbourne Beach, Florida, and two from Mississippi Sound, Miss., were taken in somewhat deeper water with trawls. It is not known to enter brackish water.

Synonyms and References:

Engraulis perfasciatus Poey, Memorias, *2*, 1860: 312 (orig. descr.; type local. Cuba; type MCZ 17955; cf. several species); Günther, Cat. Fish. Brit. Mus., *7*, 1868: 391 (descr., San Domingo, Cuba; doubtfully distinct from *E. argyrophanus* Cuvier and Valenciennes).

Stolephorus perfasciatus Swain and Meek, Proc. Acad. nat. Sci. Philad. (1884), 1885: 34 (descr., Key West, Florida, and Havana, Cuba); Henshall, Bull. U. S. Fish Comm. (1889), *9*, 1891: 373 (more abund. at Marco than elsewhere in w. Florida); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 441 (descr., range); Evermann and Marsh, Bull. U. S. Fish Comm. (1900), *20*, 1902: 88 (descr., range, Aguadilla, Puerto Rico); Metzlaar, Bijdr. Dierk. Amst., 1922: 136 (Curaçao, taken with *S. brownii* and *Jenkinsia lamprotaenia*).

Anchovia perfasciata Jordan and Thompson, Bull. U. S. Bur. Fish. (1904), *24*, 1905: 233 (Tortugas, Florida); Fowler, Proc. Acad. nat. Sci. Philad., *63*, 1911: 211 (Aguadilla, Puerto Rico); Nichols, New York Acad. Sci., *10* (2), 1929: 204, fig. 34 (diagn., distr., Puerto Rico); Hildebrand, Copeia, 1941: 224 (Beaufort, North Carolina).

Anchoviella perfasciata Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67*, 1926: 394 (descr. of "type" from Cuba; range, Florida Keys to Cuba); Jordan, Manual Vert. Anim. NE U. S., ed. 13, 1929: 44 (descr., range, New York to Cuba); Breder, Field Bk. Mar. Fish. Atl. Cst., 1929: 70, fig. (range; strays northward to N. Y.); Fowler, Proc. Acad. nat. Sci. Philad., *82*, 1930: 269 (Grenada, B. W. I.); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 47 (range, Florida Keys to Jamaica); Howell-Rivero, Bull. Mus. comp. Zool. Harv., *82*, 1938: 172 (types MCZ 17955; 9 specimens, 82–103 mm, includ. 100-mm specimen as holotype, Poey's No. 422); Longley and Hildebrand, Publ. Carneg. Instn. Wash., 535, 1941: 13 (Tortugas, Florida; taxon. notes); Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 116, fig. 49 (descr., cf. *A. eurystole*, range).

Doubtful References:

Engraulis argyrophanus Cuvier and Valenciennes, Hist. Nat. Poiss., 1848, *21*: 49 (orig. descr.; type local. "equitorial Atlantic"; cf. *A. hepsetus*; specimen said to have been taken in equatorial Atlantic on a voyage from Europe to Batavia. The specimen, therefore, may not have been taken near America, and the description is too inadequate for positive identification with any American species. Thus it seems inadvisable to use this name. Recent writers generally have referred specimens possessing a short maxillary, taken between New Jersey and Cape Cod, to *argyrophanus*, a procedure that in the light of present knowledge seems to be incorrect).

Stolephorus miarchus Jordan, Proc. U. S. nat. Mus. (1884), 7, 1885: 106 (Key West, Florida; indistingu. from types of this species; probably young *A. perfasciata*).

Anchovia perfasciata Nichols and Breder, Zoologica, N. Y., *9* (1), 1927: 42, fig. (diagn., vic. of New York City, range; distingu. characters of this species and of *eurystole* [*argyrophanus*] are not stated correctly;

the figure looks somewhat like *perfasciata*; it is the same one used by Nichols [1929: 204] and may have been based on a West Indian specimen).

Negative References:

Stolephorus perfasciatus Swain, Bull. U. S. Fish Comm. (1882), *2*, 1883: 55 (descr. of specimen from Woods Hole, Massachusetts, which was *A. eurystole*); Jordan and Gilbert, Bull. U. S. nat. Mus., *16*, 1883: 272 (descr. of specimen from Woods Hole, Mass., which was *A. eurystole*; West Indies includ. in range, where *eurystole* does not occur); Bean, T. H., Bull. N. Y. St. Mus., 60, Zool. 9, 1903: 217 (descr. of specimens from Noank, Connecticut, and Gravesend Bay, Long Island, N. Y.; specimens, in part at least, exam. by me and found to be *A. eurystole*).

Anchoviella brevirostris (Günther) 1868

Study Material. Two small soft specimens, 26 and 24 mm SL, from Lago Maximus, far up the Amazon Basin, Brazil, and six specimens that have been more or less dry, 17–22 mm SL, from Teffé, also far up the Amazon Basin, which may be of this species, all in MCZ. Another, 40 mm TL, from Lake Rogagua, Bolivia, also may be of this species (part of CAS 9398). Because of the poor condition and small size of the specimens and the inadequacy of the original description, identification is uncertain.

Description. Proportional dimensions in per cent of standard length, based on two of the larger and better specimens, 26 and 24 mm SL, respectively.

Body: depth 15.3, 16.1.
Head: length 20.4, 24.4.
Snout: length 3.8, 4.15.
Eye: diameter 7.7, 7.3.
Postorbital: distance 12.7, 12.5.
Maxillary: length 15.4, 12.5.
Mandible: length 15.4, 13.7.

Anal fin: length of base 19.2, 17.5.
Pectoral fin: length ?, 11.2.

Gill rakers: 13 or 14+19 (4 specimens).
Fin rays: dorsal 12 or 13; anal 16–19; pectoral 11 or 12 (4 specimens).

Body slender, its depth 6.2, 6.5 in SL. Head 4.1, 4.9. Snout projecting about half of its length beyond mandible, 5.5, 6.3 in head. Eye 3.0, 3.2. Postorbital part of head 1.75, 1.9 in head. Maxillary nearly straight, rounded distally, extending about an eye's diameter beyond posterior rim of orbit but not quite to joint of mandible, 1.5, 1.75 in head. Mandible 1.57, 1.6.

Dorsal origin about equidistant between base of caudal and tip of snout. Anal origin under base of last 2 or 3 rays of dorsal; anal base 5.2, 5.7 in SL. Pectoral failing to reach pelvic by an eye's diameter, 2.0 in head.

Color. Very old specimens, in alcohol, faded, except for the silvery lateral band, which is somewhat narrower than the eye.

Digest of Günther's Description, type 87 mm TL. Head 4.5, its depth 5.33. Snout much shorter than eye, projecting only slightly beyond mandible. Eye 3.5 in head.

MAXILLARY dilated and rounded distally, not extending to joint of mandible. DORSAL origin equidistant between base of caudal and tip of snout. ANAL origin below last rays of dorsal. PECTORAL ending "a great distance" from the pelvic. FIN RAYS: dorsal 15, anal 18. SCALES 41. Sides with a well-defined silvery band, this band nowhere wider than eye.

It is most unfortunate that the number of gill rakers was not stated.

Range and Habitat. If the specimens examined have been correctly identified and are the same species, the range extends from "Caxoeira,[10] Province of Bahia," Brazil, type locality, to Lago Maximus and Teffé, both far up the Amazon; and probably to Rio Chapare and Lake Rogagua, Bolivia. This species, then, seems to live in fresh water. That its distribution is as wide as indicated remains to be confirmed from the study of more and better specimens.

Synonyms and References:

Engraulis brevirostris Günther, Cat. Fish. Brit. Mus., *7*, 1868: 392 (orig. descr.; type local. "Caxoeira, Province of Bahia," Brazil); Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67*, 1926: 411 (refer it to *Amplova*, herein regarded incorrect).

Amplova brevirostris Myers, Proc. Calif. Acad. Sci., *23*, 1940: 440 (notes).

Anchoviella brevirostris Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 119 (descr., range).

Doubtful Reference:

Anchoviella carrikeri Fowler, Proc. Acad. nat. nat. Sci. Philad., *92*, 1940: 73, fig. 28 (orig. descr.; type local. mouth of Rio Chaparé, Cochabamba, Bolivia; type ANSP 68980; placed here with considerable doubt because scales [31–33] and gill rakers on the lower limb [14 or 15] seem to be too few, and the pectoral fin as shown in figure may be too long).

Negative References:

Anchoviella brevirostris Pearson, Indiana Univ. Stud., 64, 1925: 50 (Lake Rogagua, Bolivia; cf. paratype of *Stolephorus guianensis* Eigenmann by Myers and found to be that species; see ref. under *A. guianensis*); Fowler, Proc. Acad. nat. Sci. Philad., *92*, 1940: 94 (listed, after Pearson).

Anchoviella guianensis (Eigenmann) 1912

Figure 47

Study Material. A paratype, 50 mm TL, from the Demerara River, British Guiana, CM 2449; and a rather poorly preserved specimen, 62 mm, from Itacoatiara, Amazonas, Brazil, CNHM 15480.

Distinctive Characters. This species differs from the specimens herein assigned to *A. brevirostris* chiefly in the greater number of gill rakers.

Description. Proportional dimensions in per cent of standard length, and counts, based on *Study Material*, 50 and 62 mm, respectively.

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10. Dr. G. S. Myers has advised that "Caxoeira" and "Cachoeira" are alternative spellings in Brazilian Portuguese for "rapids," and that both are pronounced alike. Cachoeira is the generally accepted spelling today. —Y. H. O.

Body: depth 20, 17.4.
Head: length 23.7, 24.2.
Snout: length 4.5, 5.0.
Eye: diameter 7.5, 7.0.
Postorbital: distance 10.7, 14.2.
Maxillary: length 12.5, 13.3.
Mandible: length 14, 13.8.
Anal fin: length of base 16.8, 15.5.
Pectoral fin: length 15.2, 16.8.

Scales: *ca.* 41, 38.
Gill rakers: 16+22, 17+24.
Fin rays: dorsal 13, 14; anal 18, 19; pectoral 12, 13.

BODY compressed, its depth 5.0, 5.7 in SL. HEAD 4.2, 4.1 in SL, its depth about equal to its postorbital part and half of eye. SNOUT projecting nearly half of its length beyond mandible, 5.3, 4.9 in head. EYE 3.2, 3.5. POSTORBITAL rather short, 2.2, 1.8 in head. MAXILLARY extending about 75% of diameter of eye beyond orbit, but not to joint of mandible, 1.9, 1.8 in head. MANDIBLE 1.7, 1.75. CHEEK broad, very slightly longer than eye, its posterior angle about 60°.

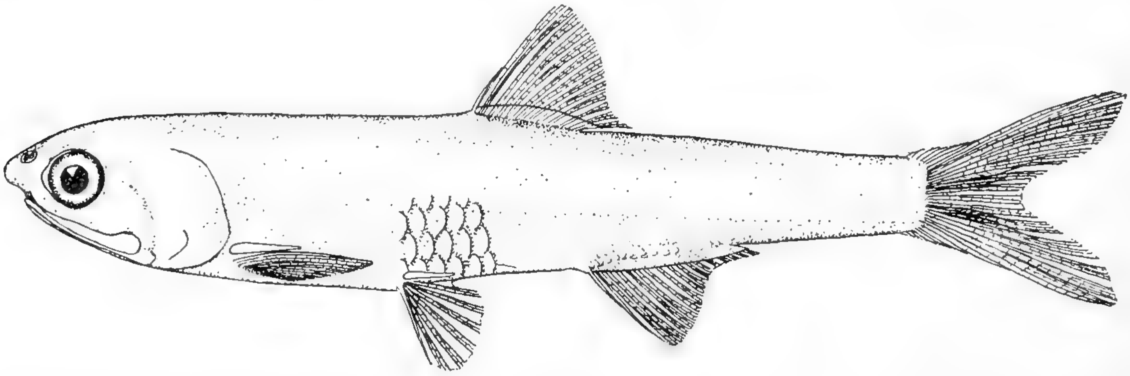

FIGURE 47. *Anchoviella guianensis*, 62 mm TL, from Amazonas, Brazil, CNHM 15480. Drawn by Louella E. Cable.

DORSAL fin with longest rays reaching somewhat beyond tip of last ray if deflexed, its origin equidistant between tip of snout and caudal base. ANAL originating under, or a little in advance of, base of last dorsal ray, its base 5.95, 6.5 in SL. PELVIC inserted equidistant between pectoral base and anal origin. PECTORAL failing to reach pelvic by diameter of pupil, 1.55, 1.45 in head. AXILLARY SCALE of pectoral narrow, reaching well beyond midlength of pectoral, 2.4, 2.45 in head.

Color. In alcohol, pale (probably preserved originally in formalin). Side of head silvery. Pale streak, probably silvery in life, on side. Back with dark punctulations arranged in two more or less definite rows behind dorsal fin; dusky punctulations along base of anal, and a median dark stripe behind anal; paratype with dusky punctulations present also on dorsal, caudal, anal, and upper rays of pectoral.

Range and Habitat. Its range extends from Trinidad, B.W.I., and Venezuela to northern Brazil and the upper Amazon Basin in Bolivia. In addition to the holotype from Bartica Rocks, British Guiana, Eigenmann had paratypes from the Morawhanna and Demerara rivers, British Guiana. It is recorded for La Brea Beach, Trinidad, and for Caño de Guanoco, Venezuela, without comment by Fowler (see reference below). Fresh water seems to be its chief habitat.

Synonyms and References:

Stolephorus guianensis Eigenmann, Mem. Carneg. Mus., 5, 1912: 447, pl. 62, fig. 5 (orig. descr.; type local. Bartica Rocks, British Guiana; type in CM; paratypes from Morawhanna and Demerara rivers, Brit. Guiana).

Anchoviella guianensis Fowler, Proc. Acad. nat. Sci. Philad., *83*, 1931: 392, 406 (La Brea Beach, Trinidad, and Caño de Guanoco, Venezuela); Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 122, fig. 52 (synon., descr., relation.); Schultz, Proc. U. S. nat. Mus., *99*, 1949: 48 (refs.).

Anchovia brevirostris Pearson (not of Günther), Indiana Univ. Stud., 11 (64), 1924: 50 (two immatures, 30 and 37 mm, IU 17354, now in CAS, rec. from Lake Rogagua, Bolivia; cf. paratype of *Stolephorus guianensis* Eigenmann by Myers and found to be that species).

Amplova guianensis Myers, Proc. Calif. Acad. Sci., (4) *23*, 1940: 440 (descr., exam. specimens from Morawhanna [paratype]; Lagoa Grande, lower Amazon, near Obidas, Brazil; and Lake "Rogoagua," Bolivia; those from last mentioned place are the ones ident. as *A. brevirostris* by Pearson; see above).

Anchoviella alleni (Myers) 1940

Study Material. The holotype and 6 paratypes, 80–84 mm TL, from Peruvian Amazon drainage system; the holotype and 4 paratypes in CAS, 2 paratypes in USNM.

Distinctive Characters. This species is close to *A. guianensis*, from which it differs in having a somewhat smaller eye, a shorter anal base, a shorter and broader cheek, a longer axillary scale on the pectoral, and in color.

Description. Proportional dimensions in per cent of standard length, and counts, based on the type material noted above, 80–84 mm TL.

Body: depth 18.8–20.
Head: length 22.7–25.
Snout: length 3.4–4.2.
Eye: diameter 5.5–6.25.
Postorbital: distance 11.3–12.
Maxillary: length 11.8–13.
Mandible: length 12.7–13.2.

Anal fin: length of base 13.3–15.
Pectoral fin: length 14.7–16.5.

Scales: *ca.* 44–46.
Gill rakers: 16–18 + 23–26.
Fin rays: dorsal 14 or 15; anal 18 or 19; pectoral 12 or 13.
Vertebrae: 42 (1 specimen).

BODY slender, moderately robust, its depth 5.0–5.3 in SL. HEAD 4.0–4.4 in SL, its depth only slightly less than its postorbital length and eye. SNOUT projecting about half of its length beyond mandible, 5.5–6.0 in head. EYE 3.7–4.1 in head, 1.9–2.1 in postorbital part of head. POSTORBITAL 1.9–2.0 in head. MAXILLARY slightly expanded and rounded distally, extending as much as diameter of pupil beyond posterior rim of orbit, failing to reach joint of mandible by about half of diameter of pupil, 1.7–2.0 in head. MANDIBLE 1.63–1.77. CHEEK very short and broad, slightly rounded posteriorly, scarcely as long as eye, and scarcely forming an angle.

DORSAL fin with longest rays reaching to or beyond tip of last ray if deflexed, its origin generally a little nearer to caudal base than to tip of snout. ANAL originating immediately behind vertical from base of last ray of dorsal, its base 6.7–7.4 in SL. PELVIC reaching a little more than halfway to anal, inserted nearer to base of pectoral than to origin of anal by diameter of pupil. PECTORAL moderately falcate, failing to reach pelvic by diameter of pupil, 1.4–1.6 in head. AXILLARY SCALE of pectoral reaching opposite distal third of fin, 2.0–2.2 in head.

Color. In alcohol, pale, probably preserved originally in formalin. Lateral band bright silvery, nearly as broad as eye, bounded above by a dark line. Tip of snout and back with dusky punctulations, these sometimes arranged in two more or less definite rows posterior to dorsal fin. Caudal with dusky markings and sometimes with a broad dusky margin.

Range. Known only from the Peruvian Amazon country, from Lake Cashiboya, and Gosulima Cocha, Upper Rio Morona, Peru, 2,000 miles from the sea.

Synonyms and References:

Amplova alleni Myers, Proc. Calif. Acad. Sci., (4) *23*, 1940: 441 (orig. descr.; type local. Lake Cashiboya, Peru; type CAS 6421; cf. *Stolephorus guianensis* Eigenmann and *Engraulis brevirostris* Günther; paratypes from Lake Cashiboya, Rio Ucayale; Gosulima Cocha, Upper Rio Morona; and Rio Morona, all in Peru); Eigenmann and Allen, Fishes West. S. Amer., Univ. Ky., 1942: 333 (add. specimens from upper Amazon basin).

Anchoviella alleni Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 124, fig. 53 (descr. of type material; cf. *Stolephorus guianensis* Eigenmann).

Anchoviella nattereri (Steindachner) 1879

Study Material. None.

Distinctive Characters. In general, *A. nattereri* seems to be related to *A. blackburni* and *A. lepidentostole*, but it differs from each of them in the rather more numerous anal rays, the more posterior origin of the anal in relation to the dorsal, and the much longer pectoral fin, which overlaps the pelvic.

Description. Based on original account, translated and condensed from Steindachner, of a specimen 50 mm long.[11]

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[11] A description with figure of an anchovy from Iquitos, Peru (upper Amazon Basin), designated *Engraulis iquitensis* by Shoji Nakashima (*14*: 6), shows some of the characters of *A. nattereri*. At least the general shape of the body, the number of anal rays, and the long pectoral overlapping the base of the pelvic seem to agree. However, Nakashima did not describe the maxillary, and its outline is not clearly shown in the figure; the number of gill rakers is not stated; and the description and figure do not agree in several respects. Therefore, it is impossible to place the fish in any genus with a degree of certainty, or to determine the validity of the species. As the author designated no type and failed to compare his fish with any known species, the name probably is without standing and no further reference will be made to it.

Body: depth 4.0.
Head: length 3.33.
Scales: *ca.* 40.
Fin rays: dorsal 12; anal 28 or 29.

BODY with dorsal profile anterior to dorsal fin less convex than ventral profile. SNOUT reaching well beyond mandible, 4.0 in head. EYE 3.6. MAXILLARY nearly square distally, not quite reaching to joint of mandible. Longest GILL RAKERS about as long as eye.

DORSAL origin slightly nearer to base of caudal than to tip of snout. ANAL origin about under middle of dorsal base. PECTORAL slightly longer than postorbital part of head, reaching middle of pelvic. The silvery lateral band is definitely marked.

Range. Known only from the type from Belém (Pará), Brazil.

Synonyms and References:

Engraulis nattereri Steindachner, Ichthyol. Beitr., 8, 1879: 56 (orig. descr.; type local. Pará, Brazil; cf. *Engraulis surinamensis* Bleeker = *E. edentulus* Cuvier).

Anchoviella nattereri Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 133 (descr. after Steindachner; relation.).

Negative Reference:

Anchovia nattereri Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67*, 1926: 413 (descr. based on specimens from Pará, Brazil, MCZ 18044; exam. by me and found to be *Anchovia clupeoides*, differing from Steindachner's descr. of *A. nattereri* in the longer pointed maxillary, in the apparently shorter anal fin and its more posterior origin with respect to dorsal, and in the much shorter pectoral fin, not extending beyond base of pelvic).

Anchoviella pallida (Starks) 1913

Figure 48

Study Material. Three specimens, 72, 80, and 102 mm TL, the first two being the holotype and paratype of *Anchoviella venezuelae* Fowler, the third one, the holotype of *Anchovia pallida* Starks, from Caño de Guanoco, Venezuela, and Pará, Brazil, respectively. The specimens agree so well that they almost certainly are one species.

Distinctive Characters. In general shape this species resembles *Cetengraulis edentulus*; however, it differs from it in lacking a membrane connecting the gill covers across the isthmus, and in having a longer and narrower cheek, a higher dorsal, and a longer pectoral. From the other members of its genus it is well differentiated by the deep body, long head, long pectoral, and numerous gill rakers.

Description. Proportional dimensions in per cent of standard length, and counts, based on the study specimens, 72–102 mm TL.

Body: depth 25.6–28.5.
Head: length 28.5–29.4.
Snout: length 4.5–4.8.
Eye: diameter 6.36–6.9.
Postorbital: distance 15.8–17.
Maxillary: length 19–20.
Mandible: length 18.8–20.
Anal fin: length of base 27.7–28.5.
Pectoral fin: length 18.8–20.

Scales: *ca.* 36–38.

Gill rakers: 28–34+36–45.

Fin rays: dorsal 12–14; anal 24–26; pectoral 12 or 13.

BODY strongly compressed, its depth 3.5–3.9 in SL. HEAD 3.4–3.5, its depth equal to its postorbital length and about half of eye. SNOUT projecting about 0.66 of its length beyond mandible, 6.0–6.4 in head. EYE 4.2–4.9. POSTORBITAL part of head 1.7–1.85 in head. MAXILLARY somewhat expanded, rounded distally, extending about 1.5 times diameter of eye beyond posterior rim of orbit, not quite reaching joint of mandible, 1.4–1.55 in head. MANDIBLE 1.43–1.55. CHEEK narrow, equal to length of snout and eye in large examples, somewhat shorter in smaller ones, its posterior angle about 35°. GILL RAKERS close-set, numerous, about as long as eye (possibly increasing in number with age).

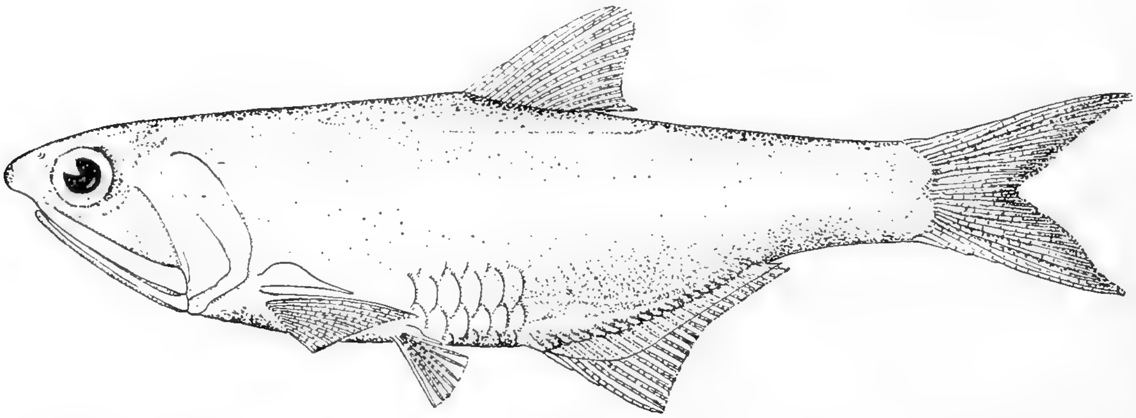

FIGURE 48. *Anchoviella pallida,* type specimen, 102 mm TL, from Pará, Brazil, SU 22216. Drawn by Alice C. Mullen.

DORSAL fin with longest rays reaching beyond tip of last ray if deflexed, its origin about equidistant between caudal base and tip of snout. ANAL originating about under middle of dorsal base, 3.5–3.6 in SL. PELVIC reaching about 0.66 of distance to anal, inserted a little nearer to origin of anal than to base of pectoral. PECTORAL reaching beyond base of pelvic by as much as diameter of pupil in largest specimen examined, somewhat shorter in smaller examples, 1.4–1.85 in head. AXILLARY SCALE of pectoral broad at base, tapering abruptly, about a third to half as long as the fin, 3.3–3.6 in head.

Color. In alcohol, plain. No silvery lateral band evident. Side of head silvery. Back with dusky punctulations. Caudal fin with a dusky margin in the largest specimen examined (holotype), but not evident in the others.

Variation. The number of gill rakers in the three specimens examined shows a rather wide variation, not attributable to age and size; the smallest specimen, according to my counts, has 34+42 rakers (34+36 according to Fowler's original description of *A. venezuelae*), the largest 34 + 45, and the intermediate one 33 + 40 on one side and 28 + 36 on the other.

Range. Known from only three specimens, two from Caño de Guanoco, Venezuela, and the type from Pará, Brazil.

Synonyms and References:

Anchovia pallida Starks, Stanf. Univ. Publ., Univ. Ser., 1913: 9, pl 1 (orig. descr.; type local. Pará, Brazil; type SU 22216; cf. *Engraulis endentulus* Cuvier, *E. vaillanti* Steindachner and *Cetengraulis juruensis* Boulenger).

Anchoviella venezuelae Fowler, Proc. Acad. nat. Sci. Philad., *83*, 1931: 406, fig. 6 (orig. descr.; type local. Caño de Guanoco, mouth of Rio San Juan, Venezuela; type ANSP 53322; cf. *Anchovia parva* Meek and Hildebrand).

Anchoviella pallida Fowler, Proc. Acad. nat. Sci. Philad., *93*, 1941: 126 (synon., descr., Ceará, Brazil); Fowler, Arqu. Zool. estad. São Paulo, *3* (6), 1941: 134 (ref. Brazilian rec.); Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 134, fig. 59 (descr., *A. venezuelae* in synon.); Schultz, Proc. U. S. nat. Mus., *99*, 1949: 48 (synon., refs.).

Anchoviella elongata (Meek and Hildebrand) 1923

Figure 49

Study Material. Specimens 65–100 mm: the type material from Mindi, Canal Zone, one specimen from Porto Bello, Panama, and 22 from Puerto Pilon, Panama.

Distinctive Characters. This species is readily recognized by the slender body, the very large eye, and the moderately few anal rays and gill rakers. In the length and shape of the maxillary it approaches the genus *Anchoa* rather closely.

Description. Proportional dimensions in per cent of standard length, and counts, based on at least 14 specimens in *Study Material.*

Body: depth 17.5–20.
Head: length 25.5–27.
Snout: length 4.5–5.1.
Eye: diameter 8.2–9.0.
Postorbital: distance 12.1–13.3.
Maxillary: length 19–20.
Mandible: length 17.8–18.8.
Anal fin: length of base 22–23.7.
Pectoral fin: length 15.3–16.3.

Scales: *ca.* 36–40.
Gill rakers: 17 or 18 + 22–24.
Fin rays: dorsal 13 or 14; anal 22–24; pectoral 12 or 13.
Vertebrae: 39 (2 specimens).

Body slender, moderately compressed, its depth 5.0–5.7 in SL. Head 3.6–3.9 in SL, its depth equal to postorbital part of head and half of eye. Snout projecting about half of its length beyond mandible, 5.3–5.8 in head. Eye large, 3.0–3.3 in head. Postorbital part of head 2.0–2.25 in head. Maxillary moderately blunt distally, reaching nearly or quite to joint of mandible (approaching the genus *Anchoa* in these respects), extending nearly an eye's diameter beyond posterior rim of orbit, 1.3–1.45 in head. Mandible 1.45–1.5. Cheek about equal to length of eye, its posterior angle approximately 60°.

Dorsal fin moderately high anteriorly, its longest rays reaching beyond tip of last ray if deflected, its origin about equidistant between caudal base and anterior margin of eye. Anal originating under or slightly behind middle of dorsal base, its base 4.2–4.5 in SL. Pelvic generally reaching more then halfway to anal, inserted rather nearer to pectoral base than to anal origin. Pectoral usually extending scarcely to base of pelvic, 1.6–1.75 in head. Axillary scale of pectoral about half as long as fin, 2.8–3.75 in head.

Color. In alcohol, pale (originally preserved in formalin). Silvery lateral band poorly defined, narrower than eye. Upper surface of head and back with dusky punctulations; dark spots at base of anal, and a median dark line posterior to anal.

Size. The largest specimen in the collection, about 100 mm (4 in.) TL, is the largest individual reported.

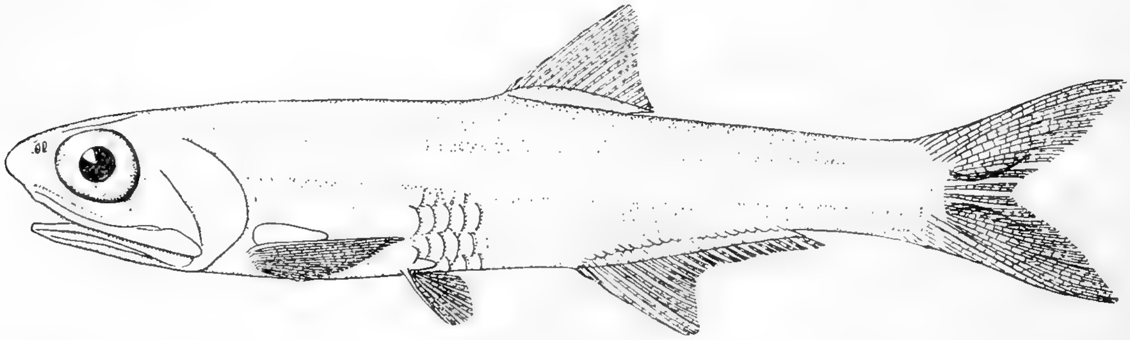

Figure 49. *Anchoviella elongata*, 101 mm TL, from Porto Bello, Panama, USNM 82093. Drawn by Louella E. Cable.

Range and Habitat. Known only from the Atlantic coast of Panama, where it apparently is not rare. Specimens have been collected from brackish water at Mindi (near Gatun), and from Gatun Spillway, Canal Zone; and from Porto Bello and Puerto Pilon, Panama.

Synonyms and References:

Anchovia elongata Meek and Hildebrand, Field Mus. Publ., Zool., *15* (1), 1923: 198, pl. 12, fig. 2 (orig. descr.; type local. Mindi, Canal Zone; type USNM 81768; cf. *A. cubana*); Breder, Zoologica, N. Y., *4* (4), 1925: 141 (common at Gatun Spillway, Canal Zone).

Anchoviella elongata Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 49 (ref. to orig. descr.); Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 126, fig. 54 (descr., generic relations., range).

Anchoviella lepidentostole (Fowler) 1911

Figure 50

Study Material. The type, about 96 mm (caudal fin damaged), 84 mm SL, and a paratype 76 mm long, 63 mm SL, from "Surinam."

Description. Proportional dimensions in per cent of standard length, and counts, based on study specimens, 84 and 63 mm SL, respectively.

Body: depth 25, 22.2.
Head: length 22.7, 23.8.
Snout: length 3.2, 3.7.
Eye: diameter 6.9, 7.1.
Postorbital: distance 10.7, 11.
Maxillary: length 16.4, 15.
Mandible: length 16.4, 15.8.

Anal fin: length of base 23.8, 23.8.
Pectoral fin: length 16.3, 15.8.

Scales: *ca.* 38.
Gill rakers: 17 + 19 right side, 18 + 20 left side; 17 + 19 both sides.
Fin rays: dorsal 14, 15; anal 25, 23; pectoral 12 (?), 14.

BODY rather robust, its depth 4.0, 4.5 in SL. HEAD 4.4, 4.2 in SL, its depth nearly equal to its length without snout. SNOUT extending about half of its length beyond mandible, 7.0, 5.5 in head. EYE 3.3, 3.3. POSTORBITAL part of head 2.1, 2.15 in head. MAXILLARY not quite square distally, scarcely reaching joint of mandible, 1.4, 1.6 in head. MANDIBLE 1.35, 1.5. CHEEK as long as eye, the posterior angle about 50°.

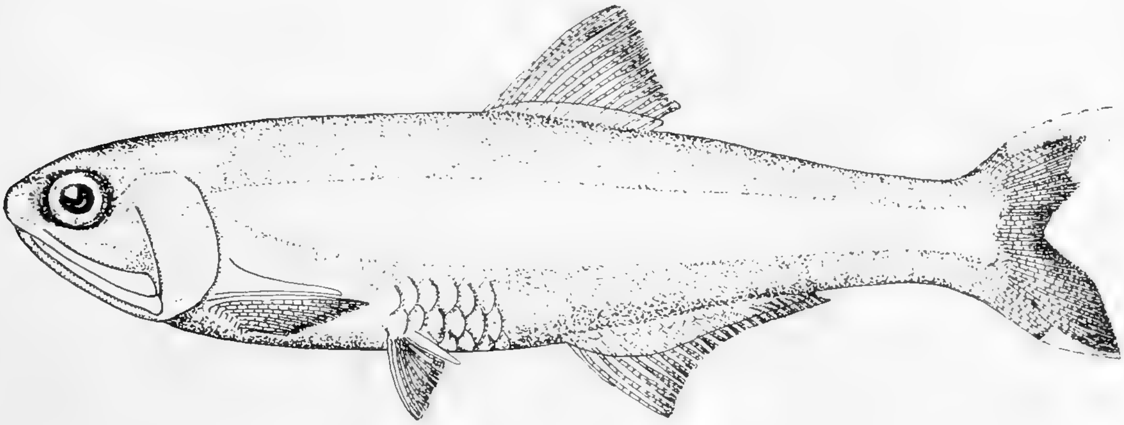

FIGURE 50. *Anchoviella lepidentostole*, type specimen, 96 mm TL, from "Surinam," ANSP 1346, modified after Fowler (1911: 214, fig. 3). Drawn by Alice C. Mullen.

DORSAL fin with longest rays failing to reach tip of last ray if deflexed, its origin a little nearer to caudal base than to tip of snout. ANAL originating under middle of dorsal base, its base 4.2, 4.2 in SL. PELVIC reaching scarcely halfway to anal, inserted a little nearer to anal origin than to pectoral base. PECTORAL failing to reach pelvic by diameter of pupil, 1.45, 1.5 in head. AXILLARY SCALE of pectoral failing to reach tip of fin by half of diameter of pupil, 2.0, 2.15 in head.

Color. In alcohol, brown. Lower parts silvery. Silvery lateral band strikingly prominent, much wider than eye.

Range. Known only from "Surinam."

Synonyms and References:

Anchovia lepidentostole Fowler, Proc. Acad. nat. Sci. Philad., *63*, 1911: 214, fig. 3 (orig. descr.; type local. "Surinam"; type ANSP 1346; cf. *Engraulis brevirostris* Günther and *E. januarius* Steindachner).

Anchoviella lepidentostole Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 49 (ref. to orig. descr.); Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 127, fig. 55 (descr. of type material).

Anchoviella blackburni Hildebrand 1943

Figure 51

Study Material. Type material, 11 specimens, about 33–38 mm TL (caudal fins damaged), all from the Gulf of Venezuela. The specimens probably are not full-grown, but the maxillary, which is shorter and blunter in very young than in adults, probably has acquired the approximate length and shape of a mature fish. At least it is shorter and much more rounded than in specimens of *Anchoa parva* and *A. mitchilli* of similar size.

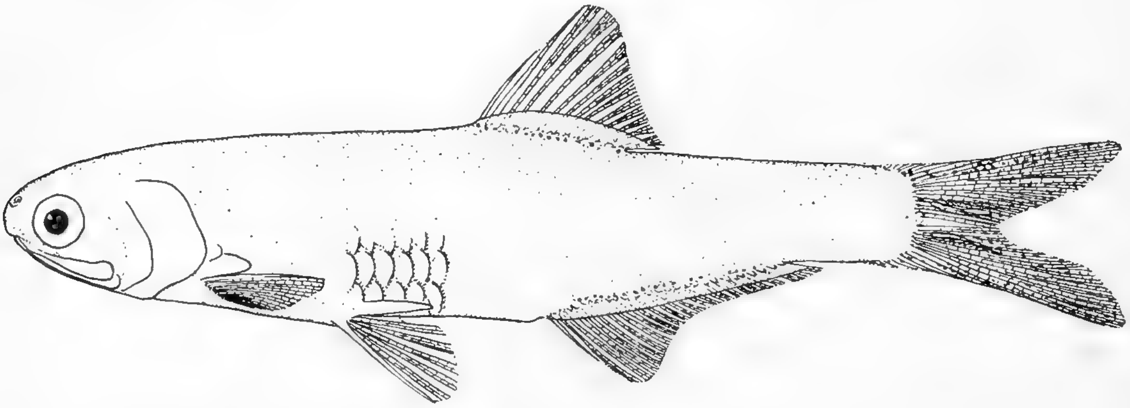

FIGURE 51. *Anchoviella blackburni*, type specimen 35 mm TL, from Gulf of Venezuela, USNM 119793. Drawn by Louella E. Cable.

Distinctive Characters. The long anal fin, the small number of gill rakers, the short head, and the very short, blunt snout distinguish this species from related forms.

Description. Proportional dimensions in per cent of standard length, and counts, based on the 11 type specimens, about 33–38 mm TL.

Body: depth 18.2–20.8.
Head: length 21.7–25.
Snout: length 3.6–3.8.
Eye: diameter 5.0–7.5.
Postorbital: distance 11–14.3.
Maxillary: length 12–15.
Mandible: length 12.3–14.8.

Anal fin: length of base 23.5–26.5.
Pectoral fin: length 13.8–16.6.

Scales: *ca.* 38–41.
Gill rakers: 10–12 + 15–17.
Fin rays: dorsal 13–15; anal 25–27; pectoral 13 or 14.
Vertebrae: 43 (1 specimen).

Body quite strongly compressed, its depth 4.8–5.5 in SL. Head 4.0–4.6 in SL, its depth equal to postorbital part of head and about half of eye. Snout very short, projecting little beyond mandible, about 5.0–7.0 in head. Eye 3.5–4.5. Postorbital part of head 1.6–1.9 in head. Maxillary slightly expanded and rounded distally, extending about half of diameter of eye beyond posterior rim of orbit, not quite to joint of mandible, 1.6–2.0 in head. Cheek only a little longer than eye, the posterior angle about 60°.

Dorsal fin with the longest rays failing to reach tip of last ray if deflexed, its origin about equidistant between caudal base and middle of eye. Anal originating about under origin of second third of dorsal base, its base 3.75–4.25 in SL. Pelvic reaching more than halfway to anal. Pectoral failing to reach base of ventral by somewhat less than diameter of eye, 1.25–1.6 in head.

Color. In alcohol, pale (originally preserved in formalin), with only a suggestion of a narrow silvery lateral band. A row of dark spots along base of anal, continued as a median dark line posterior to anal; a similar row along base of dorsal to upper lobe of caudal.

Range. Known only from the Gulf of Venezuela, where it was taken in Estauques Bay and Jacque Point.

References:

Anchoviella blackburni Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 129, fig. 57 (orig. descr.; type local. Jacque Point, Gulf of Venezuela; type USNM 119793; cf. *Anchoa parva* [Meek and Hildebrand] and *Anchoviella lepidentostole* [Fowler]); Schultz, Proc. U. S. nat. Mus., *99*, 1949: 48 (ref., counts).

Anchoviella (*Amplova*) *jamesi* (Jordan and Seale) 1926

Study Material. Two paratypes, about 47 and 37 mm TL, 36 and 32 mm SL, from fresh water as listed under *Range*; MCZ 17783 and 17784, respectively.

Distinctive Characters. This species has an extremely small mouth for an anchovy and is thus related to *A. balboae* Jordan and Seale of the Pacific coast of Panama, which was made the type of the genus *Amplova* Jordan and Seale, herein regarded as a subgenus. But it differs from *A. balboae* in having fewer anal rays, fewer gill rakers, a more posteriorly placed dorsal fin, and apparently a more slender body. *A. balboae* has 24–27 anal rays and 19–21 + 29–35 gill rakers; its dorsal origin is about equidistant between the base of caudal and middle of eye; and the depth in specimens 75–100 mm TL is 3.5–4.1 in SL.

Description. Proportional dimensions in per cent of standard length, and counts, based on study specimens 36 and 32 mm SL, respectively.

Body: depth 22.2, 23.8.
Head: length 22.2, 22.7.
Snout: length 3.04, 3.1.
Eye: diameter 5.8, 6.6.
Postorbital: distance ?, 12.8.
Maxillary: length 11.6, 11.9.

Anal fin: length of base 21, 18.7.
Pectoral fin: length 16.6, 18.7.

Scales: *ca.* 40.

Gill rakers: 13+21, 12+20.
Fin rays: dorsal 13, 12; anal 21, 19; pectoral 11, 11.
Vertebrae: 40, ?.

Body moderately compressed, its depth 4.5, 5.3 in SL. Head 4.5, 4.4 in SL, its depth equal to postorbital length and about half of eye. Snout very short, projecting about a third of its length beyond mandible, 7.2, 7.3 in head. Eye 3.8, 3.5. Postorbital part of head 1.85 in head. Maxillary distally rounded, scarcely reaching beyond posterior rim of orbit, and not to articulation of mandible, 2.0, 1.9 in head. Cheek very short and broad, scarcely forming a triangle, much shorter than eye.

Dorsal fin with the longest rays reaching far beyond tip of last ray if deflexed, its origin nearer to base of caudal than to eye. Anal with a prominent lobe anteriorly, its origin slightly in advance of middle of dorsal base, its base 4.8, 5.3 in SL. Pelvic reaching more than halfway to anal, inserted about equidistant between base of pectoral and origin of anal. Pectoral nearly reaching base of pelvic, 1.2, 1.25 in head. Axillary scale of pectoral missing in specimens examined.

Color. Old specimens, in alcohol, faded, pale. Silvery lateral band rather diffuse, narrower than eye.

Range. Known from the type material from fresh water, the holotype being from Jutahy River, the two paratypes from Lago Alexo, Brazil. Two small specimens also are reported from the Rio Ucayali, in Peru.

Synonyms and References:

Amplova jamesi Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67*, 1926: 410 (orig. descr.; type local. Jutahy R., Brazil; type MCZ 18014; two paratypes listed from Lago Alexo, Brazil); Myers, Proc. Calif. Acad. Sci., (4) 23, 1940: 441 (descr. after Jordan and Seale; Rio Ucayali, Peru).

Anchoviella jamesi Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 137, fig. 61 (descr., relation. with *Amplova balboae* Jordan and Seale).

Genus *Pterengraulis* Günther 1868

Pterengraulis Günther, Cat. Fish. Brit. Mus., 7, 1868: 384, 398; type species by monotypy, *Clupea atherinoides* Linnaeus 1758.

Characters. Body rather deep, strongly compressed. Gill rakers short and broad, especially in large examples, only about 11 on upper limb and about 14 on lower limb. Dorsal origin about equidistant between margin of opercle and base of caudal. Pelvic inserted about midway between pectoral base and dorsal origin.

Size. A large size is attained, specimens 250 mm long being included in the collections studied.

Remarks. The anal fin is long, with about 30–33 rays, its origin being under, or more usually in advance of, the dorsal origin. The teeth are small and of nearly uniform size. The maxillary extends to, or nearly to, the joint of the mandible and is rounded distally.

Range. Venezuela to northern Brazil.

Species. Only one, *P. atherinoides.*

Pterengraulis atherinoides (Linnaeus) 1766

Hareng gras Sardinha

Figure 52

Study Material. A total of 20 specimens, 66–250 mm TL, from Caño de Guanoco and Rio Apure, San Fernando de Apure, Venezuela; and from the "Amazon River," Pará, Fortaleza, Cametá, and Ararý, Brazil.

Description. Proportional dimensions in per cent of standard length, and counts, based on study specimens, 66–250 mm TL.

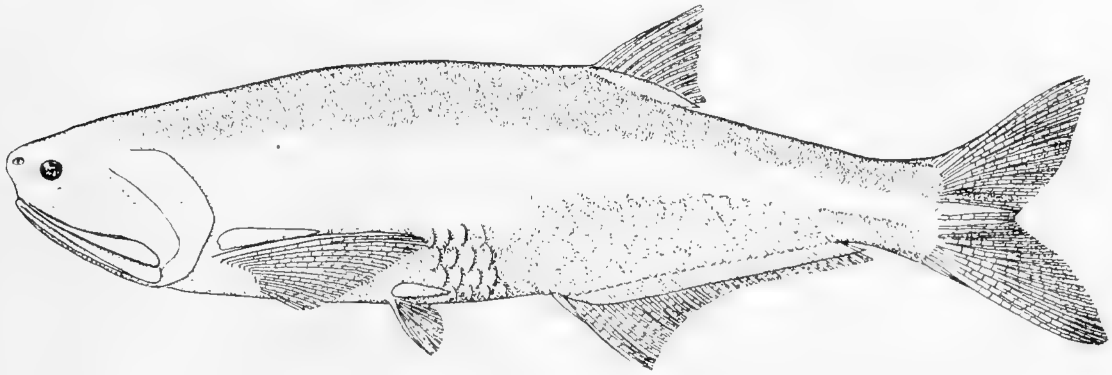

Figure 52. *Pterengraulis atherinoides,* 245 mm TL, from "Amazon River," USNM 72551. Drawn by Louella E. Cable.

Body: depth 22–26.
Head: length 22.6–28.5.
Snout: length 2.4–3.1.
Eye: diameter 4.0–5.1.
Postorbital: distance 14.3–16.7.
Maxillary: length 16.5–19.2.
Mandible: length 15.4–18.

Anal fin: length of base 30–34.5.
Pectoral fin: length 20.4–23.7.

Scales: 42–47.
Gill rakers: 10–12 + 12–15.
Fin rays: dorsal 12–14; anal 29–35 (usually 31 or 32); pectoral 13–15.
Vertebrae: 43 and 45 (2 specimens).

Body strongly compressed, its depth 3.5–4.4 in SL. Head 3.8–4.5 in SL, its depth usually equal to its length posterior to middle of eye. Snout blunt, 8.0–10 in head. Eye 4.0–6.0. Postorbital part of head moderately long, 1.4–1.55 in head.

Maxillary rounded distally, often failing to reach joint of mandible, 1.3–1.5 in head. Mandible 1.3–1.5. Cheek increasing in proportionate length with growth, much longer than eye and snout in large examples, its posterior angle about 40°.

Dorsal fin with the longest rays reaching beyond tip of last ray if deflexed, its origin about equidistant between caudal base and margin of opercle. Anal long, its origin under or more usually somewhat in advance of dorsal origin, its base 2.9–3.3 in SL. Pelvic reaching only about a third of distance to anal, usually inserted a little nearer to base of pectoral than to anal origin. Pectoral reaching to or beyond middle of pelvic, 1.0–1.3 in head. Axillary scale of pectoral reaching to or somewhat beyond midlength of fin, 1.8–2.1 in head.

Color. In alcohol, pale brownish above. Sides of head and lower parts of body silvery. Silvery lateral band broad anteriorly, narrower on caudal portion of body, becoming diffused with the silvery shade on lower part of body anteriorly in large specimens, apparently persisting posteriorly.

Size. Examples 300 mm TL have been reported.

Commercial Importance. This fish has been reported as very common in the market at Belém (Pará), Brazil.

Range. Its range extends from Venezuela to northern Brazil, possibly as far south as Rio de Janeiro. It ascends streams.

Synonyms and References:

Clupea atherinoides Linnaeus, Syst. Nat., ed. 12, *1*, 1766: 535 (orig. descr.; type local. Surinam; type lost).

Engraulis atherinoides Cuvier and Valenciennes, Hist. Nat. Poiss., *21*, 1848: 31 (descr., relations., Surinam); Günther, Cat. Fish. Brit. Mus., 7, 1868: 398 (descr., Surinam, British Guiana, and Pará, Brazil); Steindachner, Ichthyol. Beitr., *8*, 1879: 59 (descr., Surinam; British Guiana; Pará, Cametá, Gurupá, Rio de Janeiro, and Capim R., Brazil).

Pterengraulis atherinoides Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 450 (descr., range); Schreiner and Miranda-Ribeiro, Arch. Mus. nac., Rio de J., *12*, 1903: 94 (range, Guianas to Brazil); Starks, Stanf. Univ. Publ., Univ. Ser., 1913: 10 (common in market at Pará, Brazil); Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67*, 1926: 386 (descr., Pará, Cametá, Gurupá, and Ararý, Brazil); Fowler, Proc. Acad. nat. Sci. Philad., *83*, 1931: 407 (Caño de Guanoco, Venezuela); Puyo, Bull. Soc. Hist. nat. Toulouse, *70*, 1936: 170, fig. 36 (descr., habitat in French Guiana); Fowler, Proc. Acad. nat. Sci. Philad., *93*, 1941: 126, fig. 3 (Rio Jaguaribe, Ceará, Brazil; refs.); Arqu. Zool. estad. São Paulo, *3* (6), 1941: 135 (refs., Brazil); Campos, Arqu. Zool. estad. São Paulo, *3* (7) 1941: 200 (synon., descr., range); Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 139, fig. 63 (descr., synon., range); Puyo, Faune Emp. Franç., 12, Poiss. Guyane Franç., 1949: 158, fig. 81 (descr., habitat, French Guiana); Schultz, Proc. U. S. nat. Mus., *99*, 1949: 48 (San Fernando de Apure, Venezuela).

Clupea pilchardus de Magalhaes (not of Linnaeus), Monogr. Brazil, Peixes Fluviaes, 1931: 194, fig. 104 (descr., local name, length, habitat).

Doubtful Reference:

Engraulis atherinoides Knerr, "Novara," Zool., Fische (1), 1865: 332 (descr. insufficient for ident.; Rio de Janeiro, Brazil).

Genus *Hildebrandichthys* Schultz 1949

Hildebrandichthys Schultz, Proc. U. S. nat. Mus., *99*, 1949: 49; type species by original designation, *Hildebrandichthys setiger* Schultz.

Characters. Body slender, rather strongly compressed, its depth about equal to postorbital part of head. Head long and low. Eye entirely in anterior half of head. Maxillary rounded posteriorly, not quite reaching joint of mandible. Teeth all small. Gill rakers slender, those at angle of first arch about as long as eye, about 33 on lower limb. Dorsal fin far back, its origin about twice the distance from tip of snout as from caudal base. Anal fin beginning well in advance of origin of dorsal, about 25 rays. Pelvic inserted about equidistant between base of pectoral and anal origin.

Remarks. The numerous long gill rakers and the posterior position of the dorsal fin are the chief distinguishing characters of this genus. *Hildebrandichthys* resembles *Anchovia* in the numerous long, slender gill rakers, but it differs in the very rearward position of the dorsal fin. In the position of the dorsal it tends to agree more or less with *Pterengraulis*, with which it differs in the numerous, long slender gill rakers.

This genus is founded on one species, which in turn is based on only a single small (juvenile) specimen. Though it is quite distinctive, it offers some difficulties because the adult generic characters apparently are not fully developed. The maxillary, for example, is short and rounded, which, so far as known, is true of all young Engraulidae; it may or may not become produced and pointed in the adult, as shown in other generic descriptions.

Range. Known only from the Maracaibo Basin, Venezuela.

Hildebrandichthys setiger Schultz 1949

Figure 53

Study Material. A single small specimen, about 37 mm TL (caudal damaged), 31 mm SL, from the mouth of Rio Caño de Sagua, Lake Maracaibo, Venezuela. This specimen retains some of the juvenile color markings, and the maxillary may not have acquired its adult length and shape.

Distinctive Characters. The numerous gill rakers, which may increase in number with age, in general agree with the rakers in *Anchovia clupeoides*; the posterior position of the dorsal fin calls to mind *Pterengraulis atherinoides*. See also *Remarks* under genus.

Description. Proportional dimensions in per cent of standard length, and counts, based on young specimen, 31 mm SL.

Body: depth 19.2.
Head: length 32.
Snout: length 5.1.
Eye: diameter 8.7.
Postorbital: distance 17.
Maxillary: length 17.
Mandible: length 16.

Anal fin: length of base 22.6.
Pectoral fin: length 12.

Scales: mostly lost, *ca.* 38 pockets.
Gill rakers: *ca.* 23 + 33.
Fin rays: dorsal 12; anal 25; pectoral 13.

Body slender, rather strongly compressed, its depth 5.2 in SL. Head 3.1, its depth about equal to its postorbital length. Snout projecting about 67% of its length beyond tip of mandible, 6.25 in head. Eye small but longer than snout, 3.7 in head. Postorbital length 5.9. Maxillary rounded posteriorly, not quite reaching joint of mandible, 1.9 in head. Mandible 2.0. Cheek a little longer than eye, its posterior angle about 60°. Gill rakers slender, those at angle of first arch about as long as eye (too close-set for accurate counting), about 23 on the upper limb and about 33 on lower limb.

Dorsal fin small, damaged, apparently with a convex margin, the anterior rays not reaching beyond tip of last ray if deflexed, the fin placed very far back, its origin about twice as far from tip of snout as from caudal base. Anal originating about an eye's diameter in advance of dorsal origin and about equidistant between joint of mandible and caudal base, its base 4.4 in SL. Pelvic fin noticeably more than halfway to origin of anal, inserted about equidistant between pectoral base and anal origin, 3.33 in head. Pectoral fin failing to reach base of pelvic by a little less than diameter of eye, 8.4 in SL, 2.6 in head. Axillary scale of pectoral not evident, lost or undeveloped.

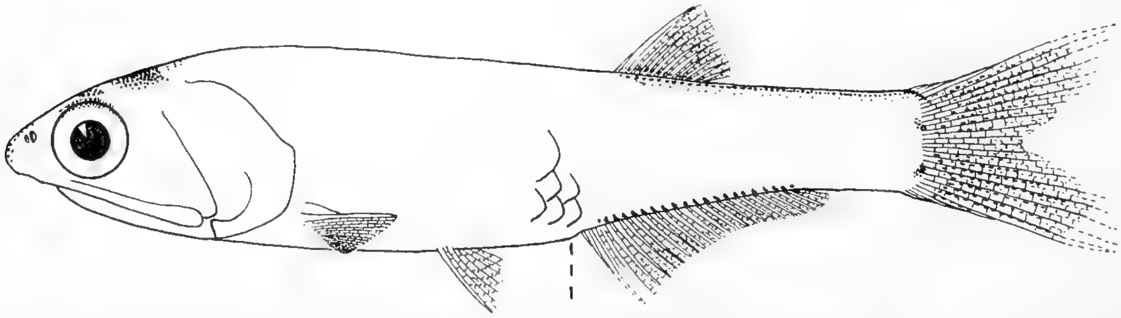

Figure 53. *Hildebrandichthys setiger*, type specimen, 37 mm TL, from Maracaibo Basin, Venezuela, USNM 121779. Drawn by A. M. Awl.

Color. This specimen retains some of the juvenile color markings. In alcohol, rather pale. Side of head and abdomen silvery. A rather faint narrow silvery lateral band present. Dusky dots present on upper surface of head and snout, along base of dorsal, and mostly in two rows behind the dorsal; a series of rather large black dots along base of anal, continued as a single median row behind anal fin (presumably juvenile markings); dusky dots generally distributed over the caudal fin; other fins pale or at most with suggestions of dusky markings.

Range. Known only from the mouth of the Rio Caño de Sagua, Lake Maracaibo, Venezuela.

Reference:

Hildebrandichthys setiger Schultz, Proc. U. S. nat. Mus., 99, 1949: 49, fig. 7 (orig. descr.; type local. Caño de Sagua, Sinamaica, Venezuela; type USNM 121779).

Genus *Lycengraulis* Günther 1868

Lycengraulis Günther, Cat. Fish. Brit. Mus., 7, 1868: 385, 399; type species *Engraulis grossidens* Cuvier 1828, designated by Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 451.

Characters. BODY slender, compressed, the depth generally less than 27% of SL. MOUTH very large. MAXILLARY extending far beyond eye, generally to or beyond joint of mandible, rounded or pointed distally. MANDIBLE curved upward near tip. GILL RAKERS variable in length, about 10–20 + 12–25 on first arch. ANAL originating definitely posterior to dorsal origin, with about 24–28 rays. PELVIC inserted about midway between base of pectoral and origin of anal. Young with a silvery lateral band that disappears with age.

Size. About 250 mm is the maximum size attained in this genus.

Remarks. The genus is distinguished by the prominent teeth in the jaws: unequal in size in older specimens but rather even in young; larger in the lower than in the upper jaw, some of them often canine-like; variable in number among the species, about 16–25 enlarged teeth in lower jaw and 40–85 in upper jaw.

Species. Eight species have been recognized, one from the Pacific ranging from Panama Bay to Peru, and seven from the Atlantic ranging from the Gulf of Venezuela to northern Argentina. Five of the Atlantic species come within the scope of the present work.

Key to Species of the Western North Atlantic

1a. Gill rakers long and slender, those at angle equal to or longer than pupil.
    2a. Gill rakers 13–20 + 17–25 on first arch; cheek scarcely longer than snout and eye in adults.
        3a. Depth of body 23–24.5% of SL; maxillary reaching margin of opercle; pelvic fin usually inserted nearer to origin of anal than to pectoral base, occasionally equidistant between these; vertebrae usually 43 or 44 (occasionally 42 or 45). *grossidens* (Cuvier) 1829, p. 234.
        3b. Depth of body 21–23% of SL in specimens upward of about 100 mm TL; maxillary not reaching margin of opercle; pelvic fin inserted nearer to pectoral base than to anal origin; vertebrae usually 41 (occasionally 42). *limnichthys* Schultz 1949, p. 237.
    2b. Gill rakers 9–13 + 12–15 on first arch; cheek much longer than snout and eye in adults. *batesii* (Günther) 1868, p. 240.
1b. Gill rakers short and broad, the longest scarcely exceeding half of length of pupil.
    4a. Maxillary sharply pointed distally, extending well beyond joint of mandible; origin of dorsal about equidistant between caudal base and middle of eye; gill rakers 11 or 12 + 16 or 17. *abbotti* (Fowler) 1915, p. 242.
    4b. Maxillary rounded distally, scarcely reaching joint of mandible; origin of dorsal much nearer to base of caudal than to posterior margin of eye; gill rakers 9–11 + 12–14. *barbouri* Hildebrand 1943, p. 243.

Table VIII. Comparison of *L. grossidens* with *L. olidus*. Proportional Dimensions in Per Cent of Standard Length.

	L. grossidens 40 specimens & others (40–220 mm TL) from northern Brazil and Venezuela	*L. olidus* 44 specimens (97–240 mm TL) from southern Brazil, Paraguay, Uruguay, and Argentina
Body: depth	21–24.3*	19.2–22.7
Head: length	22.6–26.6	22.2–25
Snout: length	3.3–4.3	2.7–3.4
Eye: diameter	4.8–7.0	4.3–5.7
Postorbital: distance	13–15	13–15.5
Maxillary: length	18.2–21.5	16.5–19.5
Mandible: length	15.2–18.2	15.5–17.5
Anal fin: length of base	23.7–26.5	22–25.5
Pectoral fin: length	16.6–20.0	15.8–17.8

	L. grossidens 40 specimens & others (40–220 mm TL) from northern Brazil and Venezuela	*L. olidus* 44 specimens (97–240 mm TL) from southern Brazil, Paraguay, Uruguay, and Argentina
Scales:	*ca.* 40–44	*ca.* 40–45
Gill rakers:	13–17 + 17–21 (most frequently 14 + 19 or 20)	15–19 + 19–23 (most frequently 16 + 21)
Fin rays:		
dorsal	14 or 15	14 or 15
anal	24–28	26–28
pectoral	14 or 15	14 or 15
Vertebrae:	43 or 44 (4 specimens)	46–48 (3 specimens)

* 23–24.3 in specimens 100 mm upward.

Lycengraulis grossidens (Cuvier) 1829

Sardinha Prata (Brazil)

Figure 54

Study Material. A total of 40 specimens, 40–220 mm TL, and many others as well [presumably from Rio de Janeiro, Brazil and northward, as implied by Dr. Hildebrand under *Relationship and Variation*–Y.H.O.]. Also 44 specimens, 97–240 mm TL, from southern Brazil, Paraguay, Uruguay, and Argentina, representing *L. olidus* (Günther), used as basis for measurements and counts in Tables viii–x.

Distinctive Characters. See *Relationship and Variation.*

Description. Proportional dimensions and counts, based on 40 specimens from Rio de Janeiro, Brazil, and northward, 40–220 mm TL, in Table viii.

Body strongly compressed, increasing in depth with age, its depth 3.85–4.4 in SL in specimens 100 mm or more. Head with depth nearly equal to its length without snout, 4.1–4.7 in SL. Snout projecting somewhat less than half of its length beyond mandible, 5.6–6.9 in head. Eye 4.2–4.9. Postorbital part of head 1.6–1.7 in head. Maxillary little expanded, pointed distally, extending beyond joint of mandible, often nearly to margin of opercle, 1.15–1.25 in head. Mandible 1.33–1.6. Cheek somewhat longer than eye and snout in large examples, shorter than snout and eye in specimens less than 100 mm, its posterior angle about 35°. Gill rakers slender, those at angle fully as long as pupil.

Dorsal fin with the longest rays usually reaching about to tip of last ray if de-

Table IX. Frequency Distribution of Gill Rakers in *Lycengraulis.**

Species	Number of Gill Rakers on Upper Limb of First Arch											
	9	10	11	12	13	14	15	16	17	18	19	20
grossidens	—	—	—	—	4	15	6	7	1	—	—	—
olidus	—	—	—	—	—	—	3	15	8	4	1	3
batesii	3	2	4	5	2	—	—	—	—	—	—	—
abbotti	—	—	1	1	—	—	—	—	—	—	—	—
barbouri	1	3	4	—	—	—	—	—	—	—	—	—

* When the number of counts exceeds the number of specimens reported in the text, the gill rakers were counted on both anterior arches of at least some of the fish.

Table X. Frequency Distribution of Gill Rakers in *Lycengraulis.**

Species	Number of Gill Rakers on Lower Limb of First Arch													
	12	13	14	15	16	17	18	19	20	21	22	23	24	25
grossidens	—	—	—	—	—	1	9	13	15	8	—	—	—	—
olidus	—	—	—	—	—	—	2	5	6	20	7	5	2	1
batesii	—	3	7	2	—	—	—	—	—	—	—	—	—	—
abbotti	—	—	—	—	1	1	—	—	—	—	—	—	—	—
barbouri	1	6	1	—	—	—	—	—	—	—	—	—	—	—

* When the number of counts exceeds the number of specimens reported in the text, the gill rakers were counted on both anterior arches of at least some of the fish.

flexed, its origin rather variable, most frequently nearer to base of caudal than to posterior margin of eye. ANAL with base 3.75–4.2 in SL, its origin generally under middle of dorsal base. PELVIC small, extending much less than halfway to anal, usually inserted nearer to anal origin than to pectoral base. PECTORAL often reaching nearly to base of pelvic, 1.15–1.35 in head. AXILLARY SCALE of pectoral about 0.75 of length of fin, 1.5–1.9 in head.

Color. In alcohol, grayish above. Sides of head and lower 67 % of body uniform silvery in adults. Young under 90 mm long with a distinct silvery lateral band narrower than eye, much broader than eye and less distinctly outlined ventrally in specimens 120 mm long, intergrading completely with the silvery color of lower parts of body in somewhat larger individuals. Margin of caudal blackish in adults.

Size. Examples having a maximum total length of 280 mm (11.2 in.) have been reported, but the largest in the collections studied is only 220 mm TL.

Relationship and Variation. L. olidus (Günther) is a very near relative of *L. grossidens*, the two probably intergrading in southern Brazil. If specimens from Venezuela or northern Brazil are compared with examples from extreme southern Brazil, Uruguay, and Argentina, it is at once evident that those from the more southern localities have a more slender and less strongly compressed body, a shorter and less pointed maxillary, smaller teeth in the upper jaw but still much larger than those of other American genera, a greater average number of gill rakers, and more numerous vertebrae. See Table VIII for comparison of *L. grossidens* with *L. olidus.*

L. poeyi of the Pacific coast of Panama is also a near relative of the Atlantic species, but it differs in having: a shorter and blunter snout that projects little beyond the mandible; smaller teeth of more uniform size in the lower jaw; a longer pectoral that reaches to, or a little beyond, the base of the pelvic and has 16 or 17 rays (1 or 2 more than in *grossidens* and *olidus*); and apparently a dark vertebral band, which is missing in the *L. grossidens* and *L. olidus* examined. In depth of body and in length and shape of the maxillary it agrees with *L. olidus* rather than with *L. grossidens.*

Commercial Importance. As some of the specimens in the collections studied were purchased in markets, this species must be of some commercial value.

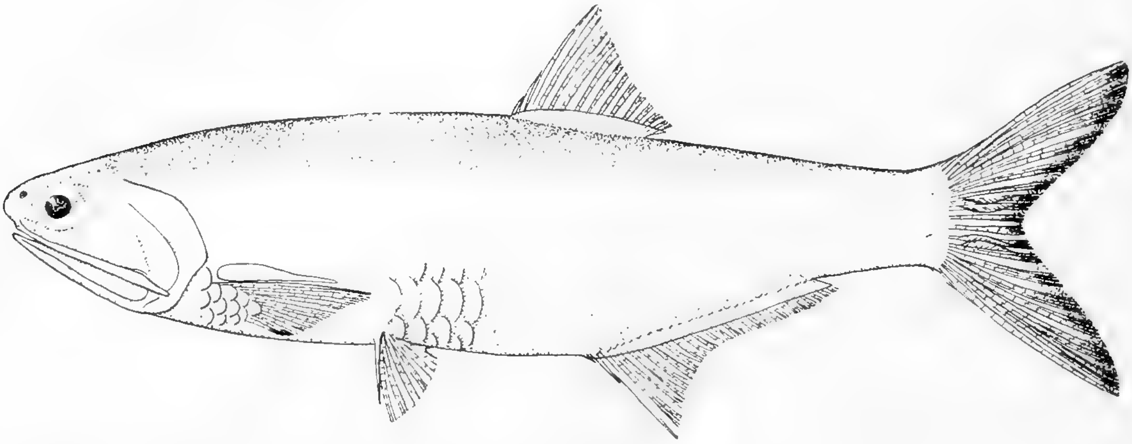

FIGURE 54. *Lycengraulis grossidens,* 214 mm TL, from Porto Inhauna, Brazil, USNM 100835. Drawn by Louella E. Cable.

Range and Habitat. The range of *L. grossidens* extends from the Gulf of Venezuela south about to Rio de Janeiro, Brazil, and of *L. olidus* from southern Brazil to northern Argentina; both species ascend freshwater streams. The rather numerous records of *L. grossidens* from Uruguay and Argentina are apparently referable to *L. olidus.*

Synonyms and References:

Engraulis grossidens Cuvier, in Spix and Agassiz, Pisc. Brazil., 1829: 50, pl. 24, fig. 1 E (orig. descr.; type local. Rio de Janeiro, Brazil); Günther, Cat. Fish. Brit. Mus., 7, 1868: 399 (descr., synon., British Guiana).

Engraulis janeiro Agassiz, in Spix and Agassiz, Pisc. Brazil., 1829: pl. 24, fig. 1 (type local. Rio de Janeiro, Brazil; name and fig. only).

Engraulis dentex Cuvier and Valenciennes, Hist. Nat. Poiss., *21*, 1848: 28 (orig. descr.; type local. Rio de Janeiro, Brazil); Kner, Reise "Novara," Zool., Fische, *1*, 1865: 332 (descr., Rio de Janeiro); Steindachner, Ichthyol. Notiz., 6, 1867: 35 (descr., Rio de Janeiro and La Plata; the latter undoubtedly referable to *L. olidus*).

Lycengraulis grossidens Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 451 (descr., range, synon.); Gilbert, Proc. Wash. Acad. Sci., *2*, 1900: 163 (descr., Pernambuco, Brazil); Starks, Stanf. Univ. Publ., Univ. Ser., 1913: 11 (descr., Natal, Brazil); Jordan and Gilbert, Bull. Mus. comp. Zool. Harv., *67*, 1926: 383 (descr., Brazil and Uruguay; those from south of Rio de Janeiro, Brazil, probably *L. olidus*; those from Rio Poty, Brazil, are *L. barbouri*); von Ihering, Rev. Indust. Anim., Anno 1 (3), 1930: 233 (size, diagn.); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 51 (range, synon.); Fowler, Arqu. Zool. estad. São Paulo, *3* (6), 1941: 135 (refs., Brazil); Hildebrand, Bull. Bingham oceanogr.

Coll., *8* (2), 1943: 143, fig. 64 (descr., range, synon.); Schultz, Proc. U. S. nat. Mus., *99*, 1949: 54 (synon., refs.).

Negative References:

Lycengraulis grossidens Berg, An. Mus. nac., Buenos Aires, *4*, 1895: 21 (fairly abund. in markets, Buenos Aires and Montevideo; *L. olidus*); Devincenzi, An. Mus. nac., Montevideo, *2* (5), 1924: 189 (*L. olidus*); Thompson, Proc. U. S. nat. Mus., *50*, 1916: 405 (numerous from Montevideo, two from Buenos Aires; in part *L. olidus*).

Lycengraulis limnichthys Schultz 1949

Figure 55

Study Material. Type material of many specimens, 24–150 mm TL, 20–116 mm SL, from Lake Maracaibo, Venezuela, and the lower parts of its tributary streams.

Distinctive Characters. This species is related to *L. grossidens* and *L. olidus*, the latter being extralimital from southern Brazil to Argentina. *L. limnichthys* differs from *grossidens* in having a more slender and apparently less strongly compressed body, specimens of nearly equal size compared. In *limnichthys* the maxillary is a little shorter, scarcely reaching beyond the joint of the mandible and not to the margin of the opercle, whereas in adults of *grossidens* it is longer, reaching well beyond the joint of the mandible and often to the margin of the opercle. In *limnichthys* the pelvic fins are inserted nearer to the base of the upper pectoral ray than to the anal origin, whereas in *grossidens* they are equidistant between these two points, or more usually nearer to the anal origin. And *limnichthys* differs from both *grossidens* and *olidus* in having fewer vertebrae.

Description. Propertional dimensions in per cent of standard length, and counts, based on at least 11 study specimens.

Body: depth 21–23, in specimens 90 mm TL and upward.
Head: length 23–25.
Snout: length 3.0–4.15.
Eye: diameter 5.4–6.5.
Postorbital: distance 12.5–15.
Maxillary: length 17.2–19.2.
Mandible: length 16.3–18.5.
Anal fin: length of base 21–23.5.

Pectoral fin: length 16–19.

Scales: *ca.* 35–45.
Gill rakers: 15–18 + 20–23 (rarely 24 or 25).
Fin rays: dorsal 13–16; anal 23–25 (rarely 26 or 27); pectoral 14 or 15 (rarely 13).
Vertebrae: 41 or 42 (11 specimens).

BODY moderately compressed, its depth 4.35–4.75 in SL in specimens 73–116 mm SL. HEAD 4.0–4.35, its depth slightly exceeding its postorbital length. SNOUT blunt, extending about a third of its length beyond tip of mandible, 6.1–7.0 in head. EYE 3.6–4.5. POSTORBITAL length 6.65–8.0 in SL, 1.6–1.8 in head. MAXILLARY scarcely pointed, extending somewhat beyond joint of mandible in the large examples but not to margin of opercle, 1.25–1.35 in head. MANDIBLE 1.27–1.4. CHEEK moderately short and broad, generally about as long as snout and eye, its posterior angle about 30°. GILL RAKERS moderately slender, those at angle of first arch about as long as pupil, rather spinulose along inner margin, scarcely expanded at tip.

DORSAL fin with longest rays not reaching tip of posterior ray if deflexed, its margin generally slightly concave, its origin usually about equidistant between posterior margin of eye and base of caudal. ANAL with a definite lobe anteriorly, its base 4.25–4.75 in SL, its origin about under middle of dorsal base and equidistant between pectoral base and caudal base, or a little nearer to the former. PELVIC generally extending a little less than halfway to anal, inserted somewhat nearer to pectoral base than to origin of anal, 2.4–2.8 in head. PECTORAL reaching to or a little beyond base of pelvic in small specimens, frequently failing to reach pelvic in large ones, 1.25–1.4 in head. AXILLARY SCALE of pectoral variable in length, reaching somewhat beyond midlength of pectoral to beginning of its distal fourth, 1.4–2.25 in head.

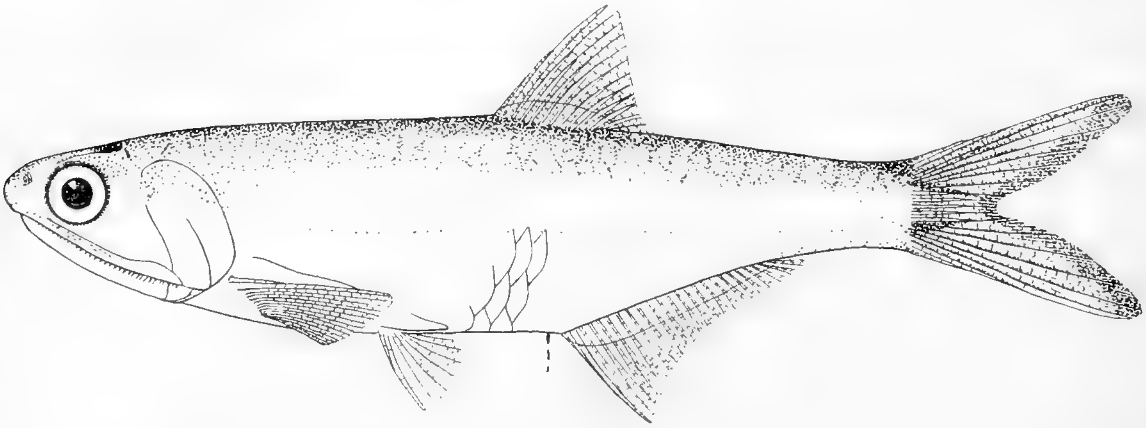

FIGURE 55. *Lycengraulis limnichthys*, type specimen, from Rio Agua Caliente, above Maracaibo Basin, Venezuela, USNM 121751. Drawn by A. M. Awl.

Color. Back pale, with a median dark streak, much more distinct in some specimens than in others. Sides with a broad silvery lateral band in adults, becoming diffused with the silvery color on the lower part of side in large examples, quite narrow in young. Dorsal and caudal fins with dusky punctulations, the margin of the latter much darker in some specimens than in others; other fins plain. Peritoneum silvery.

Size. The largest example in the collection studied is 150 mm TL and 116 mm SL, which may be near the maximum size attained.

Development. The smallest, 19 mm SL, is slender and has all fins well developed. The caudal fin is as deeply forked as that in the adult, and the other fins have acquired approximately the same shape and relative position as those in adults. The snout remains shorter and projects less strongly beyond the mandible than in larger specimens; the maxillary, also much shorter and rounder, fails to reach the joint of the mandible; and the teeth in the jaws are scarcely evident.

The juvenile color of this same specimen and of others of about equal size consists of a few dark dots over the nostrils, a group of similar dark dots at the occiput, and more or less definite rows on the back. Scattered dark points, present at and on the base of the caudal, extend prominently on the outer rays of the fin, which already has a dusky margin that remains throughout life. A series of prominent black spots along each side of the anal base continues in a single series on the peduncle behind the anal; a few scattered dark dots are present on the side of the head and on the isthmus. This small example, then, is definitely beyond the larval stage and is perhaps a young adult.

The juvenile is slender, as is usual among clupeid fishes. In three specimens, 19, 19.5, and 20 mm SL, the depth is respectively 9.0, 9.5, and 9.3 times in SL; in a group of six, ranging between 27–33 mm SL, the proportionate depth already has increased and is 8.5–6.5 in SL; and in an additional group of five, 32–50 mm SL, the depth is 6.5–5.45 in SL. Measurements of larger fish indicate that the body tends to become proportionately deeper as long as the fish grows.

The teeth in the jaws are well developed but remain minute in specimens around 25 mm SL. They do not become large (for an anchovy) and unequal in size (the chief distinguishing characters of *Lycengraulis*) until the fish attains about 65 mm SL.

In fish 25 mm SL, the snout already projects well beyond the mandible, about as in the adult, and the maxillary is now somewhat pointed and reaches to a point approximately opposite the joint of the mandible. The axillary scale of the pectoral, not detected in the smaller specimens described, is now evident and reaches about to the midlength of the pectoral; this axillary process, though rather variable in length, reaches far beyond the midlength of this fin in adults, generally to or beyond the beginning of its distal third.

The juvenile color markings are retained about as described for the 19-mm fish until a standard length of at least 40 mm is attained. Even then the juvenile markings remain in large part. However, the sides of the head and the abdomen, in part, have become silvery. A very narrow indistinct silvery lateral band has become evident, and this increases rapidly in proportionate width, being prominent and as broad as the eye in specimens of about 75 mm SL; in examples of about 85 mm SL, the band is much broader than the eye, and its lower margin generally has become indefinite. In still larger specimens it usually has become diffused with the silvery color on the lower part of the side. The dark dots along the base of the anal persist longer than any of the other juvenile markings and are visible in half-grown fish; in fact, they are visible in some specimens up to 90 mm SL.

Spawning. Several females with large eggs were taken in Lake Maracaibo on May 16 (1942), indicating that at least some spawning takes place in the spring of the year.

Range. Known only from Lake Maracaibo and from the lower sections of tributary streams, in fresh to slightly brackish water.

Reference:

Lycengraulis limnichthys Schultz, Proc. U. S. nat. Mus., *99*, 1949: 51, fig. 8 (orig. descr.; type local. Rio Agua Caliente, above Lake Maracaibo, Venezuela; type USNM 121751).

Lycengraulis batesii (Günther) 1868

Figure 56

Study Material. A total of 13 specimens, 35–185 mm TL, the larger ones from Brazil, the smaller ones from Venezuela; also 4 juveniles, 21–31 mm TL, from Venezuela.

Distinctive Characters. The slender body, the long narrow cheek, and the rather few and moderately long gill rakers distinguish this species. The statement in the original description, "Gill rakers very short, like tubercles," has been misleading, for they are fully half of the length of eye, a point that was verified from type specimens by J. R. Norman. This statement became especially bothersome upon the discovery of other species that had notably shorter gill rakers.

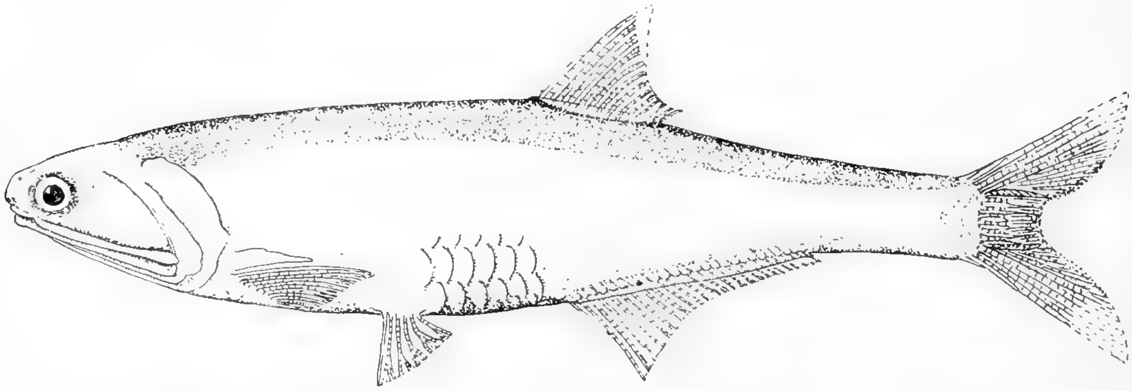

Figure 56. *Lycengraulis batesii*, 185 mm TL, 155 mm SL, from Teffé, Brazil, MCZ 18006. Drawn by Alice C. Mullen.

Description. Proportional dimensions in per cent of standard length, and counts, based on the *Study Material.*

Body: depth 16.5–19.
Head: length 21–23.
Snout: length 2.75–3.3.
Eye: diameter 4.2–4.6.
Postorbital: distance 14.3–15.6.
Maxillary: length 17.5–18.2.
Mandible: length 16.1–18.2.

Anal fin: length of base 25–26.2.
Pectoral fin: length 15.4–18.8.

Scales: *ca.* 41–45.
Gill rakers: 9–13 + 12–15.
Fin rays: dorsal 13–15; anal 26–28; pectoral 13 or 14.
Vertebrae: 47 (2 specimens).

Body slender, compressed, its depth 5.25–6.0 in SL. Head 4.3–4.7 in SL, its depth about equal to its postorbital length. Snout projecting much less than half of its length beyond mandible, 7.0–8.0 in head. Eye 4.5–5.4. Postorbital part of head 1.4–1.6 in head. Maxillary slightly expanded, scarcely pointed, reaching nearly or quite to joint of mandible, 1.2–1.3 in head. Mandible 1.27–1.4. Cheek in large examples much longer than snout and eye, proportionately shorter in small specimens, its posterior angle about 35°. Gill rakers at angle fully half of length of eye.

Dorsal fin with the longest rays extending nearly or quite to tip of last ray if deflexed, its origin much nearer to base of caudal than to eye. Anal base 3.8–4.0 in SL, its origin slightly in advance of middle of dorsal base. Pelvic failing to reach halfway to anal in adults, extending farther back in young, inserted nearer to pectoral base than to anal origin. Pectoral scarcely reaching pelvic in adults, rather longer in young, 1.25–1.5 in head. Axillary scale of pectoral about 67% of length of fin, 2.3–2.7 in head.

Color. Old specimens, in alcohol, grayish above. Side of head and lower 66% of body bright silvery. Small specimens with a broad silvery lateral band and a dark vertebral band. The original description mentioned "an oblong blackish patch on lower half of the end of the tail," but such a blackish patch is not present on the specimens studied.

Size. A total length of at least 185 mm (7.4 in.) is attained.

Development. The juvenile, as in other herring and herring-like fishes, is more slender but rounder than the adult. All juveniles show externally the convoluted intestine, which apparently has not become fully covered by the abdominal wall. The snout is very short and blunt, and in the smallest specimen it scarcely projects beyond the tip of the mandible. The blunt maxillary extends little beyond the posterior margin of the eye. Both anal fin and vent move forward with age; the anal fin has its origin under the posterior rays of the dorsal in a 21-mm specimen, about under the middle of the dorsal base in a 31-mm fish, and in advance of the middle of the dorsal, as in the adult, in a 35-mm fish.

The smallest fish has a dark line on the isthmus and chest, dark dots along the base of the anal, and a single continuous dark median ventral line on the caudal peduncle. The dark line on the isthmus and chest disappears at a length of about 30 mm, but the markings at the base of the anal and on the peduncle remain until a length of at least 52 mm is attained. The dark vertebral band, described for larger fish, first becomes partially evident at a length of about 32 mm. There is no indication of a silvery lateral band up to a length of 52 mm.

Range and Habitat. This species is known from Rio Apure (a tributary of the Orinoco) at San Fernando de Apure, Venezuela; in Brazil it has been taken from the Pará River, from Teffé on the Solimões River, and from the Jutahy River, the last two streams being tributaries of the Amazon.

Synonyms and References:

Engraulis batesii Günther, Cat. Fish. Brit. Mus., 7, 1868: 399 (orig. descr.; type local. Pará R., Brazil; types in BMNH).

Lycengraulis batesii Jordan and Seale, Bull. Mus. comp. Zool. Harv., 67, 1926: 385 (descr. not based on *batesii* throughout; 21 gill rakers on lower limb given whereas *batesii* has only 12–15; Rio Grande, Teffé, Jutahy [River] and Doce R., all in Brazil; Rio Grande specimen is *olidus*, the Doce R. specimen *schroederi*); von Ihering, Rev. Industr. Anim., Anno 1 (3), 1930: 233 (locals., diagn.); Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 148, fig. 67 (descr., range); Schultz, Proc. U. S. nat. Mus., *99*, 1949: 51 (ref.).

Negative Reference:

Lycengraulis batesii Starks, Stanf. Univ. Publ., Univ. Ser., 1913: 11 (specimen from market at Pará, Brazil, is *L. barbouri* Hildebrand).

Lycengraulis abbotti (Fowler) 1915

Figure 57

Study Material. The type and only specimen known, 180 mm long, from Port-of-Spain, Trinidad.

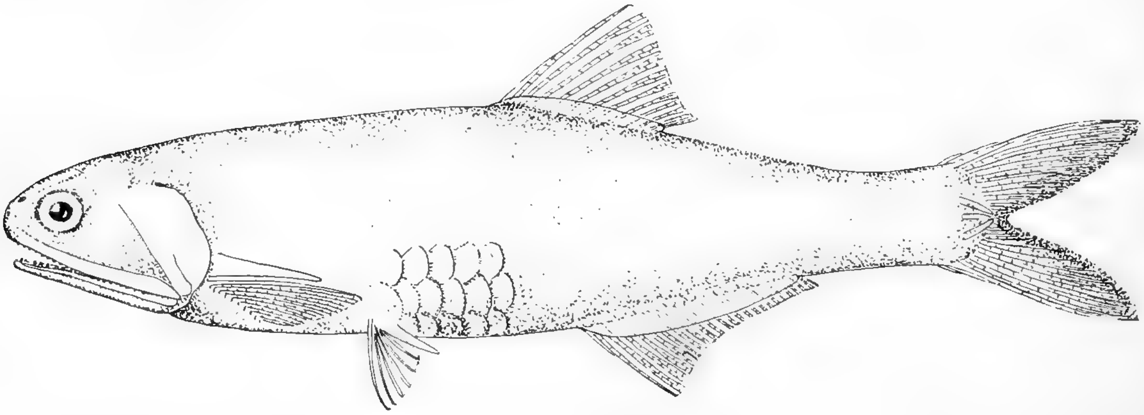

Figure 57. *Lycengraulis abbotti*, type specimen, 180 mm TL, from Port-of-Spain, Trinidad, modified after Fowler, (1915: 523, fig. 1), ANSP 45079. Drawn by Alice C. Mullen.

Distinctive Characters. This fish is related to *L. barbouri*, having similar short spiny gill rakers, but it differs in the number of gill rakers, the longer and more pointed maxillary, and the more anterior position of the dorsal fin.

Description. Proportional dimensions in per cent of standard length, and counts, based on the type, 180 mm TL.

Body: depth 27.
Head: length 23.5.
Snout: length 3.37.
Eye: diameter 4.95.
Postorbital: distance 14.8.
Maxillary: length 21.
Mandible: length 18.3.

Anal fin: length of base 25.6.
Pectoral fin: length 18.2.

Scales: *ca.* 37.
Gill rakers: 12 + 16 and 11 + 17, including rudiments.
Fin rays: dorsal 13; anal 25; pectoral 16.

Body fairly robust, its depth 3.7 in SL. Head 4.25 in SL, its depth scarcely less than its length without snout. Snout projecting less than half of its length beyond mandible, 7.0 in head. Eye 4.8. Postorbital part of head 1.6 in head. Maxillary pointed, extending nearly to margin of opercle, 1.13 in head. Mandible 1.3. Cheek much longer than snout and eye, its posterior angle about 30°. Gill rakers short, broad, very spinose, partly rudimentary, none exceeding half of diameter of pupil.

Dorsal fin with the longest rays not quite reaching tip of last ray if deflexed, its origin equidistant between base of caudal and middle of eye. Anal origin slightly in advance of middle of dorsal base, its base 3.9 in SL. Pelvic reaching less than halfway to anal, inserted nearer to base of pectoral than to origin of anal. Pectoral not quite reaching base of pelvic, 1.3 in head. Axillary scale of pectoral fully 75% of fin, 1.8 in head.

Color. Grayish above. Sides silvery. No lateral band. Caudal with a narrow dark margin.

Range. Known only from the type taken at Port-of-Spain, Trinidad.

Synonyms and References:

Anchovia abbotti Fowler, Proc. Acad. nat. Sci. Philad., 1915: 522, fig. 1 (orig. descr.; type local. Port-of-Spain, Trinidad; type ANSP 45079; cf. *Stolephorus surinamensis* Bleeker = *Engraulis edentulus* Cuvier).

Anchoviella abbotti Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 50 (name, local.).

Lycengraulis abbotti Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 150, fig. 68 (cf. *L. barbouri* Hildebrand and *L. schroederi* Hildebrand).

Lycengraulis barbouri Hildebrand 1943

Figure 58

Study Material. Type material, 3 specimens 237, 230, and 205 mm long, from the Rio Poty, Brazil, and a fourth specimen, 220 mm long, from the fish market at Pará; holotype and one paratype, MCZ 35277 and 18017, respectively; second paratype USNM 118997; and fourth specimen SU 22086.

Distinctive Characters. This species differs from *L. batesii* in having a deeper body, a somewhat more posteriorly placed anal fin, and much shorter and broader gill rakers; however, the rakers are about equal in number in the two species. *L. schroederi* Hildebrand, known only from Rio Doce in southern Brazil, is another related species; it has more numerous but equally short, broad, spiny, partly rudimentary gill rakers (17 or 18 + 21 or 22 on the first arch), a larger eye, about 4.9 in head, and a more posteriorly placed anal, its origin under the posterior third of dorsal base.

Description. Proportional dimensions in per cent of standard length, and counts, based on the four study specimens, 205–237 mm.

Body: depth 21.2–23.2.
Head: length 22–25.5.
Snout: length 2.75–3.0.
Eye: diameter 4.25–4.45.
Postorbital: distance 14.5–17.7.
Maxillary: length 18.2–21.
Mandible: length 17.5–20.8.

Anal fin: length of base 24.3–26.2.
Pectoral fin: length 17–18.2.

Scales: *ca.* 40–45.
Gill rakers: 9–11 + 12–14.
Fin rays: dorsal 14 or 15; anal 26–28; pectoral 14 or 15.

Body rather strongly compressed, its depth 4.3–4.7 in SL. Head 3.9–4.5 in SL, its depth about equal to its postorbital length. Snout projecting much less than half of its length beyond mandible, 7.8–9.2 in head. EYE 5.0–5.8. POSTORBITAL part of head 1.37–1.5 in head. MAXILLARY rounded distally, scarcely reaching joint of mandible, 1.2 in head. MANDIBLE 1.2–1.27. CHEEK narrow, its length nearly twice snout and eye, its postorbital angle about 30°. GILL RAKERS short, flat, the longest not more than half of length of pupil.

DORSAL fin with the longest rays extending to, or a little beyond, tip of last ray if deflexed, its origin about equidistant between base of caudal and upper anterior angle of gill openings. ANAL with a rather prominent lobe anteriorly, its origin under, or somewhat in advance of, middle of dorsal base, its base 3.8–4.1 in SL. PELVIC reaching much less than halfway to anal, inserted somewhat nearer to base of pectoral than to origin of anal. PECTORAL reaching to, or slightly beyond, base of pelvic, 1.3–1.4 in head. AXILLARY SCALE of pectoral about 75% of length of fin, 1.95–2.1 in head.

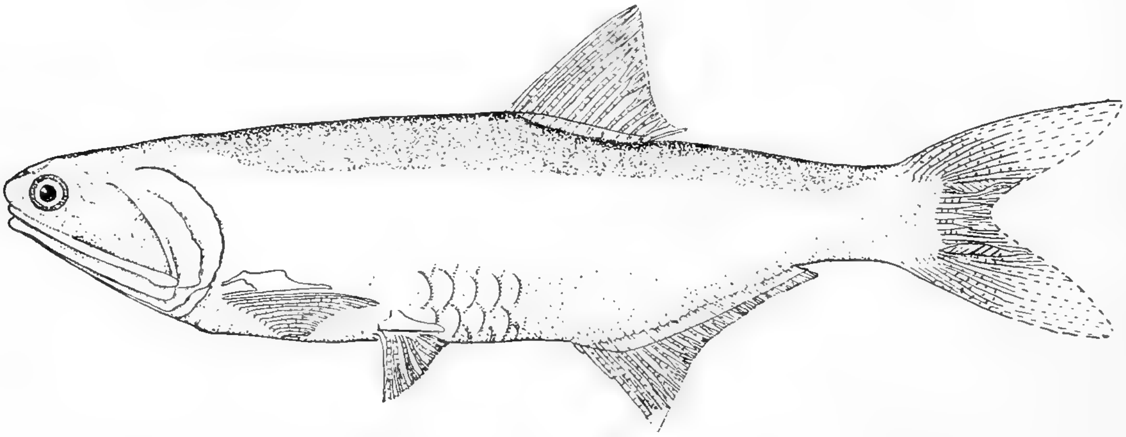

FIGURE 58. *Lycengraulis barbouri,* type specimen, 290 mm TL, 237 mm SL, from Rio Poty, Brazil, MCZ 35277. Drawn by Alice C. Mullen.

Color. Old specimens, in alcohol, grayish above. Lower 75% of body and head plain silvery. Fins unmarked, except for an indication of a black margin on caudal.

Range and Habitat. Known only from northern Brazil, from the Rio Poty, a tributary of the Rio Parnahyba, and from the Belém (Pará) market. [That this species was obtained in the Belém market, far removed from Rio Poty, seems to indicate that the species may well be marine.—Y. H. O.]

Synonyms and References:

Lycengraulis batesii Starks (not of Günther), Stanf. Univ. Publ., Univ. Ser., 1913: 11 (specimen from Pará, Brazil; found to be *L. barbouri*).

Lycengraulis grossidens Jordan and Seale (in part not of Cuvier), Bull. Mus. comp. Zool. Harv., *67*, 1926: 383 ("Rio Puty"= Rio Poty, Brazil; specimens are *L. barbouri*).

Lycengraulis barbouri Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 151, fig. 69 (orig. descr.; type local. Rio Poty, tributary of Rio Parnahyba, Brazil; type MCZ 35277; cf. *L. batesii*).

Genus *Cetengraulis* Günther 1868

Cetengraulis Günther, Cat. Fish. Brit. Mus., 7, 1868: 383; genotype *Engraulis edentulus* Cuvier, first designated by Jordan and Evermann, Bull. U. S. Nat. Mus., 47 (1), 1896: 450.

Characters. Body rather deep in adults but much more slender in young, quite strongly compressed. Maxillary short, distally rounded or very bluntly pointed, usually extending about to articulation of mandible. Teeth in jaws all very small (apparently not disappearing with age as has been stated). Gill rakers long, close-set, numerous, increasing with age (about 25 on lower limb in small specimens to about 60 in large ones). Pelvic inserted under, or a little in advance of, dorsal origin. Silvery lateral band present only in specimens about 100 mm TL or less.

Remarks. Gill covers connected across the isthmus by a thin transparent membrane (easily torn); narrow in very young.

Range. The genus is represented on the Atlantic side by two species, ranging from the West Indies to southern Brazil, and on the Pacific side by one species, *C. mysticetus*, known from the Gulf of California to Peru.

Key to Atlantic Species

1a. Depth of body 3.0–3.4 in length; head 4.6–5.3; eye 3.7–4.6 in head; pectoral failing to reach base of pelvic. *edentulus* (Cuvier) 1829, below.
1b. Depth of body 5.0 in length; head 3.5; eye 5.5 in head; pectoral reaching a little beyond base of pelvic. *juruensis* Boulenger 1898, p. 247.

Cetengraulis edentulus (Cuvier) 1829

Bocón (Cuba)

Figure 59

Study Material. About 70 specimens, mostly small, 35–160 mm TL; from Puerto Rico; Jamaica; Cuba; and New Grenada; Colón, Panama; Gulf of Venezuela; Rio de Janeiro, "Barro Santas," "Sambaia," and Cachoeira, Brazil.

Distinctive Characters. See Key to Atlantic Species, above.

Description. Proportional dimensions in per cent of standard length, based on 20 specimens, 70–160 mm, and most of the counts on many more.

Body: depth 25–34.4.
Head: length 30–34.5.
Snout: length 3.8–4.75.
Eye: diameter 6.5–8.0.
Postorbital: distance 18.2–21.2.
Maxillary: length 17.2–19.
Mandible: length 17.3–18.5.
Anal fin: length of base 21.5–23.
Pectoral fin: length 13.3–16.7.
Scales: *ca.* 40–43.
Gill rakers: *ca.* 30 + 36 in specimens around 65 mm, about 52 + 55 in specimens about 130 mm TL.
Fin rays: dorsal 14–16; anal 23–26; pectoral 14 or 15.
Vertebrae: 42 (3 specimens).

BODY strongly compressed, the ventral outline much more strongly convex than the dorsal outline, the depth increasing with age, 2.9–3.3 in SL in specimens 75 mm TL and upward. HEAD 3.0–3.5 in SL. SNOUT quite pointed, extending nearly its full length beyond mandible, 5.5–8.0 in head. EYE 3.7–4.8. POSTORBITAL part of head 1.55–1.75 in head. MAXILLARY bluntly pointed or rounded distally, 1.72–1.8 in head. MANDIBLE 1.67–1.73. CHEEK nearly or quite as long as snout and eye, its posterior angle narrow, about 30°. GILL RAKERS long, slender, close-set, increasing greatly in number with age.

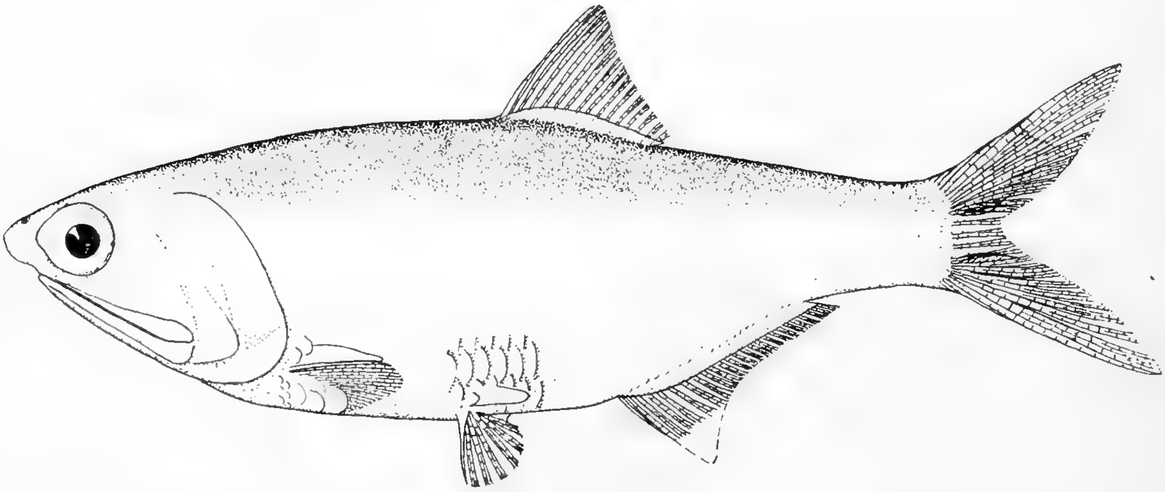

FIGURE 59. *Cetengraulis edentulus,* 120 mm TL, 100 mm SL, from Havana, Cuba, USNM 35159. Drawn by Louella E. Cable.

DORSAL fin with the longest rays failing to reach tip of last ray if deflexed, its origin generally about equidistant between anterior margin of eye and caudal base. ANAL with origin usually under last fourth of dorsal base, its base 4.3–4.6 in SL. PELVIC inserted nearer to anal origin than to pectoral base, generally reaching fully halfway to origin of anal. PECTORAL usually failing to reach base of pelvic, 1.9–2.3 in head. AXILLARY SCALE of pectoral broad, with a somewhat thickened ventral edge, 3.25–3.7 in head.

Color. In alcohol, bluish gray above; lower 75% of side silvery. Small specimens with a silvery lateral band, becoming wider and less distinct with age, generally disappearing at a length of about 100 mm.

Size. Specimens as much as 165 mm (6.6 in.) TL have been reported.

Range and Habitat. Reported for the West Indies and the Atlantic coast of Panama to southern Brazil. It ascends freshwater streams.

Synonyms and References:

Engraulis edentulus Cuvier, Règne Anim., ed. 2, 2, 1829: 323 (orig. descr.; type local. Jamaica); Cuvier and Valenciennes, Hist. Nat. Poiss., *21*, 1848: 51 (descr., abund., distr.).

Cetengraulis edentulus Günther, Cat. Fish. Brit. Mus., 7, 1868: 383 (descr., range); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 450 (descr., range, synon.); Meek and Hildebrand, Field Mus.

Publ., Zool., *15* (1), 1923: 214 (descr., range; *Stolephorus garmani* Evermann and Marsh and *S. gilberti* Evermann and Marsh put in synon.); Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67*, 1926: 414 (descr., Cuba and Brazil); Beebe and Tee-Van, Zoologica, N. Y., *10* (1), 1928: 49, fig. (descr., Port-au-Prince, Haiti); Nichols, N. Y. Acad. Sci., *10* (2), 1929: 206, fig. (synon., diagn., Puerto Rico); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 51 (range, synon.); Fowler, Proc. Acad. nat. Sci. Philad., *80*, 1931: 393 (Trinidad, B.W.I.); Beebe and Hollister, Zoologica, N. Y., *19* (6), 1935: 211 (Union I., B.W.I.); Fowler, Arqu. Zool. estad. São Paulo, *3* (6), 1941: 135 (Brazilian recs.); Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 155, fig. 71 (descr., synon., range); Schultz, Proc. U. S. nat. Mus., *99*, 1949: 54 (refs.).

Engraulis brevis Poey, Repert. Fisico-Nat. Cuba, *1*, 1866: 379 (orig. descr.; type local. Cuba; cf. *E. edentulus* Cuvier); Howell-Rivero, Bull. Mus. comp. Zool. Harv., *82*, 1838: 172 (holotype, MCZ 24296, Poey's No. 716).

Stolephorus robertsi Jordan and Rutter, Proc. Acad. nat. Sci. Philad., *49*, 1897: 95 (orig. descr.; type local. Jamaica; type SU 4853; cf. *Stolephorus opercularis* Jordan and Gilbert, a Pacific coast *Cetengraulis*); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (3), 1898: 2815 (descr. after Jordan and Rutter).

Stolephorus gilberti Evermann and Marsh, Rep. U. S. Comm. Fish. (1899), 1900: 352 (orig. descr.; type local. Palo Seco, Puerto Rico; type USNM 49359; cf. *Engraulis productus* Poey = *Engraulis clupeoides* Swainson and *Stolephorus garmani* E. and M. = *Engraulis edentulus* Cuvier); and Bull. U. S. Fish Comm. (1900), *20* (1), 1902: 90, fig. 15 (orig. descr.); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (4), 1900: 3146 (descr. after Evermann and Marsh).

Stolephorus garmani Evermann and Marsh, Rep. U. S. Comm. Fish. (1899), 1900: 352 (orig. descr.; type local. Puerto Real, Puerto Rico; type USNM 49360; cf. *Engraulis productus* Poey = *Engraulis clupeoides* Swainson, and *Stolephorus gilberti* E. and M. = *Engraulis edentulus* Cuvier); and Bull. U. S. Fish Comm. (1900), *20* (1), 1902: 89, fig. 14 (orig. descr.); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (4), 1900: 3146 (descr. after Evermann and Marsh).

Anchoviella robertsi Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 49 (range, synon.).

Cetengraulis gilberti Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 51 (range, synon.); Howell-Rivero, Proc. Boston Soc. nat. Hist., *41* (4), 1936: 55 (Cuba).

Cetengraulis garmani Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 51 (range, synon.).

Doubtful References:

Stolephorus surinamensis Bleeker, Tijd. Dierk. Amst. (1865) *3*, 1866: 178 (orig. descr. of 96-mm specimen; type local. Surinam; nothing in descr. inconsistent with *C. edentulus* of similar size); Eigenmann, Mem. Carneg. Mus., *5*, 1912: 448 (descr. of 27- and 37-mm specimens from Bartica Rocks, British Guiana); Puyo, Bull. Soc. Hist. nat. Toulouse, *80*, 1945: 103, fig. 2 (descr., French Guiana); Puyo, Faune Emp. Franç., 12, Poiss. Guyane Franç., 1949: 155, fig. 78 (descr., French Guiana).

Stolephorus manjuba Miranda-Ribeiro, Kosmos, Rio de J., Feb., 1908, 5—no pagination (orig. descr. inadequate; type local., Rio de Janeiro, Brazil).

Anchovia gilberti Fowler, Proc. Acad. nat. Sci. Philad., 1916: 401 (Colón, Panama, without comment).

Anchoviella surinamensis Fowler, Proc. Acad. nat. Sci. Philad., *80*, 1931: 392 (three specimens, 34–36 mm long, from Icacos Beach, Trinidad, B.W.I.; notes suggest *C. edentulus*).

Cetengraulis juruensis Boulenger 1898

Study Material. None.

Distinctive Characters. See Key to Atlantic Species, p. 245.

Description. Based on original description and figure, which is all that is known. Body depth 20 % of SL. Head 28.5 in SL. Snout projecting strongly (extending nearly its full length beyond mandible, according to a published figure). Eye 5.5 in head. Maxillary extending to joint of mandible. Gill rakers long, finely denticulate, about 40 on lower limb.

DORSAL origin equidistant between tip of snout and caudal base; 13 rays. ANAL origin under posterior rays of dorsal; rays 23. PELVIC fin inserted somewhat nearer to base of pectoral than to origin of anal. PECTORAL extending a little beyond base of pelvic, its length a little more than half of length of head. AXILLARY SCALE of pectoral extending somewhat beyond midlength of fin (according to figure). SCALES 38.

Color. Olive above, silvery on sides and below. Snout blackish above. Fins pale orange; caudal rays blackish at tips.

Range and Habitat. Known only from the holotype, a specimen 140 mm TL, from fresh water, from the Juruá River, a tributary of the Amazon in Brazil.

References:

Cetengraulis juruensis Boulenger, Trans. zool. Soc. London, *14* (10), 1898: 427, pl. 41, fig. 3 (orig. descr.; type local. Rio Juruá, Brazil; cf. *C. edentulus*); Eigenmann, Rep. Princeton Exped. Patagonia, 1896–1899, *3* (4), 1910: 452 (refs. to orig. descr., habitat); Campos, Arqu. Zool. estad. São Paulo, *3* (7), 1941: 202, fig. 15 (descr., range); Hildebrand, Bull. Bingham oceanogr. Coll., *8* (2), 1943: 158 (descr. after Boulenger).

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2. Fowler, Proc. Acad. nat. Sci. Philad., *83*, 1931.

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Interim Account of *Family* Alepocephalidae

HENRY B. BIGELOW

Museum of Comparative Zoology
Harvard University

Characters. Essentially as in the Clupeidae, except with the DORSAL fin considerably posterior to the midlength of body, its base partly or entirely over anal fin and preceded in a few (*Anomalopterus*) by a fleshy fold or ridge. LATERAL LINE present in most (described as indistinct or lacking in *Xenodermichthys*, *Leptoderma*, and *Anomalopterichthys*). SWIM BLADDER lacking. COLOR ranging between dark blue, purple, and black, below as well as above; transparent but never silvery. BARBELS lacking on chin and throat. BONY GULAR PLATE absent in throat region. EXTERNAL TUBULAR PAPILLA absent on shoulders (present in Searsiidae, p. 254). ABDOMEN rounded, its midline without keeled scales (scutes). SNOUT less than twice the length of mouth in most, not tubular, but tubular and more than twice the mouth in a few (*Aulostomatophora*). MOUTH ranging from very small, at tip of tubular snout (see above), to a little more than half as long as head (*Anomalopterus* and *Bathytroctes*). PECTORAL fins very small; rudimentary in a few (*Mirognathus*). PELVIC fins present, at least in most. TEETH small, feeble, present on premaxillaries in most (upper jaw toothless in *Anomalopterichthys*, *Leptochilichthys*, and *Asquamiceps*), and on maxillaries, palatines, and mandible in some. SCALES present or absent; if present, thin, rounded. LUMINESCENT ORGANS (photophores) lacking in most but present in a few; situated on nodules of raised skin if present. VENT posterior to midlength of trunk in most (anterior to midlength of trunk in *Leptoderma*). GILL MEMBRANES free from isthmus and overlapping. OPERCULAR SYSTEM thin but complete. GILL RAKERS long, numerous. BRANCHIOSTEGAL RAYS 5 or more. PYLORIC CAECA 2–21 reported (rudimentary in some).

Genera. Parr, in his recent synopsis of the family, recognized 22 genera, six of which were described by him as new (*4*: 1–14); to these he added two more new genera a year later (*5*: 263, 265).

Remarks. The Alepocephalidae differ externally from the true herrings (Clupeidae) in their very soft texture, in their uniformly dark, dull coloration (below as well as above), and in the position far rearward of their dorsal fin. They differ internally from the herrings in lacking a swim bladder.

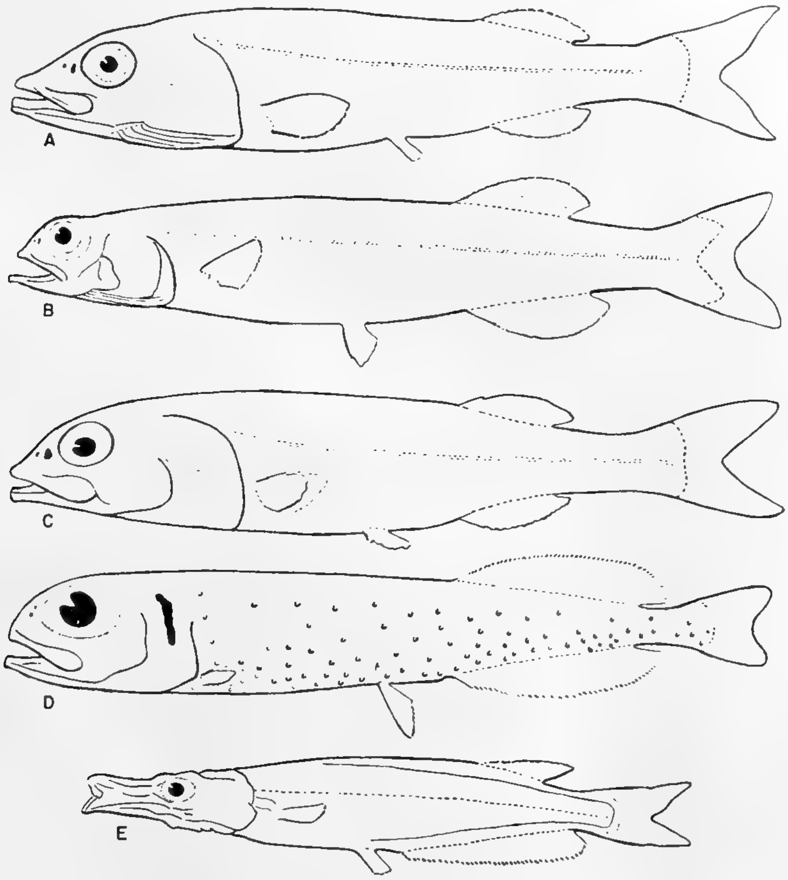

FIGURE 60. A. *Alepocephalus productus,* from ALBATROSS St. 2030, off New Jersey, 39°30′N, 71°43′W, in 588 fms.; after Goode and Bean. B. *Alepocephalus bairdii,* from Grand Banks off Newfoundland, at 200 fms.; after Goode and Bean. C. *Alepocephalus agassizii,* from off New Jersey; after Goode and Bean. D. *Xenodermichthys copei,* from off Chesapeake Bay; after Goode and Bean. E. *Aulostomatophora phosphorops,* from the Arabian Sea; after Goode and Bean, based on Alcock.

The members of the family as a whole are creatures of the deep sea, seldom taken in depths less than 250 fms. or so; a cursory examination of the literature revealed only two records for shallower depths—200 fms. for the Grand Banks off Newfoundland for *Alepocephalus bairdii* (*1*: 55) and 180 fms. north of Celebes for *Bathytroctes macrolepis* (*3*: 225). The alepocephalids can be described as "universal" in all oceans, down the lower part of the slopes and on the ocean floors at depths to at least 3000 fms. (5490 m) or so, and very likely deeper still.

Table I. Hauls from off Southern Nova Scotia to Virginia Containing Alepocephalids

Depth (fms.)	Total Hauls	Hauls with Alepocephalids	% of Hauls with Alepocephalids	Av. no. Specimens in Hauls with Alepocephalids
50–250	76	0	0	0
251–300	18	1	6	1
301–350	22	4	18	16
351–400	15	6	40	7
401–450	21	8	38	8
451–500	21	13	62	19
501–550	8	8	100	12
551–600	4	4	100	6
601–650	4	4	100	13
651–700	2	2	100	8
701–750	2	2	100	9

During the experimental cruises that were carried out from the Woods Hole Oceanographic Institution by Mr. William C. Schroeder on the dragger CAPN. BILL II in 1952–1953 along the continental slope of North America between the offings of southern Nova Scotia and Virginia, the shallowest haul that brought up an alepocephalid was at 251–350 fms.[1] Alepocephalids, however, of one kind or another were taken in more than a third of the hauls from deeper than 351–400 fms. and in all of the hauls from deeper than 500 fms., as shown in Table 1, contributed by Mr. Schroeder.

A detailed account of the family is unavoidably postponed until a subsequent volume. The general appearance of typical members is represented in the accompanying outline drawings (Fig. 60, 61 A).

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[1] A depth of "68" fms. given by Goode and Bean for *Concara macroptera* should read 687 fms. (*2*: 40); see Townsend (*6*: 403).

TEXT AND FOOTNOTE REFERENCES

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6. Townsend, Rep. U. S. Comm. Fish., 1901.

Interim Account of *Family* Searsiidae

HENRY B. BIGELOW
Museum of Comparative Zoology
Harvard University

Characters. Essentially as in the Alepocephalidae, except that there is a voluminous sac extending forward underneath the skin of each shoulder and opening rearward through a TUBULAR PAPILLA so conspicuous that it affords a convenient and reliable field mark by which a member of this family can be recognized. This shoulder apparatus appears to be a secretory organ, probably producing luminous mucus. PELVIC fins are wanting in a few (*Platytroctes*).

Remarks. The type genus *Searsia* was described by Parr in 1937 (1:12), but it was not until 1951 (2:2) that he proposed and defined the family Searsiidae to include the genera *Searsia* Parr 1937, *Platytroctes* Günther 1878, *Platytroctegen* Lloyd 1909, *Holtbyrnia* Parr 1937, *Barbantus* Parr 1951, *Normichthys* Parr 1951, *Pellisolus* Parr 1951, and *Persparsia* Parr 1956. [As this paper goes to press, Parr's recent extensive and complete monograph of the known Searsiidae is at hand (3). To the genera already listed above, he has added *Mirorictus* Parr 1947, *Sagamichthys* Parr 1953, *Maulisia* Parr 1960, and *Mentodus* Parr 1951, with *Mirorictus* in the subfamily Mirorictinae, *Platytroctes* and *Platytroctegen* in the subfamily Platytroctinae, and all the other genera in the subfamily Searsinae.—Y.H.O.]

The Searsiidae, like the Alepocephalidae (p. 250), are deep-sea fish, thus far reported in the western North Atlantic for the offing of Delaware Bay; the Caribbean; the offing of Pernambuco, equatorial Brazil; and the vicinity of Bermuda; also for the middle and eastern Atlantic off northwestern Africa, Cape Verde, and the Gulf of Gascony; the offing of southern Africa in the eastern South Atlantic; the Bay of Bengal; and the eastern equatorial Pacific off the Bay of Panama. The shallowest haul from which any searsiid has yet been reported was from 500 fms., in the Bay of Bengal.

The detailed account of the Searsiidae, like that of the Alepocephalidae (p. 250), is unavoidably postponed until a subsequent volume. The general appearance of a member of the Alepocephalidae (Fig. 61 A) and two of the included genera in Searsiidae (Fig. 61 B, C) are shown in the accompanying outline drawings.

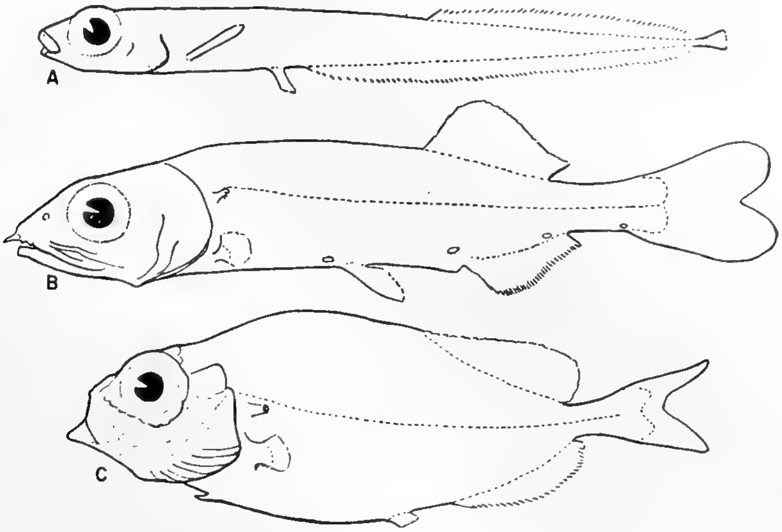

FIGURE 61. A. *Leptoderma macrops* (Alepocephalidae), from off northwestern Africa; after Goode and Bean, based on Vaillant. B. *Searsia koefoedi*, from off the Bahamas; after Parr. C. *Platytroctegen mirus*, from the Bay of Bengal; after Lloyd.

TEXT REFERENCES

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Family Clupeidae[1]

SAMUEL F. HILDEBRAND[2]

excepting

Genus *Harengula* by Luis R. Rivas
Genus *Dorosoma* by Robert R. Miller

Characters. BODY usually slender in most but short and deep in a few species; slightly to excessively compressed in most but almost round in some. SCALES covering body; cycloid, serrate, or pectinate; head naked. Chest and abdomen compressed into a sharp edge, armed with BONY SCUTES, except in the Dussumierinae (see 1a in Key to Genera). LATERAL LINE wanting. MOUTH moderately large, terminal, superior or inferior. TEETH in jaws small, or canine-like in Chirocentrinae (see 11b in Key to Genera), sometimes wanting in large adults of *Alosa*. GILL RAKERS usually long, slender, numerous, increasing in number with age and growth in some species, in moderate numbers in others. GILL MEMBRANES not united, free from the isthmus. PSEUDOBRANCHIAE present. DORSAL fin, if present, usually about at midlength of the standard length, but sometimes posterior (present in American species). ADIPOSE fin absent. CAUDAL fin forked. ANAL moderately long to very long. PELVIC fin moderately large, small, or absent. PECTORAL fin well developed. VERTEBRAE in species of the western North Atlantic about 39–59.

Remarks. This large family, composed of about 70 genera and perhaps 150 or more species, of which 16 genera and 36 species come within the scope of this work, is economically one of the most important groups of fishes in the world. Many of the species occur in great schools, making it easy for either man or natural predators to

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[1] Edited, with some revision and expansion, by George S. Myers, Henry B. Bigelow, Mywanwy M. Dick, and Yngve H. Olsen.
Some of the subfamilies recognized herein, particularly the Dussumierinae and Dorosomatinae, have been treated as separate families in some recent works. Nevertheless their affinities are with the Clupeidae. For practical purposes, therefore, the characters of the subfamilies have been sufficiently indicated in the Key to Genera (p. 259) for the major subdivisions to be recognized without further treatment elsewhere.

[2] August 15, 1883 – March 16, 1949.

catch them in large quantities; and the supply of some, such as those of the genus *Clupea*, seems to be almost inexhaustible. Fresh herring are used extensively as food by man in nearly all parts of the world, and in many areas large quantities are eaten after they have been salted and smoked or canned. Great quantities, especially of *Brevoortia*, are reduced to oil, fish meal (feed for livestock and poultry), and fertilizer. The smaller species and the young of the larger ones serve still another useful purpose in providing extensive forage for larger predatory fishes, many of which enter into the diet of man. Aquatic mammals, birds, and turtles also feed on them. All this food is provided for man and beast at virtually no cost, as the herring feed almost entirely on small organisms that are not suitable food for man or for the other predators named.

Although the members of the family Clupeidae have no lateral line, nearly all of the species described in this work have numerous mucous pores and canals about the head and shoulders that may in part compensate for the absence of a lateral line. An air bladder with a very thin wall is present in all the species of the genera examined, namely *Clupea*, *Alosa*, *Pomolobus*, *Brevoortia*, *Opisthonema*, *Harengula*, *Sardinella*, and *Etrumeus*, and it may be assumed that the other members of the family also have an air bladder. Its walls are so thin and delicate that dissections must be made with care to find it undamaged.

Range. Herring (Clupeidae) occur in all seas of the world except those of the Arctic and Antarctic regions. Many species ascend freshwater streams to spawn, and others live in fresh water permanently.

Preparation of Descriptions and Location of Study Material. Nearly all *Descriptions* were prepared directly from specimens, but a few are included for which no specimens were available. In such instances it is stated in the accounts that they were compiled or quoted from publications. The specimens used are in the USNM unless otherwise stated. Freshwater species occurring in the rivers draining into the western North Atlantic are not numerous and have been included for the sake of completeness; it is possible that all of these forms occasionally enter brackish or salt water.

Measurements and Counts. The proportions used in *Description* are based on measurements made with vernier calipers having sharp straight points. Many of the measurements of small fish (sometimes even of larger ones) and of the small structures such as eye, snout, and maxillary were made under magnification. See also Measurements and Counts under *Brevoortia*, p. 343.

TOTAL LENGTH: distance between margin of snout or tip of lower jaw (whichever is longer), more or less along the body axis to a vertical at tip of longest lobe of caudal fin.

STANDARD LENGTH: distance between anterior margin of snout and base of caudal.

BODY DEPTH: greatest depth unless otherwise stated; this may occur over base of pectoral or as far back as origin of dorsal fin.

HEAD: if used without a modifier, the distance between anterior margin of snout and most distal point of bony (not membranous) margin of opercle.

Head depth: distance from a slight crossgroove at the occiput, between the naked head and scaly body, to margin of first ventral scute; this line may be vertical or may slope somewhat backward from the occipital crossgroove.

Snout: distance from anterior margin of snout to anterior margin of orbit.

Eye: horizontal diameter of eyeball, not of orbit.

Maxillary: distance from anterior rim of snout to maxillary's posterior margin.

Mandible: distance from its tip to its joint.

Interorbital: width of bone over or between middle of eyes.

Cheek: the bone, usually with a glossy surface in the herrings, lying below and usually somewhat behind the eye, its depth measured from lower rim of orbit to its lowest or deepest point.

Predorsal length: distance between anterior margin of snout and origin of dorsal.

Caudal lobes: distance from midbase of this fin to tip of lobe.

Pelvic and Pectoral fins: distance from base of outer or upper ray to tip of fin.

Fin ray count: includes all rays, whether rudimentary, simple, or branched; the last ray, even though nearly double, counted as one.

Scales: range in scale numbers, e.g. 56–62, obtained by counting the oblique rows (upward and slightly forward) that cross the side between upper anterior angle of gill opening and base of caudal; any deviation from that procedure is stated.

Gill rakers: number present on first gill arch, including rudiments if present; all enumerations based on adult fish unless stated otherwise.

Ventral scutes: three sets of counts are given: the range of the total number present, the number in front of the pelvic fins, and the number behind these fins; the scute ending nearest to the insertion of the pelvics is included in the number in advance of these fins; the rest compose the number behind.

Vertebrae: total number, including the hypural.

Key to Western North Atlantic Subfamilies and Genera of Clupeidae[3]

1a. Body little compressed; abdomen rounded, covered with ordinary scales, without bony scutes. Subfamily Dussumierinae.

Atlantic coast of North America; eastern and western Pacific; southeastern coasts of Africa and Australia.

  2a. Pelvic fin much smaller than pectoral, inserted behind base of dorsal; dorsal fin with about 17–20 rays; chest round. *Etrumeus* Bleeker 1853, p. 262.

  2b. Pelvic fin nearly as large as pectoral, inserted under base of dorsal; dorsal fin with only about 9–14 rays; chest slightly keeled. *Jenkinsia* Jordan and Evermann 1896, p. 267.

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[3] This Key is drawn up simply for the ready identification of representatives of the subfamilies and genera that are known from the western North Atlantic without reference to those outside of this range. Therefore, some characters are used that apply only to the representatives described in this work and for that reason are not of generic value.

1 b. Body moderately to very strongly compressed; chest and abdomen compressed into a sharp keel armed with bony scutes.

- 3 a. Median line of back in front of dorsal fin with ordinary or modified scales, thus without a prominent median naked strip; stomach not gizzard-like, but wall somewhat thickened in some species.
  - 4 a. Pelvic fin well developed, inserted under base of dorsal, with 7–9 rays; mouth gently oblique, the lower jaw usually included but occasionally projecting; body moderately compressed. Subfamily Clupeinae. Virtually all temperate and tropical waters of the world, with some species entering frigid zones; inhabiting salt, brackish, and fresh water.
    - 5 a. Vertical edge on rim of shoulder girdle (cleithrum) underneath free edge of gill cover (opercle) smooth or even, without dermal lobes.
      - 6 a. Back in front of dorsal fin with ordinary scales like those on rest of body; pelvic with 8 or 9 rays; pectoral fin without a free axillary process; scales not overlapping deeply, their exposed part not much deeper than long, their margin slightly irregular, not definitely serrate or pectinate.
        - 7 a. Vomer with teeth; greatest depth of body about 4.0–5.0 in SL; ventral scutes weak, numerous, total number about 39–46. *Clupea* Linnaeus 1758, p. 274.
        - 7 b. Vomer toothless; depth of body generally less than 4.0 in SL; ventral scutes strong, total number about 27–38.
          - 8 a. Upper margin of lower jaw within mouth rising gently; teeth missing in examples 200 mm and upward in length; cheek deeper than long (Fig. 69). *Alosa* Link 1790, p. 293.
          - 8 b. Upper margin of lower jaw within mouth rising abruptly; teeth present, at least in lower jaw, at all ages; cheek not deeper than long, definitely longer than deep in some species (Fig. 76). *Pomolobus* Rafinesque 1820, p. 312.
      - 6 b. Back in front of dorsal fin with a row of enlarged modified scales on each side of median line; pelvic with 7 rays; pectoral fin with a free axillary process; scales overlapping deeply, their exposed part much deeper than long, their margin strongly serrate to pectinate (Fig. 85). *Brevoortia* Gill 1861, p. 342.
    - 5 b. Vertical edge on rim of shoulder girdle (cleithrum) underneath free edge of gill cover (opercle) with two dermal lobes (Fig. 100).
      - 9 a. Last ray of dorsal greatly produced, filamentous, often reaching nearly or quite to base of caudal (Fig. 94); anal with 20–25 rays. *Opisthonema* Gill 1861, p. 380.

9b. Last ray of dorsal little if any longer than the preceding ones; anal with about 15–20 rays.

10a. Last two rays of anal not enlarged; gill rakers about 25–40 on lower limb; scales about 34–41 oblique series crossing middle of side; pelvic with 8 rays.
Harengula Cuvier and Valenciennes 1847, p. 386.

10b. Last two rays of anal enlarged, finlet-like (Fig. 100); gill rakers about 70–130 on lower limb; scales about 41–47 oblique series crossing middle of side; pelvics with 9 rays.
Sardinella Cuvier and Valenciennes 1847, p. 397.

4b. Pelvic fin small or wanting, inserted in advance of dorsal fin if present; mouth strongly oblique to nearly vertical, the lower jaw projecting; body strongly to excessively compressed.

11a. Teeth in jaws all small, without canines; vomer toothless.
Subfamily Pristigasterinae.

12a. Maxillary with a short sharp spine near anterior end, just behind premaxillary (Fig. 103); anal fin small, beginning far behind base of dorsal, with only about 15–18 rays.
Rhinosardinia Eigenmann 1912, p. 411.

12b. Maxillary without a spine; anal fin much longer, beginning in front of dorsal fin, under it, or immediately behind it, with more than 30 rays.

13a. Pelvic fin present; dorsal fin moderately large, with about 15–20 rays. *Ilisha* Gray 1846, p. 415.

13b. Pelvic fin wanting; dorsal fin with about 10–15 rays.

14a. Body with chest and abdomen greatly dilated, more or less half-moon shaped (Fig. 108), its greatest depth about half of its SL; median line of back in front of dorsal fin with several short spines.
Pristigaster Cuvier 1817, p. 427.

14b. Body elongate, with chest and abdomen not greatly dilated, its greatest depth less than a third of its SL; no external spines on median line of back.

15a. Body excessively compressed; dorsal outline more or less concave over the head; a toothless membranous section between maxillary and premaxillary, the three elements forming a continuous margin; maxillary greatly produced in large adults (Fig. 111); anal fin with about 52–80 rays.
Odontognathus Lacépède 1800, p. 430.

15b. Body rather strongly but not excessively

compressed; dorsal outline convex over head; maxillary and premaxillary not separated by a membranous section; maxillary overlapping distal end of premaxillary, interrupting margin of upper jaw (Fig. 113); anal fin with only about 39–48 rays.
Neoopisthopterus Hildebrand 1948, p. 435.

11b. Teeth in jaws of unequal size, both jaws with strong canines (Fig. 115); vomer with teeth. Subfamily Chirocentrinae.
Chirocentrodon Günther 1868, p. 438.

3b. Median line of back in front of dorsal fin naked, not crossed by scales; stomach with very thick walls, like the gizzard of a fowl. Subfamily Dorosomatinae.
Dorosoma Rafinesque 1820, p. 443.

Genus *Etrumeus* Bleeker 1853

Round Herrings

Etrumeus Bleeker, Verh. Batav. Genoot., *25*, 1853: 48; genotype by monoytpy, *Clupea micropus* Temminck and Schlegel.

Generic Synonym:

Perkinsia Rosa Eigenmann, Amer. Nat., *25*, 1891: 153; type species by monotypy, *P. othonops* Rosa Eigenmann equals *Clupea micropus* Temminck and Schlegel.

Characters. BODY elongate, little compressed, especially in Atlantic species; chest and abdomen fully rounded. BONY SCUTES absent. SCALES with smooth edges, deciduous, covering chest and abdomen. SNOUT long, tapering. MOUTH terminal. MAXILLARY slender, ending about under anterior margin of eye. TEETH minute, present on jaws, vomer, palatines, pterygoids, and tongue. DORSAL fin beginning notably nearer to margin of snout than to base of caudal, with about 17–20 rays. ANAL about half as far from base of caudal as from origin of dorsal, with about 10–12 rays. PELVIC fins inserted well behind base of dorsal, with a shield of enlarged scales covering them in part, each fin with 8 rays. PECTORALS of moderate size, also shielded in part by enlarged scales, each fin with about 14–16 rays. Pelvic and pectoral each with a long AXILLARY PROCESS.

Range. Represented by one species on the Atlantic and Gulf coasts of the United States, and by two or more species in the eastern and western Pacific on the coasts of southeastern Africa and southeastern Australia.

Etrumeus sadina Mitchill 1814

Atlantic Round Herring

Figures 62, 63

Study Material. Many specimens, postlarvae to adults, 25–180 mm TL, the specimens from New Jersey northward being adults caught near or on the shore, those from off Cape Lookout, northern Florida, and the Gulf of Mexico, mostly young, taken quite a distance offshore in 5–21 fms. depth except for a lot of six small ones from Beaufort Inlet, North Carolina, taken in water only about 2–3 fms. deep.

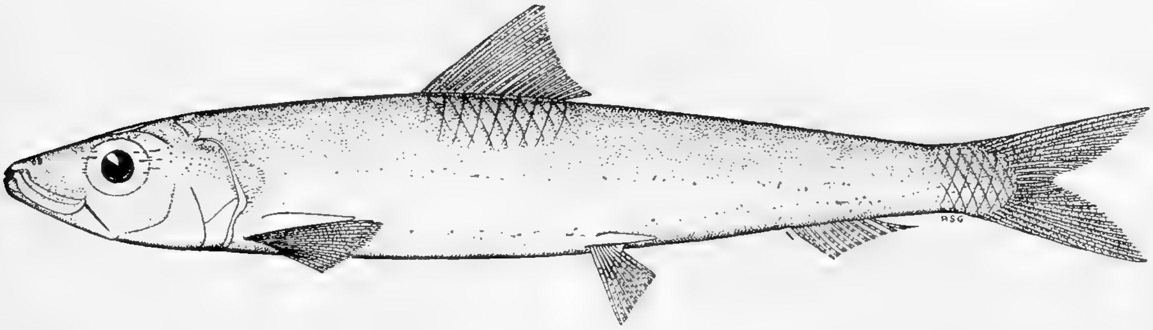

Figure 62. *Etrumeus sadina,* female, 140 mm TL, 115 mm SL, Woods Hole, Massachusetts, USNM 143574. Drawn by Ann S. Green.

Distinctive Characters. The very slender and roundish body, the roundish chest and abdomen covered with ordinary scales, the absence of bony scutes, the small anal fin situated near the base of the caudal, and the rather small pelvic fin inserted entirely behind a vertical from the base of the last dorsal ray, readily distinguish this species from other American clupeoids.

Description. Proportional dimensions in per cent of standard length, and counts, based on 22 specimens from *Study Material,* 55 mm (young adults)–180 mm TL, 45–154 mm SL.

Body: depth 16–18.5.
Caudal peduncle: depth 6.7–8.2.
Head: length 24–29.
Snout: length 6.0–9.5.
Eye: diameter 6.5–8.0.
Interorbital: width 3.0–4.4.
Maxillary: length 7.0–10.5.
Anal fin: length of base 5.6–6.9.
Pelvic fin: length 8.9–11.5.
Pectoral fin: length 14–17.

Distance from snout to origin of: dorsal 42–46.

Scales: about 48–55, usually lost in preserved specimens.
Gill rakers: 32–38 on lower limb, *ca.* 14 on upper limb.
Fin rays: dorsal 16–20, usually 18 or 19; anal 10–12, most frequently 11; pectoral 14–16.
Vertebrae: 49 (7 specimens).

Body almost round, its greatest thickness about 80 % of its depth, its greatest depth 5.4–6.25 in SL; ventral profile a little more strongly convex than dorsal profile. Caudal peduncle compressed, its depth 3.3–3.9 in head.

Scales deciduous, usually lost in preserved specimens, very thin, scarcely deeper than long, with even edges.

Head low, rather long, 3.45–4.15 in SL. Snout equal to or more usually longer than eye, tapering, 3.0–3.9 in head. Eye with much adipose tissue in adults, 3.25–4.1 in head. Interorbital bone 6.25–7.55. Maxillary obliquely rounded posteriorly, reaching about under anterior margin of eye, 2.6–3.0 in head. Mandible coterminal with snout, 1.85–2.0 in head. Gill rakers rather slender, moderately close-set, those at angle somewhat exceeding half of length of eye; apparently not increasing in number with age. Teeth small, in a single series on mandible; a few minute teeth on premaxillaries, and a row on the margin of maxillaries; very small granular teeth on vomer, palatines, pterygoids, and tongue.[4]

Dorsal fin moderately elevated anteriorly, with concave margin, its longest rays generally not reaching tip of posterior ray if deflexed, its origin about equidistant between margin of snout and vertical from middle of anal base, its distance from snout 2.15–2.4 in SL. Caudal fin forked, the lobes of about equal length, generally somewhat longer than head without snout. Anal small, rather feebly developed, placed far behind dorsal fin, a little nearer to base of caudal than to base of pelvic, its base 3.5–4.5 in head. Pelvic fin rather short and broad, with nearly straight margin, inserted a little behind vertical from base of last ray of dorsal, generally a little nearer to base of pectoral than to base of caudal, 2.3–3.0 in head; a membranous axillary process present, about 67 % of the length of fin. Pectoral fin moderately developed, reaching notably less than halfway to base of pelvic, inserted fully an eye's diameter nearer to tip of mandible than to base of pelvic, 1.5–1.8 in head; a long membranous axillary process present about 0.83 of length of fin.

Alimentary canal about half of SL. Stomach with a long blind sac and numerous pyloric caeca. Air bladder long and narrow.

Color. Fresh specimens olive green above, silvery on lower half of side and below. In old preserved specimens, back generally brownish and lower parts pale (sometimes silvery).

Size. A length of 200–250 mm (8–10 in.) is said to be attained by this species.

Development. The postlarvae and young adults are very slender, as is usual in young herrings. In postlarvae 25–28 mm TL (21–24 mm SL) the body depth is contained about 16–24 times in the SL; the jaws are weakly developed; the teeth are not evident; the snout is proportionately longer than that in adults, being 1.5–2.0 times longer than the eye; the pectoral fins are not much more than tufts of membrane; and the pelvics are incompletely developed. The larval pigment spots are still retained, chiefly in a single slightly broken dark line on the chest, in two diverging dark lines on the abdomen, in a row of dark spots along each side of the base of

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[4] To see the teeth clearly it may be necessary to dry the head.

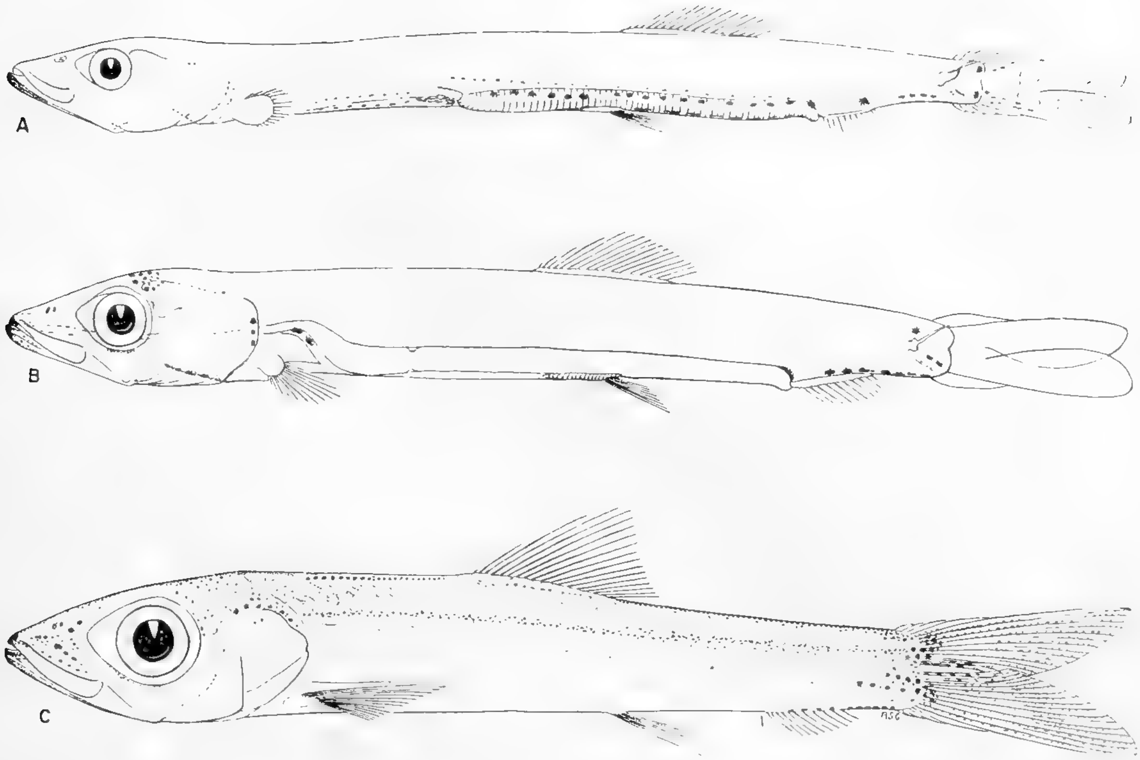

Figure 63. *Etrumeus sadina*. a, larva, 27.5 mm TL, near Pensacola, Florida. b, young, 35 mm TL, near Pensacola, Florida. c, young, 42.5 mm TL, Beaufort, North Carolina, USNM 143804. All drawn by Ann S. Green; a and b based on camera-lucida sketches by W. W. Welsh.

anal, and in a single dark median line behind the anal fin; also several dark spots are present on the base of the caudal.

At about 33–35 mm TL, the fins are all rather fully developed and the body has become proportionately much deeper, but the pigmentation remains virtually the same as in smaller examples. Specimens of this size, then, may be classed as young adults. General pigmentation is delayed and is scarcely complete at 55 mm TL. The fish continue to increase in relative depth as long as they grow.

Spawning. The smallest specimens at hand, postlarvae 25–28 mm TL, are so young that they probably were caught not far from where they were hatched; they were taken at 30°29′ N, 80°37.5′ W, off northern Florida. Still smaller larvae, 7.6–21 mm, were listed by the late W. W. Welsh in his unpublished notes, accompanied by seven camera-lucida sketches. These were taken by the Grampus at the surface in the Gulf of Mexico at 28°21′ N, 89°06′ W, 17 miles or so off the Mississippi Delta. Although these specimens are apparently no longer extant, the drawings leave no room for doubt as to their identity. Also in this as well as other collections there are young adults from northern Florida south to Cape Canaveral and from the Gulf of Mexico off Mobile Bay. The smallest young (including postlarvae) were taken on January 25 (1940), and other small young adults were taken in March off northern Florida and in the Gulf of Mexico. The smallest young were caught in water 19 fms. deep, and other small ones were taken at 21, 20, 16, and 5 fms. From these data it may be concluded that spawning in the south takes place during the winter, somewhat offshore, and in water several fathoms deep. If spawning takes place northward it seems not to have been reported.

Migration and Habitat. In the northern part of its range, as at Woods Hole, Massachusetts, this Round Herring is taken along the shore only during summer. It has not yet been determined whether this fish migrates northward during summer or whether it only comes inshore from deep water during warm weather. In southern waters it is not known to occur along the shore, for there it has been taken only offshore in water a few to several fathoms in depth. Whether it migrates at all in these waters remains unknown.

Relationships. E. sadina is the only representative of the genus in the Atlantic, but other species occur in the Pacific: off California, the Philippine Islands, Japan, Hawaii, and Galapagos Islands. Those from the western Pacific are more compressed and proportionately deeper than the Atlantic species and are therefore less typically "round herrings."

Abundance. Generally this Round Herring is rare to scarce from New Jersey to New England, where it occurs along the shore, but occasionally it is common to plentiful. It was very abundant off Woods Hole, Massachusetts, in 1905 and again in 1908 (*123*: 741). A number of specimens was also taken at Campobello Island at the mouth of the Bay in September 1937 (*82*: 5; *92*: 15). Along the coast of eastern Maine, in August-September 1953, something like 200,000 pounds were landed (*114*: 194). But apparently it has been taken only sparingly off the southern Atlantic and Gulf coast states, though commonly regarded as a warm-water fish.

Range. It is known from Passamaquoddy Bay at the mouth of the Bay of Fundy and from the eastern part of Maine to northern Florida off Cape Canaveral, and from the Gulf of Mexico.[5] Although it has been reported as not rare southward (*72*, 1896: 420), no records have been found of its occurrence from Delaware southward; and there is only one record for the Gulf, the latter being based on specimens taken from the stomachs of snappers landed at Pensacola, Florida (*74*: 143). Recent collections by the U.S. Fish and Wildlife Service include: examples from Beaufort Inlet and off Cape Lookout, North Carolina; four collections of young from off northern Florida southward to Cape Canaveral; and six collections from the Gulf of Mexico, five of these from off Mobile Bay and one from south of New Orleans. These rather recent collections are all from offshore waters of 2–21 fms. depth. Those from New Jersey northward, all adults, were caught in shallow water near or on the shore.

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[5] Bertin (*13*: 9) synonymized *E. microps* and *E. jacksoniensis*, previously recognized as valid species, and thereupon gave the range as the Atlantic coast of the United States, the coast of southeastern Australia, southeastern Japan, Hawaii, and the southeastern coast of Africa. However, from comparison of specimens from the United States and Japan, it was at once evident that the latter were different in shape, being especially more compressed. A further study of specimens from the widely separated regions where the genus occurs would be desirable.

Apparently this fish does not occur off southern Florida, for it was not reported by Longley and Hildebrand from collections made at Tortugas over many years, including dredgings at various depths down to about 400 fms (*87*). This seems to be another instance of a discontinuous range of the genus such as is reported for *Pomolobus*, *Alosa*, and *Brevoortia* (p. 343). However, in *Etrumeus* the inhabitants of the Gulf and the Atlantic appear to be identical, whereas in the other genera named, the inhabitants of the two areas differ sufficiently to be recognized as distinct species.

Synonyms and References:

Clupea sadina Mitchill, Rep. in part on Fishes of New York, 1814: 21 (orig. descr.; type local. presumably New York; type lost); Mitchill, Trans. Lit. philos. Soc. N. Y., *1*, 1815: 457 (descr., New York[6]).

Alosa teres DeKay, N. Y. Fauna, Fishes, Pt. 4, 1842: 262, pl. 40, fig. 128 (orig. descr.; type local. New York Harbor; type in State Coll.).

Etrumeus teres Günther, Cat. Fish. Brit. Mus., *7*, 1868: 467 (synon., notes, range); Jordan and Gilbert, Bull. U. S. nat. Mus., 16, 1883: 263 (diagn., refs.); Jordan and Gilbert, Proc. U. S. nat. Mus. (1883), *6*, 1884: 143 (from stomachs of snappers, Pensacola, Florida); Bean, T. H., Bull. U. S. Fish Comm. (1887), *7*, 1888: 148 (Great Egg Harbor Bay, New Jersey); Bean, T. H., Bull. N. Y. St. Mus., *60*, Zool. 9, 1903: 189 (synon., descr., New York); Fowler, Rep. N. J. St. Mus. (1905), 2, 1906: 93 (diagn., synon.); Kendall, Occ. Pap. Boston Soc. nat. Hist., 7 (8), 1908: 36 (refs., New England); Sumner, Osburn, and Cole, Bull. U. S. Bur. Fish. (1911), *31* (2), 1913: 741 (refs., parasites, Woods Hole, Massachusetts); Fowler, Proc. biol. Soc. Wash., *33*, 1920: 147 (New Jersey); Bigelow and Welsh, Bull. U. S. Bur. Fish. (1924), *40* (1), 1925: 91, fig. 39 (descr., range, Gulf of Maine); Breder, Field Bk. Mar. Fish. Atl. Cst., 1929: 63, fig. (diagn., distr.).

Etrumeus sadina Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 420 (descr., range, synon.); Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish. (1928), 2, 1930: 46 (synon., range); Bigelow and Schroeder, Bull. U. S. Bur. Fish., *48* (20), 1936: 327 (Yarmouth R. and Casco Bay, Maine); Bertin, Bull. Inst. océanogr. Monaco, 853, 1943: 9, fig. 4 (synon., descr., distr., etc.); Bigelow and Schroeder, Fish. Bull. (74) U. S. Fish Wildl. Serv., *53*, 1953: 87 (Gulf of Maine).

Genus *Jenkinsia* Jordan and Evermann 1896

Dwarf Herrings

Jenkinsia Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 418; genotype by monotypy, *Dussumieria stolifera* Jordan and Gilbert equals *Clupea lamprotaenia* Gosse.

Characters.[7] A very small species. BODY slender, compressed; abdomen rounded; chest with suggestion of a keel. BONY SCUTES absent. SCALES deciduous, very thin, with smooth edges, covering abdomen. SNOUT moderately long, tapering. MOUTH terminal. MAXILLARY narrowly rounded, terminating about under anterior margin of pupil. TEETH in a single series on the margin of maxillary and premaxillary; a short

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[6] Because of such inaccurate statements in the original description as "Mouth...toothless," "Lower jaw projecting," and "A. 15," it was long questioned whether *sadina* was available for this species. However, the description contains pertinent remarks such as "Form neat, tapering, and slender," and especially "the belly is not at all serrate, but quite smooth," which can scarcely apply to any other clupeoid. Therefore, *sadina* certainly seems available. Apparently *Alosa teres* DeKay, though much better described and rather well figured, must rest in synonymy, under the rules of zoological nomenclature.

[7] Bertin (*13*: 17) has stated that *Jenkinsia* is not separable from *Spratelloides* Bleeker.—G. S. Myers.

toothless membranous section present between these elements; no teeth on mandible or vomer; at most a few granular teeth on palatines, pterygoids, and tongue. DORSAL small, beginning rather nearer to margin of snout than to base of caudal, with about 9–14 rays. ANAL only a little larger than dorsal and placed far behind it, with about 12–16 rays. PELVIC fins nearly as long as the pectorals, each with 8 rays; a scale process present between fins at base. PECTORAL fins rather small, each with about 10–14 rays. Pelvic and pectoral both without a free AXILLARY PROCESS.

Remarks. Jenkinsia resembles *Etrumeus* in having a rather roundish, elongated body, a rounded abdomen, and no bony scutes on the ventral outline of the chest and abdomen. However, in *Jenkinsia* the chest is very slightly keeled. The rather small anal fin, situated far behind the dorsal, and the rather large pelvic fin, inserted under the anterior half of the base of dorsal, also help to distinguish this genus. The small size of these herrings, about 50–70 mm, also separates them from other herrings.

Range. Known from Bermuda, doubtfully from North Carolina, the Florida Keys, the West Indies, and from some small islands in the Caribbean Sea, off México and Central America. Only two species are known.

Key to Species

1a. Gill rakers not especially close-set, 19–24 (usually 20 or 21) on lower limb; oblique series of scales crossing silvery lateral band between margin of opercle and base of caudal, 33–37. *lamprotaenia* (Gosse) 1851, below.

1b. Gill rakers close-set, 27–30 on lower limb; oblique series of scales crossing silvery lateral band between margin of opercle and base of caudal, 39–42. *viridis* (T. H. Bean) 1912, p. 272.

Jenkinsia lamprotaenia (Gosse) 1851

Dwarf Herring, Green Fry

Figure 64

Study Material. Many specimens, 28–65 mm TL, 23–55 mm SL, collected at Key West and Tortugas, Florida, the Bahama Islands, Cuba, Isle of Pines, Jamaica, Haiti, Puerto Rico, St. Eustatius Island, Old Providence Island, and Yucatán Island off Cozumel, México.

Distinctive Characters. See Remarks, and Key to Species, above.

Description. Proportional dimensions in per cent of standard length, and counts, based on 16 specimens, 40–65 mm TL, 32–55 mm SL.

Body: depth 15–20.
Caudal peduncle: depth 6.5–8.5.
Head: length 25–29.
Snout: length 6.2–8.0.
Eye: diameter 7.6–9.7.
Interorbital: width 3.8–5.4.

Maxillary: length 9.0–12.
Mandible: length 12–14.5.
Anal fin: length of base 10–14.
Pelvic fin: length 11–15.
Pectoral fin: length 14–17.
Distance from snout to origin of: dorsal 44–50.
Scales: 33–37, generally missing in preserved specimens.
Gill rakers: 19–24 (usually 20 or 21) on lower limb.
Fin rays: dorsal 9–13; anal 12–15; pectoral 10–13.
Vertebrae: 39 or 40 (6 specimens).

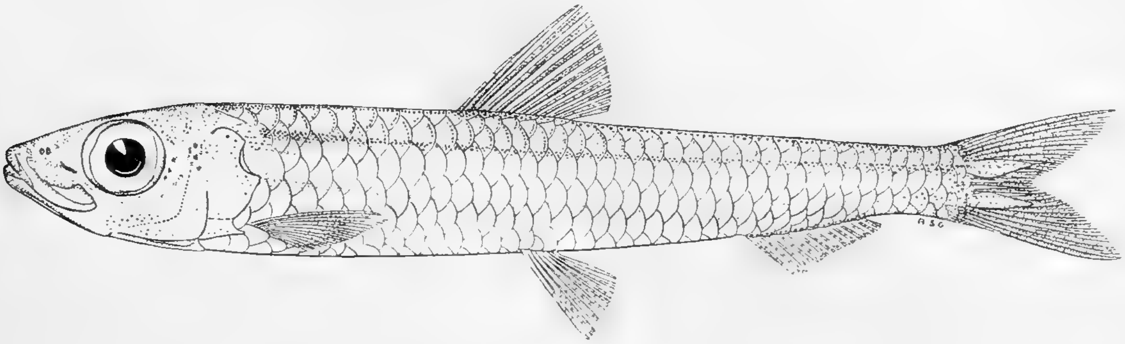

FIGURE 64. *Jenkinsia lamprotaenia*, 65 mm TL, 53 mm SL, Haiti, USNM 89600. Drawn by Ann S. Green.

BODY moderately compressed, its greatest thickness somewhat greater than half of its depth, its greatest depth 5.0–6.65 in SL; ventral outline more strongly convex than dorsal outline. CAUDAL PEDUNCLE rather strongly compressed, its depth 3.2–4.1 in head.

SCALES generally lost in preserved specimens, very thin, with smooth edges; those from middle of side below dorsal fin with a wavy ridge on anterior half, about 5 wavy radii behind it, and generally several shorter ridges at margin of scale.

HEAD rather low, 3.4–4.0 in SL. SNOUT generally shorter than eye, 3.4–4.2 in head. EYE 2.8–3.4. INTERORBITAL 5.5–7.0. MAXILLARY narrowly rounded posteriorly, reaching to or more usually a little beyond vertical from anterior margin of pupil, 2.25–2.75 in head. MANDIBLE generally included, not projecting, 1.9–2.2 in head. GILL RAKERS moderately close-set, those at angle of first arch about 75% of length of eye. TEETH missing on mandible and vomer but present in a single series on margin of premaxillary and maxillary, the series interrupted by a soft membranous section between these elements; palatines, pterygoids, and tongue at most with a few granular teeth.

DORSAL fin moderately elevated, the margin nearly straight, the longest rays reaching well beyond the tip of last ray if deflexed, the fin beginning notably nearer to margin of snout than to base of caudal, the distance from margin of snout 2.0–2.3 in SL. CAUDAL fin moderately forked, the lobes of about equal length, rather longer than head without snout; each lobe with a greatly elongated scale at base. ANAL fin much lower than dorsal, beginning far behind dorsal fin, about equidistant between insertion of pelvic and base of caudal, its base 1.9–2.6 in head. PELVIC fins only a little shorter than pectorals, with a large scaly process between them, the fins inserted under about 4th–6th dorsal ray, and generally close to an eye's diameter nearer to base of caudal than to tip of mandible; 1.9–2.5 in head. PECTORAL fins somewhat pointed, inserted about equidistant between tip of mandible and base of pelvics, 1.6–1.9 in head.

ALIMENTARY CANAL short. STOMACH with a large blind sac. PYLORIC COECA large, about 7. PERITONEUM pale, with many dark dots.

Color. In life, faintly greenish above, with a distinct silvery lateral band. Preserved specimens straw colored, the silvery band persisting. Margin of mandible brown to black. Well-preserved specimens with an elongated silvery area on abdomen behind pectoral fin, and a similar though smaller area behind pelvic. Scales above lateral band with a brownish line on middle of exposed section, paralleling the curve of the margin of the scale; dark dots also present, especially in and above upper margin of silvery lateral band; two rows of dark dots on back; generally numerous dots on snout, including an elongated one in front of lower half of eye; an irregular dark spot at base of each anal ray, continued as a single median ventral line on caudal peduncle.

Size. The largest example at hand, 65 mm (2.6 in.) TL, may be near the maximum size attained.

Spawning and Development. Nothing is known definitely concerning reproduction in this species, but examples collected in 1937 at Kingston, Jamaica, during our winter months, contain well-developed eggs, indicating that at least some spawning takes place during that time around Jamaica.

The smallest examples at hand, a little more than an inch (28–30 mm) TL, are fully developed young adults. They differ principally from large examples from the same general locality (Tortugas, Florida) in being more slender, the depth being about 6.4 times in SL; in the large adult this proportion varies between about 2.25–5.6. However, there are large specimens in the collections studied that are just as slender as the young mentioned. For further discussion of the difference in depth, see *Variations* (p. 271).

Migration and Habitat. It seems improbable that this little fish travels long distances. It does occur in large compact schools that probably consist of millions of fish, as observed by me at Key West, Florida, and as reported for Tortugas, Florida (*49*: 156; *21*: 1). It moves about more or less like the young Atlantic menhaden, *Brevoortia tyrannus*, without pursuing any definite course.

Food. This species, like many other clupeoids, feeds on plankton, which it screens from the water as the school girates or mills around at the surface.

Enemies. Many large fish feed on this species. The gray snapper was mentioned especially by Gudger, who said that the little fish exhibited little fear; it hovered over the snapper in dense swarms but left a clear space around it approximately equal to the length of the snapper (*49*: 156). Whenever the snapper moved, the rather orderly school broke up but soon re-formed. Longley said, "Exceedingly common at Tortugas (Fla.), particularly along shore, where predacious fishes often drive them too close for safety, and large numbers are cast upon the windward beaches to spring about until a wave rescues them, or until they perish" (*87*: 12).

The copepod, *Colliparvus parvus* Wilson, was found on the gills of specimens taken at Nassau, Bahamas (*135*: 79), and an unidentified trematode was reported as parasitic on it at Tortugas, Florida (*90*: 372).

Relationships. Only two species of *Jenkinsia* are recognized herein. A third nominal species, *stolifera*, long was thought to be distinct, but recent works on taxonomy agree that it and *lamprotaenia* constitute one variable species; since *lamprotaenia* is the older name, *stolifera* has become a synonym. *J. viridis* is closely related to *lamprotaenia*, as shown in the account of *viridis* (p. 272).

Variations. This species, as indicated, is very variable. While the depth of body in general increases with age, adult specimens of equal size vary greatly in this respect among themselves, as is evident from the wide range shown in the *Description.* And this in turn is reflected in the wide range in the depth of the caudal peduncle and in the length of the head. A rather wide variation in the number of dorsal, anal, and pectoral rays, and in the number of gill rakers, is also shown in the *Description.* Although some of the earlier counts may have erred because fins are often broken in preserved specimens (no doubt so in the original description of *stolifera*), this error does not enter into those given in the foregoing *Description*, for ample specimens with undamaged fins were chosen for the enumerations.

Commercial Importance. Although this little Herring has been reported among the "white bait" in the market at Port-au-Prince, Haiti (*10*: 45), no doubt its chief value is that of providing food for foodfishes.

Range. Known from the Florida Keys, the Bahamas, throughout the West Indies, and from Swan Island, Glover Reef, and Cozumel Island in the Caribbean Sea; recently reported from Venezuela; doubtfully recorded for Beaufort, North Carolina. Apparently it is chiefly a shore species.

Synonyms and References:

Clupea lamprotaenia Gosse, Naturalist's Sojourn in Jamaica, 1851: 291, pl. 1, fig. 2 (orig. descr.; type local. Jamaica; types in BMNH; found in schools with an anchovy, *Engraulis brownii* = *Anchoa hepsetus*); Günther, Cat. Fish. Brit. Mus., 7, 1868: 465 (descr., Jamaica).

Dussumieria stolifera Jordan and Gilbert, Proc. U. S. nat. Mus. (1884), 7, 1885: 25 (orig. descr.; type local. Key West, Florida; type USNM 34964; local abund.); Bean, T. H., Bull. U. S. Fish. Comm. (1888), *8*, 1890: 206 (Cozumel, Yucatán).

Jenkinsia lamprotaenia Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 419 (descr., after Günther); Evermann and Marsh, Bull. U. S. Fish Comm. (1900), *20* (1), 1902: 84 (descr., refs., Puerto Rico); Metzelaar, Rapp. Vissch. Curaçao, ed. by J. Boeke, 1, W. Indian Fishes, 1919: 9, fig. (refs., descr., range; Leeward Is., West Indies); Beebe and Tee-Van, Zoologica, N. Y., *10* (1), 1928: 43, fig. (refs., descr., range, *J. stolifera* synon.; Port-au-Prince, Haiti); Breder, Field Bk. Mar. Fish. Atl. Cst., 1929: 63, fig. (diagn., range); Nichols, N. Y. Acad. Sci., *10* (2), 1929: 201, fig. 32 (refs., distr., diagn., Puerto Rico); Parr, Bull. Bingham oceanogr. Coll., *3* (4), 1930: 3 (refs.; discus. ident. of *lamprotaenia* and *stolifera*; Bahamas, Turks Is.); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 46 (range, refs.); Longley and Hildebrand, Publ. Carneg. Instn. Wash., 535, 1941: 12 (discus. *lamprotaenia* and *stolifera*; variability; Tortugas, Florida); Hildebrand, Copeia, 1941: 224 (extension of range, Beaufort, North Carolina); Fowler, Monogr. Acad. nat. Sci. Philad., 6, 1944: 123, fig. 30

(descr., locals., pp. 434, 456); Martin, Mem. Soc. Cient. La Salle, *15*, 1955: 184–188 (descr., ills., Venezuela).

Jenkinsia stolifera Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 419 (descr., ref. to orig. descr.); Evermann and Kendall, Rep. U. S. Comm. Fish. (1899), 1900: 55 (refs., Florida); Evermann and Marsh, Bull. U. S. Fish Comm. (1900), *20* (1), 1902: 84 (descr., refs., Puerto Rico); Bean, B. A. *in* Bahama Islands, Fishes, 1905: 297 (rec. from Spanish Wells); Fowler, Proc. Acad. nat. Sci. Philad., *58*, 1906: 81, fig. 1 (descr.; assoc. with anchovies; Florida Keys); Wilson, Proc. U. S. nat. Mus., *53*, 1917: 79 (host of copepod, *Colliparvus parvus* Wilson; Nassau, Bahamas); Breder, Bull. Bingham oceanogr. Coll., *1* (1), 1927: 13 (Isle of Pines, Swan I., and Glover Reef off British Honduras); Breder, Amer. Mus. Novit., 382, 1929: 1–5 (school. behav., Tortugas, Florida); Gudger, Publ. Carneg. Instn. Wash., 391, 1929: 156, pl. 1, fig. 6 (local abund., habits, Tortugas, Florida); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 46 (range, ref.); Breder, Publ. Carneg. Instn. Wash., 435, 1932: 8 (fed on by needlefish, *Strongylura*; Tortugas, Florida); Gowanloch, Bull. La. Conserv. Dep., 23, 1933: 214 (in great schools, Gulf of Mexico; but no records for Gulf coast north of extremes Florida, therefore, apparently not of Louisiana fauna).

Spratelloides lamprotaenia Bertin, Bull. Inst. océanogr. Monaco, 853, 1943: 17 (diagn., revision).

False References:

Jenkinsia stolifera Nichols (not of Jordan and Gilbert), Proc. biol. Soc. Wash., *33*, 1920: 63 (*Stolephorus viridis* in synon., Bermuda).

Jenkinsia lamprotaenia Beebe and Tee-Van (not of Gosse), Field Bk. Shore Fish. Bermuda, 1933: 37, fig. (field char., diagn., distr.); Beebe and Tee-Van, Zoologica, N. Y., *13* (7), 1933: 136 (refs., *Stolephorus viridis* and *J. stolifera* in synon., Bermuda); Hollister (not of Gosse), Zoologica, N. Y., *21* (4), 1936: 276, figs. 40–44 (caudal skel.).

Jenkinsia viridis (T. H. Bean) 1912

Bermuda Herring, Dwarf Herring, Green Fry

Figure 65

Study Material. A total of 19 specimens, 42–58 mm TL, 32–48 mm SL, as follows: 4 "types," from Bermuda, presumably from Hamilton, USNM 74084; the holotype, USNM 100546; and 14 paratypes of *Jenkinsia bermudana* Rivas, GRAMPUS St. 10178, off Bermuda, 32°20′N, 64°21′W.

Distinctive Characters. See *Relationships* (p. 273) and Key to Species (p. 268).

Description. Proportional dimensions in per cent of standard length, and counts, based on study specimens, 32–48 mm SL.

Body: depth 15–17.5.
Caudal peduncle: depth 6.7–8.2.
Head: length 25–27.
Snout: length 6.7–8.5.
Eye: diameter 7.0–9.0.
Interorbital: width 3.6–4.75.
Maxillary: length 9.4–10.8.
Mandible: length 11.6–13.5.
Anal fin: length of base 12–14.
Pelvic fin: length 12–15.
Pectoral fin: length 14–16.
Distance from snout to origin of: dorsal 44.5–50.

Scales: about 39–42, generally lost in preserved specimens.
Gill rakers: 27–30 on lower limb.
Fin rays: dorsal 9–14; anal 14–16; pectoral 12–14.
Vertebrae: 40 (1 specimen).

Body shaped in all respects as in *lamprotaenia*, its greatest depth 5.7–6.6 in SL. Caudal peduncle 3.2–4.0 in head.

Scales as in *lamprotaenia*, except that there appear to be a few more in a lateral series.

Head low, with exceedingly numerous mucous canals and pores, its length 3.7–4.0 in SL. Snout equal to, or more usually a little shorter than, eye, 3.2–3.8 in head. Eye 2.9–3.5. Interorbital 5.5–7.1. Maxillary narrowly rounded posteriorly, generally reaching vertical from anterior margin of pupil, 2.45–2.6 in head. Mandible slightly included, about coterminal with the snout, 2.0–2.2 in head. Gill rakers very close-set, those at angle rather more than half of length of eye. Teeth apparently in all respects as in *lamprotaenia*.

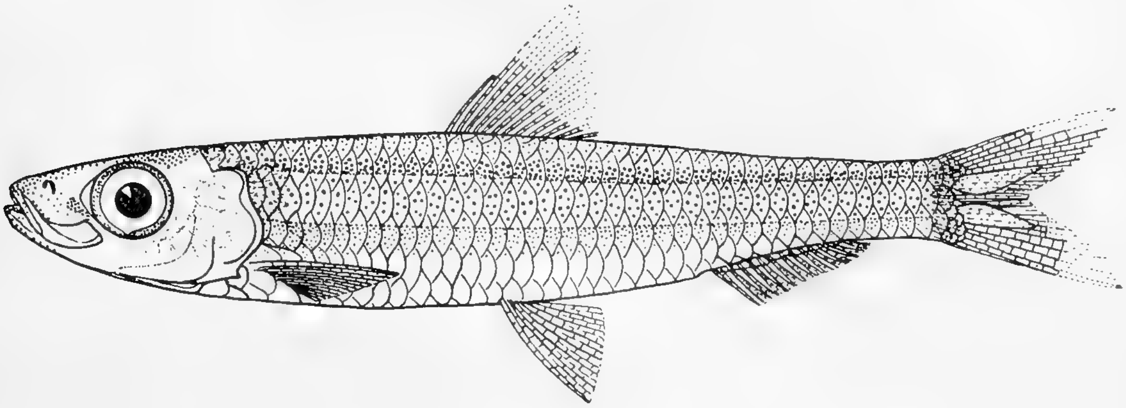

Figure 65. *Jenkinsia viridis*, 45 mm TL, from Bermuda, USNM 100546. After Rivas.

Dorsal fin elevated anteriorly, the longest rays reaching far beyond tip of last ray if deflexed, the fin generally beginning about half of an eye's diameter nearer to margin of snout than to base of caudal, the distance from margin of snout 2.0–2.25 in SL. Caudal fin as in *lamprotaenia*. Anal lower than dorsal, its origin about equidistant between insertion of pelvic and base of caudal, its base 1.8–2.2 in head. Pelvic fin only a little shorter than pectoral, inserted under the 4th or 5th dorsal ray and about equidistant between anterior margin of eye and base of caudal, its length 1.55–2.2 in head. Pectoral fin pointed, inserted a little nearer to tip of mandible than to base of pelvic fin, 1.55–1.8 in head.

Color. In all respects as in *lamprotaenia*.

Size. The largest specimens at hand, 55–58 mm TL (2.2–2.3 in.), may be near the usual maximum length attained.

Food. Although no specific information is at hand, there seems to be no reason to believe that the food of this species differs from that of *lamprotaenia*.

Enemies. No enemies have been listed. However, there can be no doubt that predatory fish and water birds feed on this species as they do on *lamprotaenia*.

Relationships. As stated in the account of *lamprotaenia*, the two species of this genus recognized herein are closely related. But they differ in the number of gill rakers on the lower limb of the first arch, *viridis* having 27–30 while *lamprotaenia* has only 19–24 (usually 20 or 21). That there is a difference between the species in the insertion of the pelvic fin, as stated by Rivas (*108*: 3), I am unable to substantiate, as it seems to be obliterated by the variations among specimens. However, according to four *viridis* and seven *lamprotaenia* that remain almost fully covered with scales, in the former 39–41 oblique rows of scales cross the lateral band between the margin of the opercle and the base of the caudal, whereas in the latter only 33–37 series cross this band. The specimens of *viridis* at hand have much more prominent mucous canals and pores about the head and on the anterior part of the body, but they may not be specifically significant.

It so happens, then, that even though T. H. Bean placed this species in the wrong genus and family (*Stolephorus*, family Engraulidae), his species still remains valid (*9*: 22).

Commercial Importance. This species is not known to be of direct commercial importance. It has been reported as exceedingly common in Bermuda (*9*: 123; *11*: 37), therefore it must be valuable as a forage fish.

Range. Known only from Bermuda and vicinity. It congregates in schools like *lamprotaenia* but ventures some distance offshore, as shown by the GRAMPUS catch noted above.

Synonyms and References:

Stolephorus viridis Bean, T. H., Proc. biol. Soc. Wash., *25*, 1912: 122 (orig. descr.; type local. Bermuda; types USNM 74084; common).

Jenkinsia stolifera Nichols (not of Jordan and Gilbert), Proc. biol. Soc. Wash., *33*, 1920: 63 (*Stolephorus viridis* in synon.).

Jenkinsia lamprotaenia Beebe and Tee-Van (not of Gosse), Field Bk. Shore Fish. Bermuda, 1933: 37, fig. (field char., diagn., distr.); Beebe and Tee-Van, Zoologica, N. Y., *13* (7), 1933: 136 (refs., *Stolephorus viridis* and *J. stolifera* in synon.; Bermuda); Hollister, Zoologica, N. Y., *21* (4), 1936: 276, figs. 40–44 (caudal skel.).

Jenkinsia bermudana Rivas, Smithson. misc. Coll., 106 (14), 1946: 1–4, 1 fig., 1 pl. (orig. descr.; type local. Bermuda; type USNM 100546; cf. *lamprotaenia*; but *S. viridis* Bean apparently overlooked, of which *bermudana* becomes a synon.).

Genus *Clupea* Linnaeus 1758

Clupea Linnaeus, Syst. Nat., ed. 10, 1758: 317; type species by implication (unquestioned), *Clupea harengus* Linnaeus.

Generic Synonym:

Rogenia Cuvier and Valenciennes, Hist. Nat. Poiss., *20*, 1847: 340; type species by monotypy, *Rogenia alba* equals *Clupea harengus* Linnaeus 1758.

Characters. BODY quite elongate, compressed. BONY SCUTES on median line of chest and abdomen, weak. SCALES with crenulate membranous borders. MAXILLARY with a large paddle-shaped supplemental bone. TEETH on vomer permanent, forming a small patch. DORSAL fin rather small, without a produced ray. PELVIC commonly with 9 rays, rarely with only 8.[8] VERTEBRAE 45–57.

Remarks. The very slender body and the presence of vomerine teeth distinguish this genus from other genera of the western North Atlantic.

Range. North Atlantic and North Pacific, ranging on the American side of the Atlantic from North Carolina to Greenland and in Europe from the Strait of Gibraltar to Spitsbergen. In the Pacific, the genus is represented from southern California to the Aleutian Islands and across to Siberia and Japan. A single species occurs in the western North Atlantic.[9] The species generally occurs in schools, which are usually seen at or rather near the shore.

Clupea harengus Linnaeus 1758

Atlantic Herring, Sea Herring, Herring

Figures 66–68

Study Material. At least 18 specimens, 75–270 mm TL, 63–224 mm SL, and smaller specimens, including postlarvae; from Kings Creek (tributary to Tangier Sound), Chesapeake Bay, Maryland; Ipswich River (estuary) and Woods Hole, Massachusetts; Sheepscot River and Eastport, Maine; St. Lawrence River; Nova Scotia; New Brunswick; and Newfoundland. This American material was compared with specimens from Norway and Sweden, and with specimens from the Pacific collected in California, Oregon, and Alaska.

Distinctive Characters. The following conspicuous field marks separate the postlarval and adult Atlantic Herring from the shads (*Alosa*) and from representatives of *Pomolobus* (alewives, hickory shad): the point of origin of its dorsal fin is about midway of its trunk (considerably farther forward in the others); its body is not as deep, a difference shown better in the illustrations than by words; and the sharp midline of its belly is less strongly serrate.

[Critical examination is required to distinguish the early stages of clupeoids of the western North Atlantic, one from another. Larvae of other species with which the Herring larva might be confused are the launce (*Ammodytes*), the so-called rock gunnel (*Pholis*), the capelin (*Mallotus*), and the smelt (*Osmerus*). But the position of the anus, about 83 °/₀ of the way back along the body, sets the larval Herring apart from all of these (about 75 °/₀ of the way back in *Mallotus* and *Osmerus*, about 66 °/₀ of the way back in *Ammodytes* and *Pholis*).—H. B. B.]

Description. Proportional dimensions in per cent of standard length, and counts, from specimens in *Study Material*, not including small specimens except for mention of their much more slender body and fewer gill rakers; specimens 63–224 mm SL.

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[8] Pelvics with 7 or 8 in South American species.—G. S. Myers.

[9] The genus *Clupea* in the present sense is also represented in Australian–New Zealand temperate waters and in southern South America. Norman has reviewed the South American forms (*102*: 37).—G. S. Myers.

Body: depth 20–25.8.
Caudal peduncle: depth 7.2–10.
Head: length 22.6–26.4.
Snout: length 5.6–7.1.
Eye: diameter 5.3–7.7.
Interorbital: width 3.0–4.5.
Maxillary: length 10.2–12.3.
Pelvic fin: length 9.4.–11.3.
Pectoral fin: length 14.2–17.7.

Scales: *ca.* 56–62.
Ventral scutes: *ca.* 39–46.
Gill rakers: 37–52.
Fin rays: dorsal 16–20, usually 17–19; anal 16–20, usually 17 or 18; pectoral 17–19.
Vertebrae: 55–57 (12 specimens).

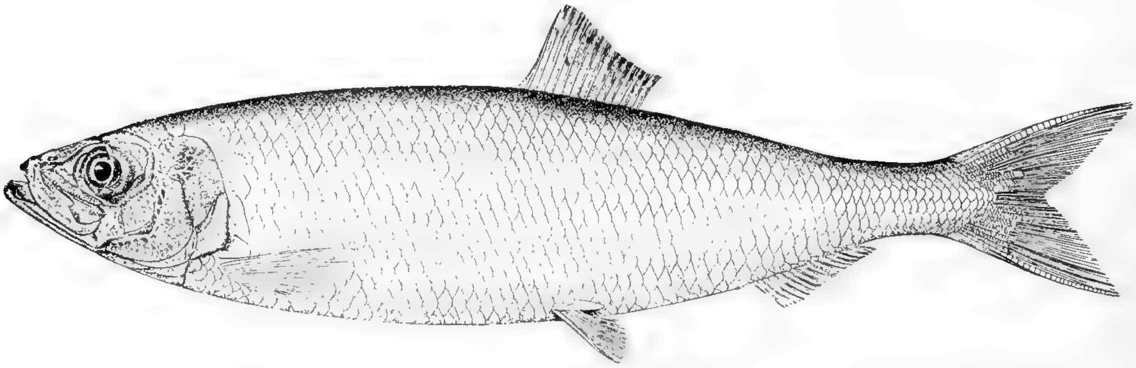

FIGURE 66. *Clupea harengus*, 315 mm TL, 12.62 inches, USNM 16667. Drawn by H. L. Todd.

BODY compressed, its greatest thickness somewhat less than half of its depth, its depth 3.9–5.0 in SL, much less in very young, 5.2–9.5 in specimens 40–70 mm.

SCALES only moderately adherent, often lost, especially in small fish; scales with crenate membranous border; about 16 or 17 longitudinal rows between ventral edge at base of pelvic and anterior ray of dorsal. VENTRAL SCUTES weak, often difficult to count, about 26–33 in front of pelvic fin and 13–15 behind.

HEAD 3.8–4.4. SNOUT 3.25–4.1 in head. EYE 3.4–4.25. INTERORBITAL 3.0–4.5. MAXILLARY rounded posteriorly, generally not quite reaching middle of eye, 2.0–2.3 in head. GILL RAKERS at angle nearly as long as eye in adults, proportionately shorter in young; increasing in number with age, the principal increase taking place before the specimens reach a length of 100 mm; specimens 36–70 mm long with only about 25–36 on lower limb. TEETH missing in upper jaw; the margin of maxillary with minute serrae; lower jaw anteriorly with about 6 rather prominent teeth on each side; middle of tongue with an elongated patch of small teeth; vomerine patch elongate, the teeth rather few and fairly strong.

DORSAL fin little elevated anteriorly, with nearly straight margin, its origin somewhat in advance of pelvics, usually nearer to base of caudal than to tip of snout. CAUDAL with lower lobe rather longer than the upper one, about as long as head. ANAL very low, its origin about equidistant between base of pelvic and base of caudal. PELVIC very near ventral edge, inserted equidistant between base of pectoral and last anal ray, 2.2–3.0 in head. PECTORAL inserted a little higher on side than pelvic, and below distal margin of opercle, 1.3–1.6 in head.

Color. According to Bigelow and Welsh (*16*: 93):

> Peritoneum quite dusky. Deep steel blue or greenish blue on the back with green reflections; the sides and belly silvery; the change from dark to pale sides often marked by a greenish band. The gill covers sometimes glisten with a golden or brassy gloss; indeed, fish just out of the water are iridescent all over with different hues of blue, green, and violet, beauties that soon fade, however, leaving only the dark back and silvery sides. The ventral and anal fins are transparent white; the pectorals, however, are dark at the base and along the upper edge; the caudal and dorsal dark grayish or shading into blue or green.

Size. The maximum size attained by the Atlantic Herring is about 450 mm (18 in.), though the usual size is only about 300 mm (12 in.).

Scope of Following Account. Much has been written about this Herring's spawning habits, food, rate of growth, seasonal migrations, and so on, by both European and American authors. Summaries of the literature about this species on the American coast, with frequent references to the European literature, have been given by Bigelow and Welsh (*16*: 92–105) and by Bigelow and Schroeder (*15*: 88–100), who drew heavily on important papers by Moore (*95*: 387–442), Lea (*78*: 75–164), and Huntsman (*63*: 165–171); furthermore, they were able to add much to the already known facts from their own studies. A review of all the literature would make this account much too long for the present work. Therefore, only a brief summary of what is known about its life history, drawn in large part from the accounts mentioned above (*15*; *16*), is given here. Nearly all of the papers cited provide bibliographies from which references to literature containing additional information may be obtained.

FIGURE 67. *Clupea harengus* (Europe) eggs attached to seaweed. After Ehrenbaum.

Development and Growth. The eggs of the Atlantic Herring, 1.0–1.4 mm in diameter (*16*: 98) or 1.2–1.5 mm (*29*: 362), are heavier than sea water, and adhesive, adhering singly or in clumps to objects in the water or to the bottom. If they fall on muddy bottom they probably smother.

The number of eggs produced by a single female is relatively small, and as usual it varies according to the size of the fish, large fish having many more eggs than small ones. The number produced by one female may vary between 21,000–47,000 (*101*: 283) or between 20,000–40,000 (*16*: 94).

The duration of incubation depends upon the temperature. Norman stated that eggs kept at 52–58°F hatched in eight or nine days, whereas others held in water at

32°F hatched in 47 days (*101*: 330). Bigelow and Welsh gave 10–15 days as the probable average incubation period for the usual temperatures prevailing in the Gulf of Maine during the hatching season; these seem to vary between about 46–55°F (*16*: 94).

The newly hatched fish, transparent and very slender, vary considerably in length, with a range of about 5.3–7.0 mm (*29*: 362) or about 5.0–6.0 mm (*16*: 97). The small yolksac is absorbed in several days, when the larvae have attained a length of 8–10 mm; no marked changes take place in the form of the body during this time. The vent is situated so far back that the length posterior to it is less than a fifth of the total body length, and the depth at this size is contained about 24 times in the total length. Considerable advancement in the development of the fins was evident in larvae around 19 mm long, taken in the tow at Helgoland; rays definitely were present in the dorsal and caudal, and the caudal had a concave margin. However, the anal and pelvic fins did not become differentiated until a length of about 29 mm was attained. In young about 41 mm long, the proportionate depth of the body has increased greatly, and the vent as well as the anal and pelvic fins have all moved forward; larvae of this size are said to be in the transition stage. However, this stage may be attained by the spring fish at a length of 31–44 mm, and by the fall fish at 44–60 mm (*29*: 363–366, figs. a–g).

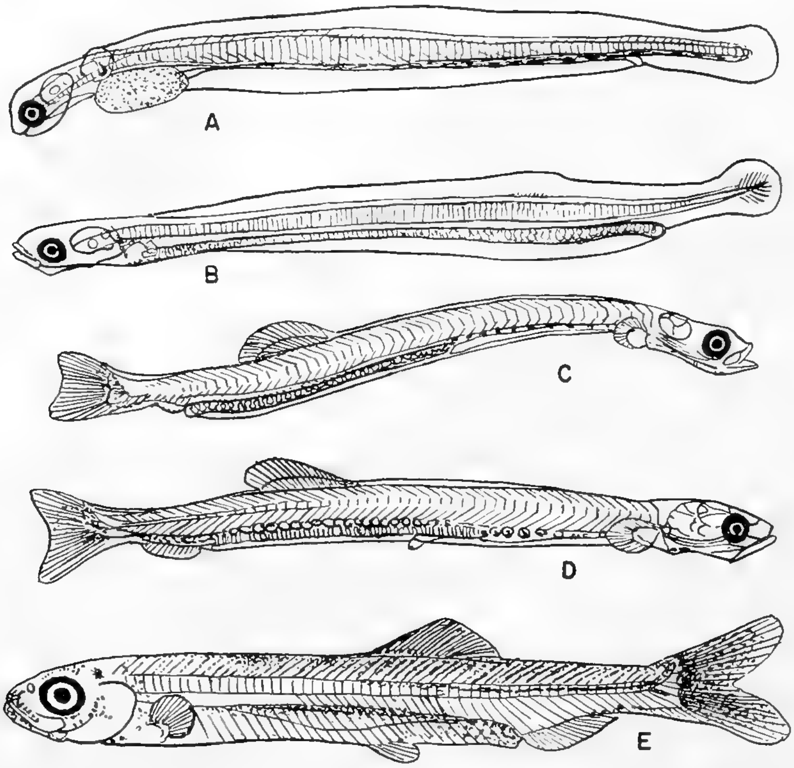

FIGURE 68. *Clupea harengus* (Europe). A–D, larval stages; A 7 mm; B 10 mm; C 19 mm; D 29 mm; E young fry, 41 mm.

Young fish from the Clyde Sea area of England lost their yolksac and began developing the dorsal fin at about 10 mm; the end of the notochord turned up at about 17 mm; pelvic fins appeared at about 22 mm; the caecal part of the stomach began to form and the air bladder became prominent at a length of 30–35 mm; and the least length at which metamorphosis took place was 42 mm (*91*: 248, 252). Marshall, *et al.* also recorded a regular weekly increase of 3 mm prior to metamorphosis, at a length of about 35–40 mm. This rate of growth of the larvae is in fair agreement with that reported for elsewhere in Europe.

Huntsman observed that, on the American coast, as at Grand Manan Island, New Brunswick, larvae hatched in late summer and early autumn had attained a length of 17–20 mm by the end of November or early in December. Fry 50–60 mm long were abundant in St. Andrews Bay in June. Yearlings were 90–125 mm long in the fall of the year in the Bay of Fundy. This rate of growth is in agreement with that observed by European investigators in examples from Norwegian waters and from the North Sea. A one-year old Atlantic Herring, then, is about 88–125 mm long.

These fish do not fall into definite size groups when more than one year old. But their subsequent rate of growth may be determined by segregating the fish into year-classes through scale reading, for the so-called winter rings are so pronounced that they can be relied upon with considerable confidence to show the age of the individual specimen.[10] Thus, Meek (*93*: 76) has indicated the following average lengths for those caught on the Dogger Banks in the North Sea: 98 mm at one year, 183 at two, 220 at three, 241 at four, 255 at five, 266 at six, 275 at seven, 281 at eight, 287 at nine, 291 at ten, 293 at eleven, and 295 mm at twelve years of age. The Norwegian fish spawned in 1899 grew more slowly at first than the Dogger Bank fish but about equaled the latter in size by their sixth year. Fish up to 19 years old have been found in many Canadian samples (*83*: 10) and some 20 years of age have been seen in Europe. However, the rate of growth after age 12 is extremely slow. According to observations by Huntsman and by Lea, the rate of growth is about the same for Atlantic Herring both here and in Europe, with Bay of Fundy fish growing a little faster than those spawned in the Gulf of St. Lawrence, and with the fish spawned along the outer coast of Nova Scotia growing a little faster than those produced in the Bay of Fundy.

On the coast of Maine, some individuals reach sexual maturity at a length of about 235 mm (9.5 in.), when three or four years old. Usually they do not spawn until they are 250–262 mm (10–10.5 in.) long, at five to six years of age. Most of the individuals in the schools of spawning fish are 300–325 mm (12–13 in.) long, the majority of which is then perhaps 10 years of age or more. It is believed that Atlantic Herring, after reaching sexual maturity, spawn every year as long as they live.

Atlantic Herring may be divided roughly into three growth stages,[11] each with its

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[10] For a detailed study of the scale of the Atlantic Herring in relation to growth, see Lea (*78*:81–93).

[11] Sometimes a greater number of growth stages has been recognized. Thus, Johnson (*69*:351), following the nomenclature of the fishermen of Passamaquoddy Bay, listed "brit" 80–100 mm, "snippers" 110–130 mm, "oils" 140–180 mm, and "mustards" 190–230 mm. In New England at least, the term "sperling" is used for young fish 75–125 mm long; they therefore come within the range of the sardine group, as used by Bigelow and Welsh (*16*:99).

own general distribution and seasonal migration. The first stage, the "sardine," consists of one- and two-year-old fish 45–200 mm long; the second is the "fat" stage, consisting of sexually immature fish about two years old, 190–200 mm long; and the third or "spawn" stage is a mature fish (see also pp. 283, 284).

Spawning Seasons. Spawning takes place in the spring, summer, or autumn, or in both spring and autumn, depending on the locality. Apparently there is no time in the year when spawning, off Europe at least, does not take place somewhere. On the southern coast of Newfoundland and in the Gulf of St. Lawrence, they are spring spawners, commencing in May or even as early as the latter part of April. In the southern and inner part of the Gulf as a whole, the season lasts only a few weeks. But on the south coast of Newfoundland, and perhaps on the west coast as well, spawning may continue until July, and some fish spawn in the Gaspé-Bay of Chaleur region in September. To the south, on the Atlantic coast of Cape Breton, Nova Scotia, spawning occurs chiefly in May or June, but also in August and September; and on the outer coast of this province to the south of Halifax, from August through September (*95*: 405; *60*: 10; *83*: 11, fig. 6).

The Bay of Fundy once harbored both spring and summer-autumn spawning schools, as did the outer coasts of Nova Scotia (by fishermen's reports); but they seem never to have been numerous; it is doubtful whether any of the spring spawners still exist anywhere south of the Gulf of St. Lawrence. At the mouth of the Bay of Fundy and off the easternmost part of the Maine coast, the heaviest spawning takes place in July-August and September in some years, with spawning continuing late in the fall; but in other years it does not commence until August, to end early in October. Passing westward–southward, the spawning run is progressively later and shorter: from mid-August until October in the general vicinity of Mt. Desert Island; in October along the east coast of Massachusetts (where only a few spawn); and early November near Woods Hole, Massachusetts.

Off northern Europe, where two principal races are recognized, namely coastal herring and sea herring, the coastal fish spawn mostly in brackish water and principally in the spring months, whereas the sea herring spawn in the open sea over widely distributed times of the year, but mostly in the late summer, autumn, and winter. The spawning periods of the different stocks are so varied that one may find spawning fish somewhere at almost any time of the year (*29*: 362). The Pacific Herring has only one spawning period, which may vary between December and June; the earliest spawning takes place in California and the latest in northern Alaska (*111*: 278).

Spawning Grounds and Depths. In northern European waters, as already indicated, at least some fish spawn in shallow inshore brackish water whereas others spawn in the open sea. But in the western side of the Atlantic they are not known to spawn in water less saline than about 31.9 ‰ or more saline than about 33 ‰. In the Gulf of Maine, spawning takes place at temperatures of about 46–55°. For the more northern part of the American range, however, precise information in this regard is lacking.

Off America, Atlantic Herring spawn in greater or fewer numbers throughout their geographic range, from north to south. Around Newfoundland they spawn chiefly within the bays. However, from the southern side of the Gulf of St. Lawrence southward as far as southern Maine there is no considerable sector of the coast, except a part of the Bay of Fundy (p. 290), that does not see a more or less plentiful spawning run. Moore has spoken of the northern coastline of the Gulf of Maine as "a continuous spawning ground," succeeded by scattered grounds wherever the bottom is suitable, extending as far southward as Block Island off the Rhode Island coast (*95*: 408). However, local spawning grounds may be abandoned for a term of years—a common occurrence (*95*: 430).

In the Gulf of St. Lawrence, Canada, they have been described as spawning in water so shallow that the eggs are sometimes washed up on the beach by the waves (*95*: 411), as happens every year in northern European waters (*15*: 99). In general, however, our Atlantic Herring spawn at depths of, say, 2–30 fms. Thus spawning takes place both along shore and on the various ledges that lie between 5–25 miles off the coast, where eggs are often found sticking to the anchor lines of fishing vessels. But the nature of the bottom makes it improbable that any eggs are laid at a depth greater than 75 fms. on the American side, though spawning at a depth of 100 fms. has been reported for Scandinavian waters (*95*: 411). Whether, or how regularly, the fish may spawn on the shallower parts of the offshore fishing areas, from Georges to Grand banks, remains to be learned.

Habits.[12] Herring are primarily wanderers of the open sea. While they also enter bays and estuaries freely, they seem never to have been reported reliably from water that is more than slightly brackish; along the American coast a salinity of perhaps 2.8 ‰ is about the lower limit of tolerance.

As a rule, all sizes of Atlantic Herring congregate in schools of hundreds or thousands of individuals, with a given school usually consisting of individuals of about the same age and size. How long a school may preserve its identity as such is not known, for while Fridriksson and Aasen have found that specimens tagged and released together may be recaptured at widely separated localities (*40*: 22), this may not apply to schools that have assembled under natural conditions.

When a school is at the surface in the daytime, as often happens in calm weather, it is betrayed by a fine rippling of the water; but the fish do not ordinarily "fin" or lift their noses above the water, as is characteristic among menhaden (p. 354). At night they are betrayed at the surface by their luminous trails if the water is "firing."

A school of Atlantic Herring is not as easily frightened as a school of mackerel by an approaching boat. Neither is it usual for them to leap clear of the water, except when young fry are pursued from below by larger pelagic fish.

A school that is actively feeding is likely to be more or less stationary, drifting as a whole with the current. At other times schools are seen traveling as if with purposeful intent, all of the members swimming side by side in the same direction. Schools

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[12] Condensed from Bigelow and Schroeder (*15*: 89).

of sardine-sized fry may often be seen streaming past some rocky headland, seemingly in an endless procession. What the directive stimulus may be we have yet to learn, for as Huntsman has pointed out, "There is no indication that herring swim against the current unless the water is somewhat turbulent" (*65*: 83). Whether they make or lose headway over the bottom while doing so depends on their swimming speed relative to the strength of the current.

No information is available as to how rapidly a school may travel at sea. But Fridriksson and Aasen have found that specimens held alive in nets swam constantly at a rate of about 0.2–0.25 sea miles per hour (6–8 m/min.) when not disturbed. It is certain that they are capable of long journeys, for individuals tagged on the east coast of Iceland have been recaptured in southern Norway, and vice versa (*40*: 26, 27).

How active Atlantic Herring are at any time and place depends primarily on the water temperature. In the Bay of Fundy region, for example, they "move very sluggishly when the water is coldest, in February and March," i. e. when the upper 20 fms. or so have cooled to about 32–36°. They become active again when the water has warmed to about 40–43°.

While the vertical range of this species extends down to an extreme depth of about 100 fms., the vast majority lives at depths shallower than 40–50 fms., living pelagically in the upper water layers for most of the year but close to the bottom during the coldest months.

Relation to Light. That light is an important factor in controlling their vertical distribution, at least in southern New Brunswick, was discovered by Johnson in 1939 (*69*: 349–354). He found that at night, in the absence of appreciable light, all sizes were quite near the surface. During weak light, as at dawn and dusk, all sizes still were a foot or so from the surface. However, as the sun rose above the horizon they left the surface, the largest fish, 190–230 mm long, descending to a depth greater than 10 feet and those 140–180 mm long to a depth of 10 feet or more; the smaller ones in general were nearer the surface. Also, on cloudy days all sizes were closer to the surface than on clear days.

Migratory Movements. Because of the economic value of this species, knowledge of the migrational habits, which would make it possible to predict runs in advance of their occurrence, has been and continues to be sought on both continents. In Europe at least, these studies have been complicated by the presence of a large but indeterminate number of local populations or races (p. 287), each with its own migratory pattern, a fact not known until comparatively recently and even now not well understood. As Norman (*101*: 263) wrote:

> At some seasons herrings may be found in huge numbers in a given locality (in Europe), at others they will disappear almost entirely; in other places they may be caught all the year round, but the numbers caught on a given ground may exhibit an immense amount of variation from one season to another.

To explain these long known and very obvious facts, an older view, widely held until about 1825, was that Atlantic Herring as a whole withdraw in winter to Arctic waters, to return to more temperate coasts in spring, some of them to the eastern side of the North Atlantic, others to the western side (for further details, see Meek, *93*: 67–87). But Perley wrote as early as 1852 that this idea was "supposed to be wholly imaginary," it being generally believed then "that the herring fattens in the depths of the ocean, and approaches the shore in shoals merely for the purpose of depositing its spawn" (*104*: 206). Successive and long continued studies at many hands have since proven that in reality we are not dealing with any widespread mass migrations, but with short-range movements (inshore and offshore) of local bodies of fish, each with its own area of occurrence and each of which may include subpopulations that spawn at different times of year, as Norman has pointed out. It is equally clear that the ranges of the races of European fish overlap—highly probable at least that more or less interchange is constantly taking place between adjacent races.

However this may be, the basic migratory pattern, essentially the same for all of them, may be conveniently divided into the three successive phases noted previously—sardine, fat, and spawn.

Those of the sardine stage, 45–200 mm long, tend to remain near their birthplace. They probably spend the winters on the bottom in a few fathoms, appear in the inshore waters of New England, New Brunswick, and Nova Scotia in the spring as one- and two-year-old fish, and remain there through the summer and autumn. How far they may journey during this period and in what direction depends chiefly on the movements of the water. For example, every summer untold millions of sardines congregate in the Passamaquoddy region at the entrance to the Bay of Fundy (p. 290), and it is now known[13] that the responsible factor is the prevailing movement shoreward of the subsurface water in which the sardines are swimming; this shoreward flow is motivated by the offshore movement of surface flow from tributary streams combined with superficial offshore currents set up by the wind. Sardine-sized fish, in other words, drift with the current much as do any planktonic animals, such as the euphausiid shrimps and copepods on which they feed. In technical language, they are denatant, which applies equally wherever young Atlantic Herring are produced.

The fat stage consists of sexually immature fish about two years old and 190–200 mm long that have accumulated a large amount of fat around the viscera and among the body tissues. During the year's period that precedes their sexual maturity, they disperse much more widely than do the sardines. Whether this wide scattering is brought about wholly by transport of water movements or whether directive swimming plays an important role remains a mystery. In either case they are encountered anywhere and everywhere throughout the range of this species. In the Gulf of Maine, for example, where more attention has been paid to the movements of these fish than has been the case anywhere else in the western North Atlantic, the fat stage has been encountered indifferently close to shore, as at the mouth of the Bay of Fundy in the northeast, and offshore in the Massachusetts Bay region in the

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[13] Studies carried out from the Atlantic Biological Station at St. Andrews, chiefly under Dr. A. G. Huntsman's leadership (*65*: 95, 96).

southwest, in the central parts of the Gulf, and over Georges Bank. Those picked up during the warmer months either in mackerel seines or in otter trawls are mostly very fat and show no signs of approaching sexual maturity. It seems that these "fat" fish, like the sardines, merely sink down close to the bottom for the winter wherever they may be.

About all that is known of the mature spawn stage in the western Atlantic is that these fish live mostly some distance offshore near bottom and appear in vast numbers in their spawning areas at spawning time. In the Gulf of Maine, most of them seem to drop out of sight after having spawned; the large ones caught there out of spawning season fall in the fat category. But there is no reason to suppose that they travel far during the interval (between spawning time and winter) when they are feeding greedily to recover condition sufficiently for spawning again the next year. In fact, it is probable that they, like the other two stages in the Gulf of Maine, merely descend into deeper water to winter, as has long been known to be their custom in European waters. How deep the great body of them may go is not known, but the contour of our continental shelf is such that no fish need swim any great distance to reach water deeper than 50–75 fms. anywhere between Cape Cod and the Gulf of St. Lawrence. It seems likely also that they spend the winter in deep water in the southern part of the Gulf of St. Lawrence, but definite information in this regard is lacking. On the southern and western coasts of Newfoundland, however, where spawning takes place in the spring, the mature fish "move off into deeper water in summer" (*125*: 35) but return late in the autumn to their natal bays, where they have long supported important November–January fisheries.

Food and Feeding. Atlantic Herring feed on plankton—first on diatoms and other unicellular organisms, then on copepods and their eggs following the yolksac stage (*91*: 252). In summing up her rather extensive investigations at Plymouth, England, Lebour (*79*: 463) listed the following by stages of growth; before disappearance of the yolksac: larval gastropods, green food (probably diatoms and flagellates), larval bivalves, nauplii and other young stages of small crustacea, as well as the eggs; after disappearance of the yolksac up to about 12 mm: the same, but with small adult copepods added; after 12 mm and probably until metamorphosis: copepods; after metamorphosis: copepods, decapod crustaceans, amphipods, and fish.

Only two kinds of food were found in about 1500 examples taken off Eastport, Maine (*95*: 401). Moore said that "One of these [foods] consisted of copepods ('red seed'), which appeared to constitute the sole food of the small herring, the so-called brit, and a considerable portion of that of the larger individuals from $5^1/_2$ inches upward." But the principal food of the larger fish was euphausiid crustaceans (*Meganyctiphanes norwegica*), known to local fishermen as "shrimp." These are so important in the diet of this species that it seems likely that the appearances and disappearances of large fish in the open waters of the Gulf are correlated with the presence or absence of euphausiids of one kind or another. Concerning their capture, Moore remarked:

> To capture such prey requires some address on the part of the herring; they frequently throw themselves almost clear of the surface and their splashings... are audible at a considerable distance. When feeding on copepods the movements of the herring are less impetuous. They swim open-mouthed,[14] often with their snouts at the surface crossing and recrossing on their tracks and eventually straining out the minute crustaceans by means of their branchial sieves.

The sieves were described by Moore (95: 401) as follows:

> An examination of the mouth cavity of the herring will disclose a series of long bristle-like processes, the gill rakers, projecting from the anterior face of each gill arch, like the teeth of a comb. When the mouth is opened widely the tips of the gill rakers stand apart, but when it is closed or partly closed they become more closely approximated and each series is pressed closely against the inner face of the series attached to the arch next in front. There is thus formed a beautifully fine and effective sieve, capable of retaining small bodies contained in the water taken in at the mouth and discharged through the gill slits.

The amphipod genus *Euthemisto* is also an important food for this species off Europe; that this is not so in the Gulf of Maine no doubt reflects the scarcity of this pelagic crustacean in our coastal waters. In default of an abundant supply of crustacea, and sometimes even when these are plentiful, the fish feed on whatever other kinds of smaller planktonic animals and plants may be available. Small fish of various kinds have been found in their stomachs: capelin, especially in Newfoundland waters in winter; and grass shrimps (*Crago*), schizopod shrimps (*Mysis*), amphipods (*Gammarus*), small squid, annelid worms, and crab larvae at Woods Hole, Massachusetts. But the smaller planktonic plants, whether diatom or peridonidian, have never been found in specimens longer than 15 mm, probably because their gill sieves are not fine enough to retain them.

Enemies. Their chief natural enemies include all kinds of marine predators, such as cod, pollock, haddock, silver hake, mackerel, dogfish and other sharks, finback whales, and the common squid (*16*: 104). An attack on a school of young Atlantic Herring by squid has been described by Hildebrand and Schroeder (*59*: 82) as follows:

> We had occasion to watch the wholesale destruction of 2 to 4 inch herring during June 1925, on the flats about Provincetown, Mass. Schools of 10 to perhaps 50 squids circled around a school of herring until they had bunched their prey into a compact mass. Individual squids then darted in and seized one, sometimes two, and then darted back for more. Along the beach there remained a silvery streak of dead herring.

A similar firsthand account of silver hake (*Merluccius bilinearis*) driving a school of large Atlantic Herring up on the beach in Massachusetts Bay has been reported (*15*: 90).

Parasites. Among the European fish, "cestode larvae and trematodes were frequently found as parasites in the gut. The latter were common and the incidence appeared to increase as the herring grew, as many as 29–30 per cent being parasitized in the large catches of May 21 and 30. Cestode larvae were less numerous, and they too were more frequent in the older fish" (Marshall, *et al.*, *91*: 253). No fatalities were specifically ascribed to these parasites; Sindermann and Rosenfield have found that infestation with trematode larvae may be fatal—at least under experimental con-

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[14] That the larger herring "swim open-mouthed" when feeding on copepods has been questioned by Battle, *et al.*, who are of the opinion that the fish seize the organisms individually (7:411). However, as to the organisms ingested there is general agreement.

ditions—"provided they are present in numbers large enough to overwhelm the host" (*117*: 12). Furthermore, it has been reported that nematodes, cestodes, and trematodes occur in the viscera and sporozoa in the muscles of small fish taken at Woods Hole, Massachusetts (*85*: 473).

Mass Mortalities and Diseases. The literature that deals with the Atlantic Herring contains many accounts of their great destruction on both sides of the North Atlantic. For June and July 1914, Cox reported widespread mortality on both the southern and western sides of the Gulf of St. Lawrence (*28*: 82–85). A few years later, a spectacular event occurred in Cohasset Harbor, Massachusetts Bay, on October 5, 1920, when an estimated 20,000 barrels of fish 100–125 mm long became stranded on the mud with a falling tide (*16*: 104). On October 10 a second but smaller run and on October 15 a run as large as the first were stranded similarly. The exact reason for the stranding and mass destruction was not determined, but fishermen thought that the fish had been driven into the nearly landlocked harbor by silver hake, *Merluccius bilinearis.* Other mass strandings of small individuals have also been reported, for Manchester Harbor, Massachusetts (*14*: 327). Pursuit by predatory fishes is the most likely cause of simultaneous mass strandings within small areas; for an eyewitness account of one such event, see page 285.

But enough evidence has now accumulated to make it practically certain that when mortality is very widespread it has been caused by disease of one kind or another. Thus Cox found that fish from the Gulf of St. Lawrence case of 1914 (above) were so evidently in a diseased condition and were so heavily infested with a myxosporidian protozoan that it seems practically certain that the latter had been responsible for the mortality (*28*: 82–85). It is known now that those along the coasts of New England, and presumably in more northern waters, suffer from fungous disease caused by *Ichthyosporidium*, from ulcer disease caused by protozoa, from pigment spot disease caused by larval trematode worms, and from tail rot caused by bacteria; it is known also that fungous disease in particular, and probably the others as well, sometimes reaches epidemic proportions, with mortality so widespread and so severe that the sardine fishery is very seriously affected.[15]

Relationships. Although the Pacific herring has been recognized as being specifically distinct from the North Atlantic Herring and has for many years been designated *Clupea pallasii* Cuvier and Valenciennes, it is difficult in the light of rather recent studies to find distinguishing characters. This difficulty was pointed out by Rounsefell, who made some studies of the relationship himself and reviewed the findings of several European investigators (*111*: 243). The distinguishing character given by Regan in his revision of the Clupeidae is "Ventral scutes all keeled" in *harengus* and "Ventral scutes in front of pelvic fins not keeled" in *pallasii* (*106*: 227). According to the material now at hand, the scutes in *pallasii* are merely less strongly developed.[16]

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15. For a general survey, with photographs, of diseased fish, and references, see Sindermann and Rosenfield (*117*).
16. Relationships with the species of temperate southern hemisphere waters have not been adequately worked out. Regan, the most recent revisor, had inadequate material (*106*: 228). Norman did not attempt to compare the South

Variations. It has long been generally appreciated that Atlantic Herring in the east do not constitute a homogeneous population, since a number of regional races is included (pp. 282, 283). Thus "it is possible," writes Norman, "to recognize North Sea, Baltic, Norwegian, Icelandic herring" (*101*). These races differ from each other in such morphologic characters as average proportional dimensions and average numbers of fin rays and vertebrae. But we ought to caution the nontechnical reader that these are numerical averages for many specimens and are not used for the identification of an individual specimen, or of even a few fish; only when the number of specimens examined is large are such figures significant. For example, if the average number of vertebrae was given as 56.3–56.5 for one locality and as 56.6–56.8 for another, it means simply that in the first case there were more fish with 56 vertebrae and less with 57; and in the second case, more fish had 57 and less had 56. No fish ever has a fractional number of vertebrae.[17]

Each of these races has its own chief center of abundance, its own pattern of seasonal migration, and its own spawning season or seasons, for some of the races include both early and late spawners. The races differ in the average size to which their members grow. A knowledge of the times and localities where these populations are catchable in greatest amount is of so much commercial importance that these matters are under continuous survey by the fisheries services of the countries chiefly concerned.

In 1914, Hjort found (*60*: 9–12) in the western Atlantic Herring: that the average number of keeled ventral scales is larger (13–14) for the autumn spawners of outer Nova Scotia and the Gulf of Maine than for the spring spawners of the Gulf of St. Lawrence; that the number of vertebrae is greatest (55–59, av. 56.8) in those from the west coast of Newfoundland; that the number of dorsal and anal rays averages higher in those caught in the open sea than in those from the more enclosed waters of the Gulf of St. Lawrence and Bay of Fundy; and that, among the spring spawning populations, the average number of vertebrae, fin rays, and keeled scales is higher in those from the west coast of Newfoundland than in those from the southern part of the Gulf of St. Lawrence. But the fishery for "fat" and for "spawn" fish plays so small a role in the general welfare of Canada and the United States (p. 288) that no additional information seems to have been contributed to the racial question on this side of the Atlantic. From analyses of extensive data, however, Day, Leim, and Tibbo showed that Canadian Atlantic Herring represent six more or less distinct populations, differing from each other in rate of growth and in average number of vertebrae: one in the northern part of the Gulf of St. Lawrence, a second in the Bay of Chaleur, a third in the southern part of the Gulf, a fourth off the outer Nova Scotian coast, a fifth along southern Newfoundland, and a sixth along western Newfoundland (see Leim, *83*: 11, figs. 6, 12).

Commercial Importance. From an economic standpoint, these fish are perhaps the most important in the world. In addition to their great value as food for man, many

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American forms with the northern ones (*102*: 37). Regan's *Clupea holodon* from New Zealand is now known as *Clupea antipodum* (Hector).—G. S. Myers.

[17] For a general survey of the races of eastern Atlantic Herring, see especially Lübbert and Ehrenbaum (*89*: 14–19); for a detailed study of the average number of vertebrae in the different races, see LeGall (*80*: 167–170).

are used for bait, and they constitute an important item in the diet of other fish that are of great economic importance. The catches have fluctuated greatly from year to year, but they have not always provided a criterion of the supply available. In America, at least, the catches have often been governed by demand and profit. Therefore the fishing efforts from year to year have not been uniform. Through 1952, the annual catches on the American side have fluctuated between 172,000,000–359,000,000 pounds,[18] the major part of the catch from Canada and Newfoundland. The catch in Europe in 1948 was 4,150,000,000 pounds (1,881,713,000 kilo; *24*: 6), and in 1956, the latest year for which information is conveniently available, it was 5,858,650,000 pounds (2,590,715,000 kilo). European waters, in short, have yielded annually something like 15 times the catch (in pounds) taken in American waters. However, the apparent discrepancy in relative productivity does not loom so large when we note that the bulk of the American catch is concentrated within a latitudinal belt of about 8°30′ at most, while the European catch is distributed along something like 19°30′, or a distance nearly 2.5 times greater.

Small fish, 75–125 mm or so in length, are canned in large quantities as sardines, not only in Norway but along the easternmost coast of Maine and in the region of Passamaquoddy Bay at the mouth of the Bay of Fundy on the New Brunswick side; these last account for the concentration of Atlantic Herring landings there. Elsewhere the American catch consists chiefly of the "fat" and "spawn" stages. Some of the large ones are consumed fresh, others are salted or pickled, some are salted and smoked in various ways, and still others are canned.

The three principal types of smoked Herring are the kipper, bloater, and red herring. The kipper is split down the back, immersed in brine for a very short period of time, slightly dried, and then smoked for several hours. The bloater is cured without splitting, only the belly being cut open for cleaning; it is lightly salted and smoked only long enough to dry the flesh. The red herring, like the bloater, is not split, but it is much more heavily salted (buried in salt for at least five days) and then smoked for ten days or so. Thus the last is a fairly durable product, which can be shipped to distant markets, whereas the kipper and bloater are perishable. The several curing processes are practiced much more extensively in Europe than in America and are sometimes carried out aboard fishing vessels. Large quantities are also frozen, to be used as bait by the hand-and-long-line fishermen: for example, 32,000,000 pounds in Canada (including Newfoundland) in 1954. While corresponding information is not conveniently available for the United States, this time-honored method of fishing is now far outstripped by the otter trawlers. The landings by line fishermen in Maine and Massachusetts in 1954 were 9,000,000 pounds, the greater part of which was hooked on frozen herring. The offal at the canneries and occasionally surplus catches of whole fish are reduced to oil, fish meal, and fertilizer.

Fluctuations in Abundance and Catch; *Year-Classes.* It is notable that a fishery such as the one for this species in European waters, exploited for centuries, has apparently

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[18] Statistics from publications issued by the governments of the respective countries named.

shown no positive or permanent decline. Of course it has been claimed from time to time that signs of exhaustion were evident, but such claims seem to have been based on the scarcity or disappearance of the fish in certain areas, not on the population as a whole. There certainly is insufficient information concerning the American stocks to furnish a basis for an answer. If a decline has taken place in American waters, it could scarcely be ascribed to overfishing, as the supply of fish generally has exceeded the demand. The fluctuations in the annual catches, then, do not necessarily mean that the fish were scarce when a small quantity was caught, or were abundant when a large catch was taken. Neither does a small annual catch necessarily indicate that the demand was light. It may mean only that the fishermen were operating in an area where the fish are usually abundant but were absent there that year. The fish are influenced in their migrations by the weather and by the presence of food, which seem to account for their abundance in one area one year and elsewhere the next. At present it is impossible to predict the time of arrival of schools in any given area.

From his studies of Atlantic Herring from the English Channel, Ford wrote, "if it could be shown that the variation from season to season followed some rule, it might yet be possible to discover that rule from the study of past data and hence to predict what is likely to occur in the future" (*36*: 369). But all uniformity seems to be lacking. "It can be regarded as certain that fishing results are dependent upon the weather, but in the present state of meteorological science, we cannot hope to receive much advanced information regarding weather conditions during a forthcoming season." Nevertheless, he found that daily forecasts had some value, for a gale warning not only indicated an interruption of operations, but it also suggested heavy catches when fishing was resumed. The prediction of calm weather, on the other hand, suggested lighter catches.

The many age analyses of Atlantic Herring, chiefly of those from European waters, have shown that a very large crop of young may survive in some years while very few do in other years, especially in more northerly spawning regions. Consequently, those spawned in a favorable year may dominate the population for several years to come. The classic example is the year-class produced in 1904 that dominated the Norwegian catches for the next six years and dominated catches on the west coast of Newfoundland until 1914 and even 1915. In the Gulf of St. Lawrence, of late years, the broods of 1939, 1941, 1943, and 1944 were highly productive, whereas those of 1940, 1942, and 1945 contributed but little to the population (*83*: 107). There is also the well-documented case of a particular body of Bay of Fundy fish that did not receive any significant recruitment for some 10 years, by which time the few remaining fish seem to have dropped out of the picture due to old age (*15*: 93, 99). Consequently, the successes or failures of reproduction in given years are reflected in the catches. Thus Ford (*36*: 370) was able to predict which year-classes would predominate in the catches of certain years, as well as the probable proportion of large fish, for as a rule old fish are larger than the younger ones, though the fish in some areas grow faster than those in others. Ford concluded his discussion on predictions as follows:

In practice it is possible to obtain advance information of the relative richness of broods and hence of the relative success of future fisheries. But there still remain possible influences which militate against a forecast of yield based entirely on this evidence, chief among these being the factors which govern migrations of herring.

Methods of Fishing. Most of the fish are caught in traps known as wiers, in floating traps, stop seines, purse seines, and drift nets; in the American bays and harbors, large numbers, especially of the smaller sizes, are taken by "torching," i. e. by netting fish attracted by a light.

Range. Atlantic Herring in American waters range from Greenland to North Carolina, but usually not in commercial abundance south of New Jersey; they are most abundant north of Cape Cod. In Europe, where certain races enter brackish water, they range from Spitsbergen, Novaya Zemlya, the Kara Sea, the White Sea, and northern Norway south to the Straits of Gibraltar.[19]

Occurrence in the Western North Atlantic. Stray specimens have been reported for as far south as Cape Hatteras, the lower part of Chesapeake Bay, Maryland, and New Jersey (*59*: 82; *119*: 120; *37*: 93); and only irregularly do a few visit the coasts of New York and Rhode Island. But they are seasonally abundant and generally distributed throughout the Woods Hole region, though not in any great numbers (*123*: 741). Although they appear sporadically in the Massachusetts Bay region, they are plentiful enough in some years to support local fisheries. Along the coast of eastern Maine, and in the Passamaquoddy region at the mouth of the Bay of Fundy,[20] they are not only far more plentiful but more regular in their comings and goings. But farther up the Bay of Fundy, on the New Brunswick side and at its head, they are far less plentiful, probably because of the turbidity of the water there. However, along the Nova Scotian side, toward the mouth of the Bay, they are sufficiently abundant so that they yielded between five and six million pounds in 1946 (Annapolis and Digby counties); indeed in the general vicinity of Yarmouth on the west coast of the province they are so plentiful that great numbers of giant tuna congregate there summer after summer to harry and destroy the schools in the local tide rips.[21] Thence eastward along the outer coast of Nova Scotia they are abundant and generally distributed; witness a reported catch between the vicinity of Cape Sable and Cape Breton of something more than 41 million pounds in 1946, and 21 million pounds in 1956, the latest year for which pertinent statistics are readily available.—H. B. B.

There are fewer, it seems, along the Nova Scotian shore line of the Gulf of St. Lawrence; landings there in 1946 were 1,330,000. But thence westward these fish are numerous again throughout the southern side of the Gulf,[22] around Anticosti Island (described there as in "bancs enormes"; *116*: 285) and along the Gaspé shore in the lower part of the St. Lawrence estuary. But they are progressively fewer up the

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[19] "With the favourable climatic conditions in Arctic regions, the Herring has spread to Jan Mayen, Spitzbergen, Nowaja Zemlya and Kara Sea" (Jensen, *67*:64).

[20] For details as to their regional and seasonal occurrence in the Gulf of Maine, see Bigelow and Schroeder (*15*:93).

[21] The annual "Tuna Tournament" is held at Wedgeport, Nova Scotia, not far from Yarmouth.

[22] 1946 catches, 36,103,600 for the New Brunswick shore of the Gulf; 6,080,100 for Prince Edward Island; 15,078,000 for the Magdalens; 15,525,000 for Bonaventure and Gaspé counties, Quebec.

St. Lawrence, and we find no report of them beyond Trois Pistoles, Quebec, about opposite the Saguenay River. Although the area of abundance does not extend to the northern shore of the Gulf, they are widespread there as well as in the Strait of Belle Isle; the 1946 catch for this entire coastline was only 923,700 pounds. They have been reported also for the banks in the northeastern corner of the Gulf between Newfoundland and Labrador (*125*).

They are so plentiful along the Newfoundland shores of the Gulf that they have long supported important fisheries in and off Bay of Islands and at Bonne Bay. Indeed, "it seems proven . . . that practically all the Newfoundland bays are frequented by spawning herring often in great numbers" (Thompson, *125*: 36). Thus Fortune and Placentia bays on the eastern part of the southern coast have been the sites of productive Atlantic Herring fisheries since the days of the early cod fishery; the local catch is used chiefly as cod bait.

The reported commercial catch of Atlantic Herring in 1946 for Newfoundland as a whole was only about 65 % of that for the southern part of the Gulf of St. Lawrence on the Canadian side[23]. This, taken at face value, suggests that the cold waters of eastern Newfoundland produce fewer Atlantic Herring than the waters of the south and west coasts. However this may be, they are at least moderately plentiful on the east coast of Newfoundland right up to the entrance of the Strait of Belle Isle; Jeffers not only reported them for Rahleigh but stated that they were numerous enough at Quirpon to supply the local inhabitants with winter food for their sledge dogs (*66*: 206). They have also been reported for the northern side of the Strait at Blanc Sablon (*121*: 124), and repeatedly for the Strait without specified locality.

But a review (perhaps not sufficiently searching) of the various lists of Labrador fishes has not yielded any reference to their presence anywhere to the north of the Strait, apart from Stearns' report that they are abundant "north of Blanc Sablon, growing more and more so all along the Labrador coast, the farther down which are the greatest catches" (*121*: 124).

The offshore boundary of their range follows in general the break in slope at the outer edge of the American continental shelf. Schools are occasionally seen at the surface or are picked up by trawlers here or there on Georges and Browns banks, fronting the Gulf of Maine (*15*: 95). It seems the situation is similar on the Nova Scotian Banks eastward to Banquereau and on the Newfoundland Banks, where they are often taken by otter trawlers in quantities (*125*: 36). All this has long been common knowledge among the banks fishermen. During the early years of the Georges Bank cod fishery, it was common practice to set herring drift nets for bait (*16*: 102). And it may well prove that they are much more plentiful on the banks than is now realized, for while the numbers reported (*15*: 95, for Georges Bank) have been insignificant, no serious attempt has yet been made to sample the offshore population with drift nets, midwater trawls, or bottom trawls of a kind adapted to the capture of this particular fish.

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[23] Data on Canadian catches are published annually in "Fisheries Statistics of Canada."

It has been known since Fabricius' day (*34*) that there were Atlantic Herring in western Greenland waters, in small numbers. They are now known to be widespread along the southwestern and western coasts, northward at least to 72°30′ N, though not in any great numbers if judged by the standards of northern Europe or the American coast. Their eggs have also been found in the Julianehaab district. The spawning extends through August and into September, and the presence of young fry is proof of successful local reproduction. In 1932 Hansen reported the presence of schools on the eastern coast in the neighborhood of Cape Walloe and Grittenfeldts Island (*53*: 42); he also reported the capture of a specimen near Angmagssalik. The evidence, in short, is strong that this species has expanded its range in Greenland waters during the past 30 years or so, as have other boreal sub-Arctic fishes (for details as to their occurrence in Greenland waters, see Jensen, *67*: 61–64).

Synonyms and References:[24]

Clupea harengus Linnaeus, Syst. Nat., ed. 10, 1758: 317 (diagn.); Cuvier and Valenciennes, *20*, 1847: 30, pl. 591 (descr., anat., life hist., distr., etc., includ. review of lit.); Günther, Cat. Fish. Brit. Mus., *7*, 1868: 415 (refs., descr., Europe and N. Amer.); Jordan and Gilbert, Bull. U. S. nat. Mus., 16, 1882: 265 (descr.); Goode, *et al.*, Fish. Fish. Industr. U. S., 1 (3), 1884: 549–568, pl. 204 (abund., import., distr., migr., reprod., food, capture, uses); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 421; 47 (4), 1900: fig. 18 (descr., synon.); Smith, Bull. U. S. Fish Comm. (1897), *17*, 1898: 91, (spawn., growth rate, Woods Hole, Massachusetts); Linton, Bull. U. S. Fish Comm. (1899), *19*, 1901: 437 (food, parasites); Bean, 7th Rep. Forest Comm. N. Y. (1901), 1902: 298, with fig. (econ. import., spawn., range); Bean, Bull. N. Y. St. Mus., 60, Zool. 9, 1903: 192 (synon., refs., descr., import., abund., spawn., distr.); Fowler, Rep. N. J. St. Mus. (1905), 1906: 93, fig. (diagn., New Jersey); Smith, N. C. geol. econ. Surv., *2*, 1907: 120 (descr., range); Ehrenbaum, Eier und Larven Fisch., Nord. Plankt., 2, 1909: 361 (develop. of eggs and larvae); Sumner, Osburn, and Cole, Bull. U. S. Bur. Fish. (1911), *31*, 1913: 741 (refs., season. abund., spawn., food, parasites, Woods Hole, Massachusetts); Cox, Contr. Canad. Biol. (1914–16), 1916: 81 (disease, Gulf of St. Lawrence, 1914); Meek, Migrations of Fish, 1916: 67–88 (genl. acct.); Regan, Ann. Mag. nat. Hist., (8) *19*, 1917: 227 (diagn. in key); Lebour, J. Mar. biol. Ass. U. K., N. S. *12* (3), 1921: 459 (food of young clupeoids); Bigelow and Welsh, Bull. U. S. Bur. Fish. (1924), *40*, 1925: 92, fig. 40 (descr., range, breed. habits, growth, size, season, movements, food, enemies, destruct. by natural causes, annu. fluct., Gulf of Maine); Jordan, Fishes, 1925: 275 (distr., abund.); Hildebrand and Schroeder, Bull. U. S. Bur. Fish. (1927), *43*, 1928: 81 (refs., descr., spawn., import., rare in Chesapeake Bay); Breder, Field Bk. Mar. Fish. Atl. Cst., 1929: 64, fig. (range, import., habits, size); Jordan, Manual Vert. Anim. NE U. S., 1929: 39 (diagn., range); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 41 (range, synon.); Perlmutter, 28th Rep. N. Y. Conserv. Dept., Suppl., 15 (2), 1939: 17 (spawn., eggs, young caught, Long Island, New York); Greeley, 28th Rep. N. Y. Conserv. Dept., Suppl., 15 (2), 1939: 82 (Long Island, New York); Bigelow and Schroeder, Bull. U. S. Bur. Fish., *48*, 1940: 327 (range extension; catch on Georges Bank; distr. of young); Warfell and Merriman, Bull. Bingham oceanogr. Coll., *9* (2), 1944: 51 (near New Haven, Connecticut; sizes and spawn.); Anonymous, Fish. Resources U. S., Senate Doc. No. 51, 1945: 61–62, with figs. (commerc. import., range, life hist., fluct.); Bigelow and Schroeder, Fish. Bull. (74) U.S. Fish Wildl. Serv., *53*, 1953: 88–100 (descr., life hist., Gulf of Maine).

[24] Numerous accounts pertaining wholly or in part to this Herring have been written, for it has been a principal subject of extensive study for centuries. A complete bibliography would occupy many pages. Therefore, the references given herein are limited to the papers actually quoted (directly or indirectly), to taxonomic works of a general nature, or to faunal lists of the American coast. Many of these also contain bibliographies. Furthermore, references are given to publications containing descriptions of the species itself and of several "species" now considered synonymous with *Clupea harengus*. For additional references bearing especially on the biology of this species, see Scattergood (*114*).

Clupea elongata LeSueur, J. Acad. nat. Sci. Philad., *1* (2), 1818: 234 (orig. descr.; type local. Marblehead and Sandy Bay, Massachusetts).

Herring, Moore, Rep. U.S. Comm. Fish. (1896), *22*, 1898: 387–442 (life hist., econ. import., Passamaquoddy Bay); Huntsman, Canad. Fish. Exped. (1914–1915), 1919: 165–171 (growth of young); Lea, Canad. Fish. Exped. (1914–1915), 1919: 75–165 (age and growth, Canad. waters); Norman, Hist. Fishes, 1931: 42, 65, 80, 91, 135, 183, etc. (genl. acct.); Anonymous, Rep. U.S. Tariff Comm., (2) 69, 1933: 78, 106, 117, 143, 149–151, 157, 161, 163–165, 218 (statist. fishery products, Europ. and Amer. countries); Ford, J. Mar. biol. Ass. U. K., N. S. *19*, 1933–34: 305 (econ. of fishery, Plymouth, England; life hist. data; forecast. catch); Battle, Huntsman, Jeffers, Johnson and McNairn, J. biol. Bd. Canad., *2* (4), 1936: 401 (fatness and food of young, Passamaquoddy Bay); Marshall, Nicholls and Orr, J. Mar. biol. Ass. U. K., N. S. *22*, 1938: 245 (growth, feed., Clyde); Johnson, J. Fish. Res. Bd. Canad., *4*, 1939: 349, 392 (effects of light on movements, feed.). Leim, Tibbo, and Day, Bull. Fish. Res. Bd. Canad., 3, 1957: 1–184 (investig. e. Canada, growth, abund. populations, year-classes).

Doubtful References:

Clupea halec Mitchill, Rep. in part, Fishes of New York, 1814: 20 (orig. descr.; type local. New York; type lost; possibly a species of *Pomolobus*); Mitchill, Trans. Lit. philos. Soc. N. Y., *1*, 1815: 451 (descr.).

Clupea coerulea Mitchill, Trans. Lit. philos. Soc. N. Y., *1*, 1815: 457 (orig. descr.; type local. New York; type lost; possibly a species of *Pomolobus*).

Genus *Alosa* Link 1790

Shads

Alosa Link, Mag. Physik. Naturg., Gotha, *6* (3), 1790: 35; type species not specified; Cuvier, Règne Anim., ed. 2, *2*, 1829: 319; type species *Clupea alosa* Linnaeus, same as *Alosa* Link.

Generic Synonym:

Alausa Cuvier and Valenciennes, Hist. Nat. Poiss., *20*, 1847: 389; type species *Alausa vulgaris* Cuvier and Valenciennes equals *Clupea alosa*, apparently a variant spelling of *Alosa* Link.

Characters. BODY compressed, rather deep to elongate. BONY SCUTES rather prominent, with sharp points; the chest and abdomen with a sharp edge. CHEEK (bone below eye) notably deeper than long (Fig. 69). MOUTH large. MAXILLARY generally extending beyond middle of eye. UPPER JAW with a definite median notch. LOWER JAW largely included in upper one, its upper margin within the mouth rising gradually (Fig. 69). TEETH in jaws minute or absent (absent in American adults); none on vomer or tongue in adults. DORSAL with 16–22 rays, its last ray not produced, its origin nearer to end of snout than to base of caudal. ANAL with 18–27 rays (18–22 in American species), the last ones not enlarged. PELVIC usually with 9 rays, inserted under base of dorsal. VERTEBRAE about 52–59.

Remarks. This genus is very close to *Pomolobus*, with some of the species being difficult to separate generically. The species herein assigned to *Alosa* have a deep median notch in the upper jaw; the lower jaw shorter than the upper, with the upper margin (within mouth) not rising abruptly; the cheek deeper than long; and the adults without teeth. A combination of these characters is required to identify the species of *Alosa*.[25]

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[25] The two "wing-like plicae of skin, covered with elongate scales (*alae*)" on the base of the caudal, designated the leading diagnostic character by Borodin in his revision of the genera *Alosa* and *Pomolobus* (*18*:175), seem unusable because too often they are indistinct on preserved specimens.

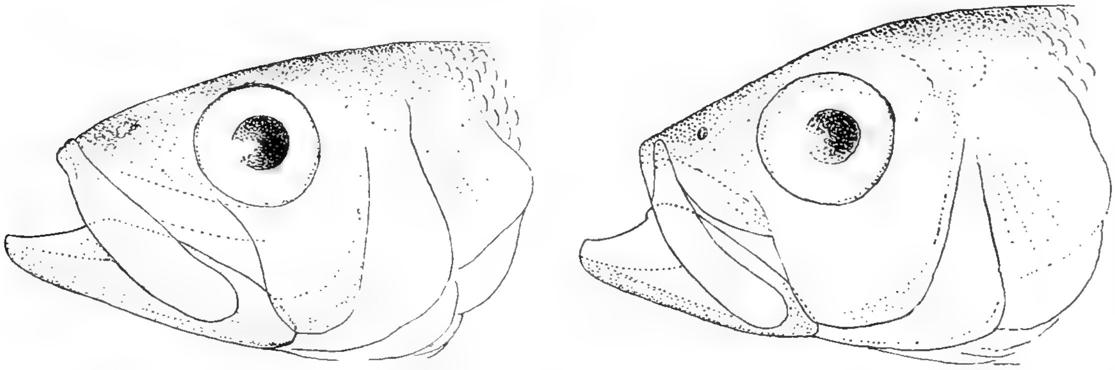

Figure 69. Heads showing shape of mandible and cheek. left, *Alosa sapidissima*, 93 mm TL, Clifton Beach, Maryland; right, *Pomolobus aestivalis*, 82 mm TL, Smith Point, Maryland. Both drawn by Louise Nash.

Range. Two species occur off Europe, another off northern Africa, and two off North America, where the recorded range extends from southeastern Newfoundland, the St. Lawrence River, Quebec, and northern Nova Scotia southward to Indian River City, Florida, and the Gulf of Mexico westward to the Mississippi River.

Key to North American Species

1 a. Lower limb of first gill arch with 59–73 rakers (26–43 in young under 125 mm). *sapidissima* (Wilson) 1811, p. 295.

1 b. Lower limb of first gill arch with 42–48 rakers in adults (27–33 in young 48–90 mm long). *alabamae* Jordan and Evermann 1896, p. 308.

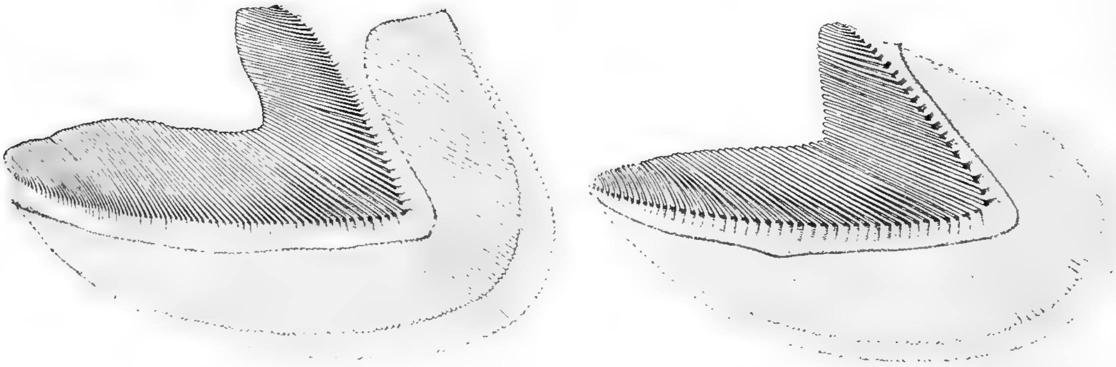

Figure 70. First branchial arch, showing numerous gill rakers: left, *Alosa sapidissima*, 550 mm TL, USNM 20969; right, *A. alabamae* (with fewer rakers), 390 mm TL, type, USNM 47689. Both drawn by Ann S. Green.

Alosa sapidissima (Wilson) 1811

American Shad, Atlantic Shad, Shad, Common Shad, White Shad

Figures 69–74

Study Material. At least 75 specimens, 35–580 mm TL, 29–475 mm SL, from St. Andrews Bay, New Brunswick; Flag Island, Eastport, and Portland, Maine; Holyoke and Woods Hole, Massachusetts; Noank, Connecticut; Long Island, and Gravesend Bay, New York; Great Egg Harbor, New Jersey; Delaware City, Delaware; many places in Chesapeake Bay and tributary streams; Avoca and Beaufort, North Carolina; and New Berlin, Florida.

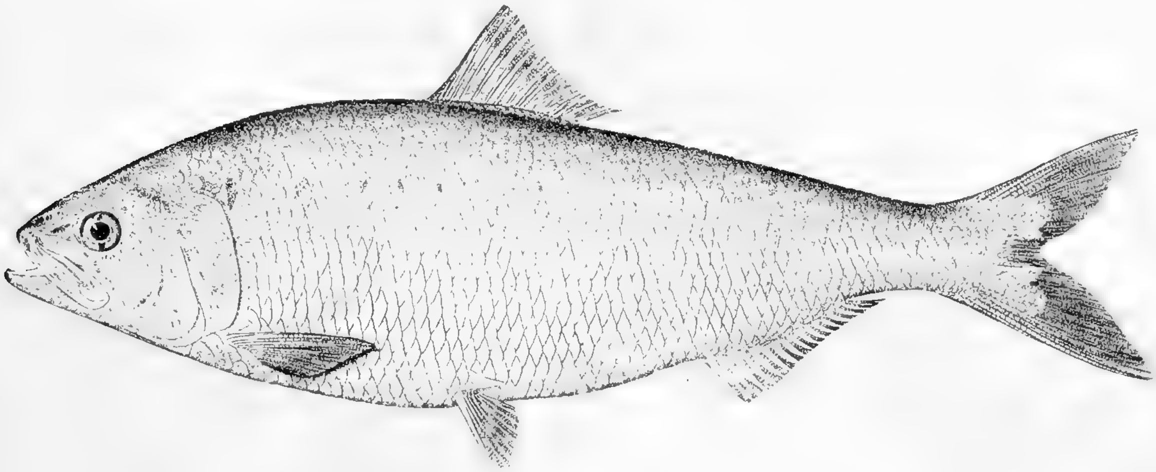

FIGURE 71. *Alosa sapidissima*, adult male, 480 mm TL, 19.13 inches, Norfolk, Virginia, USNM 25099. Drawn by H. L. Todd.

Distinctive Characters. For the features that distinguish the true shads (*Alosa*) from their close relatives, and for the difference between *sapidissima* and *alabamae*, see Key to Species, p. 294, as well as pp. 293, 304, 309, 310.

Unlike the adult with its toothless jaws and a median indentation in the upper jaw, young of 150 mm and less lack the indentation on the upper jaw and have minute teeth in the jaws. Therefore the jaw and tooth characters of the adult cannot be used in identifying the young. However, the deep narrow cheek as well as the slender mandible with its upper margin not rising abruptly to form an angle in the mouth will aid in separating young *sapidissima* from young and adult alewives of the genus *Pomolobus* (Fig. 69).

Description. Proportional dimensions in per cent of standard length, and counts, based on study specimens 29–475 mm SL.

Body: depth 30.2–36.8.

Caudal peduncle: depth 7.7–10.

Head: length 23–28.

Snout: length 4.85–7.1.

Eye: diameter 3.8–5.7.
Interorbital: width 4.55–5.95.
Maxillary: length 11–14.
Pelvic fin: length 9.9–11.9.
Pectoral fin: length 15.3–17.7.

Scales: 52–62.
Ventral scutes: 35–38.
Gill rakers: 59–73 in adults.
Fin rays: dorsal 17–20; anal 20–23; pectoral 15–17.
Vertebrae: 55–57 (4 specimens), 54–59 given in literature.

Body slender, compressed, its greatest thickness generally about half of its depth; the depth very variable, increasing with age, 2.75–4.0 in SL.

Scales moderately adherent, with crenulate membranous borders, 15 or 16 rows between base of pelvic fin and anterior dorsal rays. Ventral scutes well developed, 20–22 in front of pelvics, 14–17 behind them.

Head 3.6–4.4 in SL. Snout 3.6–4.6 in head. Eye 4.0–5.9. Interorbital 4.2–5.8. Mouth moderate, oblique; mandible included. Maxillary broad, its width about half of length of snout, with a broad supplemental bone, rounded posteriorly; reaching to middle of eye in young, generally to below posterior margin of eye in adults, 1.9–2.2 in head. Gill rakers increasing in number and proportionate length with age, those at angle shorter than snout in young but longer than snout in large specimens, 26–43 on lower limb in young 29–125 mm SL, 59–73 in specimens 300 mm SL and upward. Teeth missing in adults though present on jaws and median line of tongue in young.

Dorsal fin somewhat elevated anteriorly, its margin slightly concave, its last ray a little longer than the preceding one, its origin an eye's diameter or less in advance of pelvic fin and about equidistant between tip of snout and vertical from base of last anal ray. Caudal rather deeply forked, the lobes of nearly equal length and somewhat shorter than head. Anal low, its origin about an eye's diameter nearer to base of pelvic than to base of caudal. Pelvic near ventral edge, about equidistant between base of pectoral and origin of anal, 2.1–2.6 in head; the axillary scale equal to, or a little more than, half of length of fin. Pectoral a little higher on side than pelvic, 1.4–1.65 in head.

Color. Fresh specimens greenish to bluish with metallic luster above, gradually shading into the bright silver on sides. Dark spot on shoulder, sometimes followed by smaller spots or dots, rarely with a second parallel row of dots below the first. No dark lines along rows of scales. Fins pale to greenish, the dorsal and caudal somewhat dusky in large examples, and tips of lobes of caudal dark in some specimens. Peritoneum mostly pale to silvery.

Size. This species is the largest of the herrings. Females attain a maximum length of about 600 mm (30 in.) and a weight of 12 pounds in the Atlantic. On the Pacific coast, where the species was introduced, the maximum weight is even greater; females of 14 pounds have been reported. In the Chesapeake Bay area the average weight (and length) of females (roe shad) is probably somewhat under six pounds (about 57.5 cm; 22.75 in.), that of males (buck shad) about 3.5 pounds (about 50 cm; 20 in.).

Development and Growth. The eggs, about 3.5 mm in diameter after they are impregnated, are demersal, but they are only slightly heavier than the water in which they are deposited. As they are not adhesive, they drop loosely and singly to the bottom. According to Ryder they hatch in 52 hours at an average temperature of 57.2° F, and in less than 36 hours at an average of 74° F (*112*: 796). However, a longer incubation period was reported by Leim (*81*: 31), who said that eggs held under artificial conditions hatched in 12–15 days at 12° C (53.6° F) and in 6–8 days at 17° C (62.6° F).

The newly hatched fish, transparent and extremely slender, are about 9–10 mm long. The yolk is absorbed in four or five days at a water temperature of 62.5° F and in about seven days at 53.5° F; the fish have then attained a length of about 12–15.5 mm (*81*: 33). In some preserved specimens that show the yolk almost absorbed, the depth is only about 0.05 of the length, the large dark eyes protrude prominently, the dorsal fin fold is somewhat developed, and the alimentary canal is discernible, ending under the beginning of the posterior sixth of the body. During development, the vent moves forward as in other Clupeidae. The fins are fully developed in 21–28 days at a length of about 20 mm, when metamorphosis is nearly complete (*16*: 118). For a more detailed account of the development of the larvae, see Leim (*81*: 31–43).

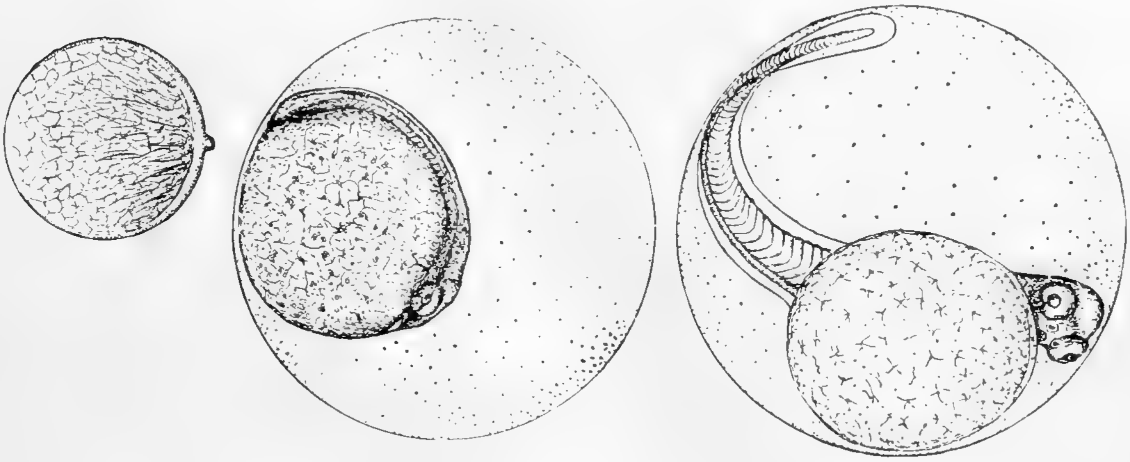

FIGURE 72. *Alosa sapidissima* egg development. LEFT to RIGHT: newly laid egg; embryo in natural position within enveloping membrane of egg (photograph); egg with embryo nearly ready to hatch. After Leach.

The young remain more slender than the adults until they are nearly grown fish, but even among sexually mature fish there is great variation in depth, seemingly not related to sex and only partly related to spawning conditions. In 25 young, 35–125 mm long, the depth varied between 26.5–30 % of SL, and in a lot of 12, 460–505 mm long, the depth was 32–48 % of SL.

A gradual increase in the number of gill rakers, as already indicated, also takes place with age and growth. For example, the number on the lower limb of the first arch varied as follows: in 18 young 35 to 65 mm long, 26 to 31; in 21 examples

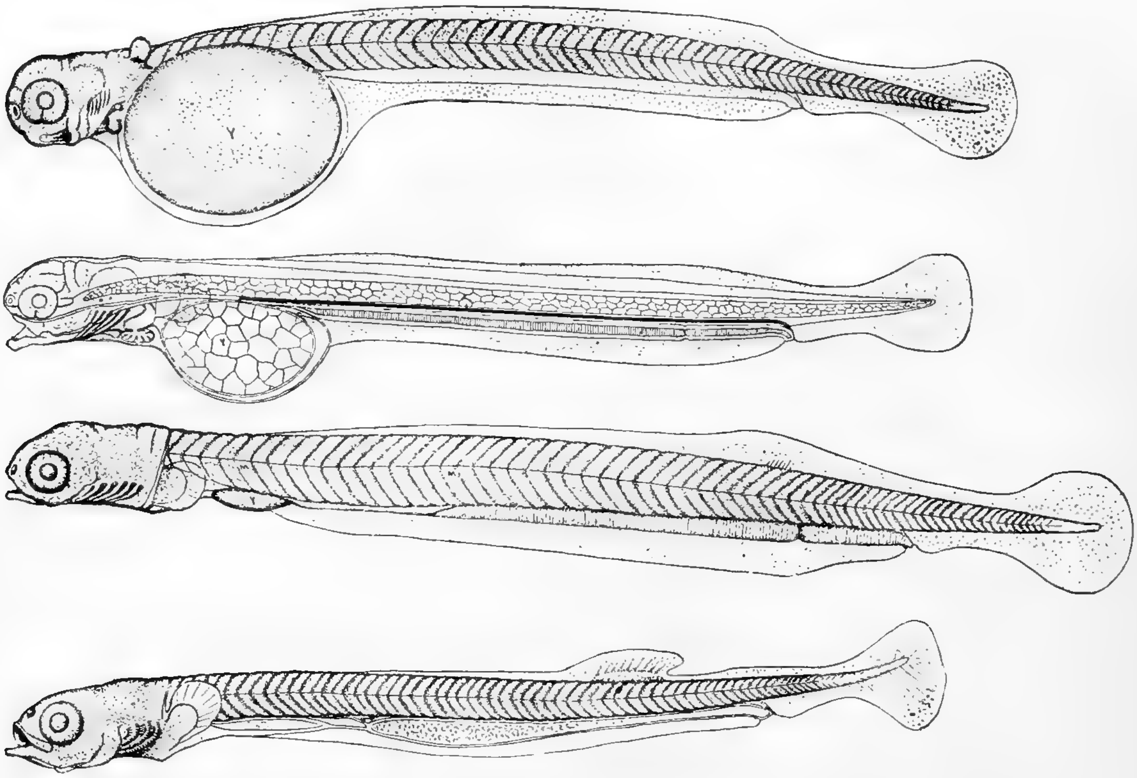

FIGURE 73. *Alosa sapidissima,* larval development. TOP, immediately after hatching; UPPER CENTER, third day after hatching; LOWER CENTER, five days after hatching; BOTTOM, 17 days after hatching. After Leach.

70 to 125 mm, 34 to 43; in 16 immature fish 190 to 270 mm, 48 to 62; and in 32 sexually mature examples 465 to 580 mm, 59 to 73.

The young grow rapidly during their first summer while in fresh water. The total lengths of 769 young taken in the Chesapeake Bay area—mostly from the Potomac River (in 1912)—ranged between 20–69 mm during June, 30–74 mm during July, 45–79 mm during August, 50–95 mm during September, 45–99 mm during October, and 60–119 mm during November (*59*: 98).

Larger young of 150, 175, and even 225 mm, at an age of seven months, have been reported. Such fish, in at least one instance, are known to have lived under specially favorable conditions in a pond well supplied with food (at Washington). Furthermore, according to Bean: "Nets set off shore in Gravesend bay [New York] in the fall frequently inclose large quantities of young shad, sometimes a ton and a half at one time, during the migration seaward ... The fish are usually about 6 to 8 inches long" (*8*: 208). One may question whether fish of such a large size, taken in such large quantities, were only six to seven months old. That the young grow faster north of Chesapeake Bay seems unlikely in the light of a statement by Bigelow and Welsh (*16*: 118) concerning this Shad in the Gulf of Maine: "The young shad remain in the rivers until fall when, at a length of $1^1/_2$ to $4^1/_2$ inches (37 to 112 mm) and resembling their parents in appearance, they move down to salt water." This range in length is close to that of fish of the same age from Chesapeake Bay and does not indicate more rapid growth in the more northern part of the range. However, Bigelow and Welsh added: "In the rivers of Maine the fry may be as long as 5 to 7 inches (125 to 175 mm) by the first week of November." Included in Hildebrand and Schroeder's data there were three specimens from the November collection that ranged somewhere between 145 and 244 mm in length (*59*); these fish were so much larger than the other 137 specimens taken in the same month that one is led again to suspect that they may have belonged to the one-year class.

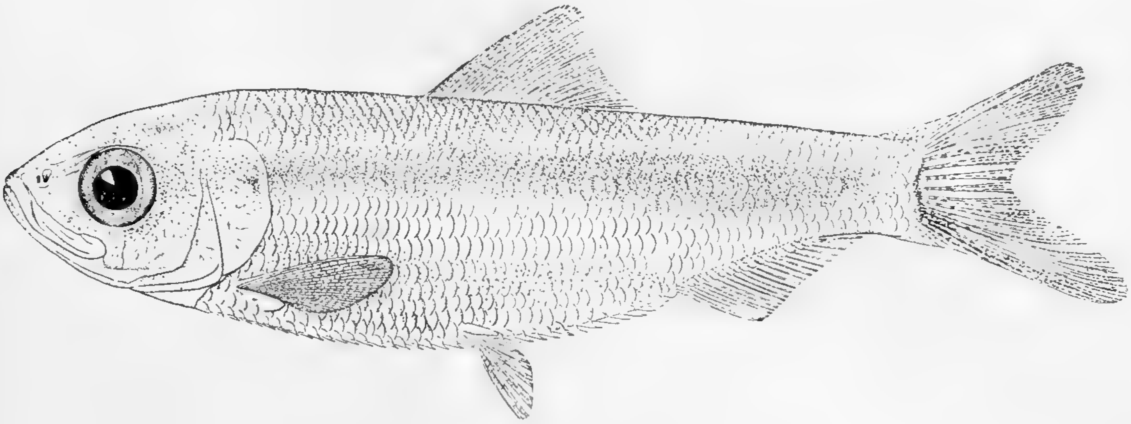

FIGURE 74. *Alosa sapidissima,* young, 47 mm TL, 1.88 inches, Beaufort, North Carolina. Drawn by Louella E. Cable.

The growth rate after the young have entered salt water is not well known because of the lack of specimens available for examination. Hildebrand and Schroeder listed 22 specimens that were spending their first winter in the deeper places of Chesapeake Bay instead of continuing their migration to sea (*59*: 98). Eight of these, taken in January, ranged between 95–124 mm and averaged 108 mm, 3 taken in February were 95, 105, and 135 mm long, 10 taken in March ranged between 105–159 mm and averaged 142 mm, and 2 taken in May were 145 and 154 mm long. Specimens of a somewhat similar size were dredged during the winter in the estuary of Newport River, Beaufort, North Carolina; 18 specimens caught in January ranged between 73–140 mm and averaged 117 mm; 14 caught in February were 100–160 mm and averaged 121 mm; and 3 caught in March were 84, 102, and 120 mm long.

Using mostly specimens from the Connecticut River, Borodin[26] (*17*: 183) determined the age of older fish from the annuli and transverse grooves on the scales, a method confirmed as practicable in Barney's study of otoliths (*5*: 168). Borodin provided a list of 10 size groups to which he assigned ages as follows: Group 1 — 58

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[26] Borodin, in determining the age of Shad from the scales, used the transverse grooves in addition to the annuli, having discovered that two complete transverse grooves are formed each year. Barney determined their age from the "limy deposits" in the otoliths, which form annual rings; he found that these annuli correspond to the annuli and crossgrooves on the scales used by Borodin.

to 113 mm long, 26 specimens from the river, all less than a year old; Group 2 — 145 to 180 mm long, 4 from salt water, in their second year; Group 3 — 210 to 290 mm, 7 from salt water, in their third year; Group 4 — 300 to 350 mm, 10 young males entering the river, in their fourth year; Group 5 — 360 to 390 mm, 22 young males entering the river, in their fifth year; Group 6 — 400 to 430 mm, 13 males and 9 females, in their fifth, sixth, and seventh years; Group 7 — 440 to 480 mm, 34 males and 9 females, in their sixth, seventh, and eighth years; Group 8 — 490 to 520 mm, 28 males and 13 females, in their seventh, eighth, and ninth years; Group 9 — 530 to 570 mm, 6 males and 43 females, in their seventh, eighth, ninth, and tenth years; and Group 10 — 580 to 660 mm long, 1 male and 23 females, in their eighth, ninth, tenth, and eleventh years.

Young fish from the Bay of Fundy reach a length of 41–45 mm in nine to ten weeks (*81*: 74–84). Leim's calculations, based on scale readings of adult fish, in general indicate a rather faster rate of growth for his fish than for those of Borodin.

Some of the males, according to Borodin, enter the Connecticut River from the sea when they are 300–350 mm long and in their fourth year, as shown in the preceding data. Although the author did not say so, these males undoubtedly were sexually mature, as migration to the rivers seems to be carried out solely for the purpose of spawning. The smallest females that returned to the Connecticut to spawn, according to the same author, were between 400 and 430 mm long and in their fifth, sixth, and seventh years. Therefore, the males seem to become sexually mature at an earlier age than the females. On the other hand, females may reach a greater age; among the older fish examined by Borodin, determined by him to be in their seventh, eighth, ninth, tenth, and eleventh years, there were only 7 males compared to 86 females. Concerning the Bay of Fundy fish, Leim said: "Most of the shad present on the spawning grounds were five years old or over and eight or nine years seems to have been the maximum age represented. Fish under four years of age apparently do not spawn at all" (*81*). The discrepancy in the rate of growth and the age of spawning fish, as determined by Borodin and by Leim, may have resulted from a difference in the interpretation of the scale markings, or from a difference in the behavior of two rather widely separated races that may respond differently to the climatic or general environmental conditions in which they live.

Reproduction. The average number of eggs produced by a single fish varies between 25,000–30,000 (*119*: 127). In the *Manual of Fish Culture* (*2*: 125) it is stated that the average number is not more than 30,000 but that a single fish has been known to yield between 60,000 and 115,000 eggs. In 1885, one from the Delaware River yielded 156,000. In this species, as among others, large fish as a rule produce many more eggs than small ones.

If all of the large number of eggs produced by a female hatched and reached maturity, the progeny would be exceedingly great. However, it is quite certain that normally only a small proportion of the eggs produces fish that live to maturity. The most critical time in the life cycle apparently comes when the larvae have absorbed the yolk and must find their own food. If food is found and if other conditions are favorable for survival, then the spawning season is a successful one. The success or failure of a spawning season in a river is usually evident from the size of subsequent catches when the fish hatched in a given year return later to spawn in the same stream. The comparatively large fluctuations in catches over a period of years no doubt result in large part from the measure of success of the particular spawnings from which the fish composing the catches were derived.

Spawning and Migrations. American Shad spawn in fresh water. Some spawn as soon as they arrive from the sea while others do not spawn until they reach the upper tributaries of rivers. Virtually all spawning, in this species as in many others, takes place in the evening between five and ten o'clock. While spawning, the fish are paired, swimming close together side by side. Since no nests are made, the eggs fall loosely in the water, and doubtless many are smothered when they fall on muddy bottom. An individual returns to spawn year after year.

The water temperature governs the date when mature American Shad approach the mouths of the rivers to spawn, about 50–55° being required. Accordingly, they appear off the Florida coast (St. Johns River) in November, to remain until March, in the sounds along the Carolina coast in February and March, in the Chesapeake Bay area in March and April, and farther north in May and June. But the precise date of arrival at any particular locality along the coast may vary by a couple of weeks from year to year, depending on the variation from year to year in the vernal warming of the water.

In large rivers, they run far upstream if their passage is not blocked. Thus they still run up 375 miles (or did recently) in the St. Johns River in Florida, 300 miles in the Altamaha in Georgia, about 200 miles in the St. John in New Brunswick, and at least 200 miles in the St. Lawrence (*122*: 11; *127*: 129, 130). American Shad ascending the estuary of the St. Lawrence may travel as much as 25–50 miles in 24 hours (*127*: 129).

The spent fish, very thin after spawning, begin their return journey to the sea immediately afterward; i.e. in March to May in the southern part of the range and in June to August in the northern part. But the young fry (product of that season's spawning) remain in the parent stream until autumn, when the temperature falls to 60° or lower. In the Chesapeake Bay region, their migration out into salt water takes place principally in October and November; but it is not until late November or December that all of them are in salt water.

Southward from Cape Cod the spent fish vanish upon re-entering salt water. While a few young fry in the Chesapeake Bay area spend their first winter in the deeper parts of the Bay, those from the Hudson may linger nearby for an entire year, for catches of 6- to 8-inch fish in Gravesend Bay in autumn have been reported (*8*: 208). The larger sizes of immature fish vanish as completely from the southern part of the coast as do the spent fish, until they reappear there for their first spawning.

Spent fish up to ten pounds and averaging about five pounds have been reported as taken in the Gulf of Maine, and schools of them have been seined from time to time in summer and autumn, even in December, at various places along the Maine coast, where they have been the object of a frozen-fish industry in some years. Immature fish (0.5–2.5 pounds) sometimes congregate also along the Maine coast and are more or less common in the Massachusetts Bay region.

Clearly these Gulf of Maine fish are far too numerous to be derived only from the streams of the Bay of Fundy, as was formerly considered likely (*16*: 116). Recently, extensive tagging experiments (*15*: 111, ftn. 18–20; *124*) have shown that, while some of them come from as far south as the Altamaha River, Georgia, others come from as far north as the St. Lawrence estuary, both of these contingents to fatten in the Gulf. By the end of December, however, they have vanished, not to reappear anywhere on the coast until the onset of the next spawning season, when the maturing fish return to the rivers of their native watersheds.

Like salmon and alewives, American Shad spend most of their life in the sea and make most of their growth there, but where they winter remains to be discovered. While in the sea, Shad are schooling fish, often in the thousands, and they never reenter fresh water until they return to spawn, although they may appear in brackish estuaries. They have been taken 25–90 miles out off southern New England, 110 miles out on Georges Bank, 40–50 miles out off the coast of Maine, and 50–60 miles off eastern Nova Scotia, and as deep as 50–68 fms.

Food. The diet of 14 young fish, 43–60 mm long, from fresh water of the Potomac River, consisted chiefly of adult and larval insects and ostracods, and in one instance a small fish (*59*: 95). Larger juveniles, 100–150 mm long, caught in Chesapeake Bay, presumably while en route to the sea, had fed mostly on *Mysis*, although one stomach contained fragments of a small fish, and another fragments of plant tissue.

Working with young specimens from the Shubenacadie River, tributary to the Bay of Fundy and its estuary, Leim found that the first food taken by larvae 11 mm long consisted of midge larvae (Chironomidae), while the somewhat larger larvae had fed principally on mature and immature copepods (*81*: 16). In fact, these organisms constituted the chief food of the young up to the time of transformation, with the relative abundance of these forms in a particular locality determining which food predominated. Dr. Leim's data show also that young adults taken in the same general vicinity continued to subsist principally on these same organisms. Other foods ingested consisted of ostracods, amphipods, insects, and fish.

Little or no food has been found in the stomachs of those caught while in fresh water en route to their spawning grounds, indicating that these fish, like salmon, do not ordinarily feed then. However, there are some records showing that adults occasionally do take food while in fresh water, at least late during the spawning season. They will often take a live minnow or an artificial fly when working upstream on their spawning run.

Many kinds of food have been found in the stomachs of those taken in salt water in estuaries and bays north of Cape Cod. But southward, examples are rarely obtainable in salt water, except during the migration to and from the spawning grounds. Therefore it is of interest that an adult female, caught in Chesapeake Bay in December, was gorged with parts of plants, among which were fragments of a mollusk shell. It has been reported also that adults taken in the vicinity of Savannah, Georgia, had fed on plants. Others caught near Fort Lee, New Jersey, had fed liberally on young shrimp, and still others, taken in Delaware Bay, had eaten small fish.

From an examination of about 350 stomachs of both mature and immature fish caught in the salt water of Scotsman Bay, Bay of Fundy, Leim found that, while copepods constituted the chief food of the smaller ones, as in fresh water, these crustaceans were unimportant in fish 400 mm and more in length (*81*: 68). Mysids, which were sparingly eaten by small fish, were the chief food of adult fish. In general, about 90 % of the specimens of all sizes from that area had eaten copepods and mysids, with ostracods, amphipods, isopods, decapod larvae, insects, mollusks, algae, fish eggs, and fish making up the remainder. After examining many stomachs of specimens taken in the Bay of Fundy, Willey also concluded that the chief foods consisted of copepods and mysids, to which he added shrimp and larval stages of barnacles (*133*: 313–320). Stomachs of fish from the Gulf of Maine have been found full of copepods (chiefly *Calanus*). American Shad also feed greedily on pelagic euphausiid shrimps.

Enemies. No doubt the larger predatory fishes are the principal enemies of the young while the latter are in the rivers. Although no records at hand show definitely that this is so, it can scarcely be otherwise, for the young are not rapid swimmers and do not ordinarily seek protection among plants or other cover. Furthermore, they are small enough, at least during the early part of summer, to be swallowed by bass and other carnivorous fishes only an inch or two long. Water birds, turtles, and water snakes no doubt feed on them too. The toll taken by predatory fishes while the young are en route to the sea may not be very great, for this migration takes place in the fall when many marine fishes (at least in Chesapeake Bay) have left the shallow waters. At sea they doubtless fall prey to all the larger predaceous fishes, and perhaps to finback whales as well.

The chief enemy of the adults is man, who has not only depleted the stock in many rivers through overfishing but has cut them off from spawning areas through the construction of barriers and by polluting the waters with deleterious wastes.

Parasites. The parasites of *A. sapidissima* have been made known principally through several papers by Edwin Linton and by Charles B. Wilson, based mostly on specimens obtained from fish caught in the vicinity of Woods Hole, Massachusetts. The findings were summarized by Sumner, *et al.* (*123*: 742) as follows: "Acanthocephala (Linton) *Echinorhynchus acus.* Nematodes (Linton) — *Ascaris adunca*, *Ascaris* sp. (immature). Copepods (C. B. Wilson) — *Caligus rapax.*" To this list was added the copepod *Lernaeenicus radiatus* (*135*: 59). Working with both young and adults from the Shubenacadie River and Scotsman Bay, Leim found no external parasites and only three internal ones, namely "distomes, nematodes, and Acanthocephali" (*81*: 74). It is not stated whether any of these parasites were considered seriously detrimental to the host.

Relationships. There are two well-marked species of this genus in Europe, *A. alosa* and *A. finta*, both of which have the deep cheek and notched upper jaw as in American species. However, *A. alosa* has smaller scales (72–80 lateral series) and more numerous gill rakers (72–86 on lower limb in adults) than the American species. *A. finta*, while agreeing with the American species as to scales, has only about 24–32 gill rakers on the lower limb, in grown examples.

The two American species recognized here, namely *A. sapidissima* and *A. alabamae*, differ principally in the number of gill rakers; mature examples of *sapidissima* have 59–73 on the lower limb whereas specimens of *alabamae* of similar size have only 41–48. The relationship of these species is discussed further in the account of *alabamae* (pp. 309, 310).

Variations. The specimens examined, from various localities within the range (p. 295) and used in preparing the *Description*, do not differ specifically or subspecifically. However, racial differences have been recognized. Vladykov and Wallace have found slight average differences in the number of vertebrae, pectoral rays, and ventral scutes between examples from the Bay of Fundy, Delaware Bay, and Chesapeake Bay; these they regarded as different "populations" (*130*: 52–66). Investigators of the U.S. Fish and Wildlife Service, in a special study of *A. sapidissima*, found that virtually every important river system within the range of this fish is inhabited by a different race (unpublished data).

Commercial Importance. This species has been an important foodfish throughout its entire range since the earliest settlers arrived, and no doubt these fish were taken by the Indians long before. Unfortunately, pollution, overfishing, and dams constructed across the streams (preventing the fish from reaching their spawning grounds) have caused partial and sometimes serious depletion, or even virtual extermination. So many streams have been dammed, particularly in New England, that, in the words of Bigelow and Welsh: "the local stock of shad has diminished until now the Gulf of Maine stock is but a shadow of its former abundance . . ." (*16*: 114). The great decline in abundance in New England is evident from the published statistics of the former United States Fish Commission, U.S. Bureau of Fisheries, and the present U.S. Fish and Wildlife Service;[27] the annual New England catch between 1889–1908 seems to have been well above 1.25 million pounds, by 1919 it had fallen somewhat below a million pounds, and between 1924–1940 it has fluctuated around a half million pounds.

The situation with respect to the American Shad fishery in the Hudson is much more encouraging, although depletion occurred in that river also; statistics from the sources previously mentioned show that the catch in that river declined from 3.75 million pounds in 1901 to only 40,000 pounds in 1916 and to 43,000 in 1917; thereafter, between 1918–1935, the catch varied from 94,000 pounds (1924) to 847,000

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[27] No adjustment for the differences in the number of persons employed, the type and number of vessels, and the different types of gear used from year to year has been made in the statistics given here and elsewhere. However, it is highly probable that the "fishing effort" for 1000 pounds of fish, for example, has increased.

pounds (1935); and in 1936–1941 it varied from 2,467,000 (1938) to 3,270,700 (1939). Although the catch in 1959 was only 1,171,212 pounds, very definite recovery has been indicated. According to investigators of the U. S. Fish and Wildlife Service, this recovery is ascribed partially to the elimination of pollution and partially to the great decrease in fishing effort at the time when depletion made it unprofitable to fish. The curtailment in fishing permitted the depleted population to reach the spawning grounds, to return to the sea, and to spawn again and again. Ultimately this resulted in the rehabilitation of the American Shad in this river system. It is decidely encouraging to have evidence that a depleted fishery can be restored.

The American Shad fishery in the Potomac, though it has fluctuated greatly, has also undergone a general decline in recent years, without evident recovery. The catches in 1896 and 1901 were above 2.5 million pounds whereas in 1909 and 1915 they were only three-quarters of a million pounds. Then from 1919 to 1923 they ranged above a million pounds, reaching the impressive totals of somewhat more than two million pounds in 1919 and over three million pounds in 1922; the latter is the greatest catch on record. In 1924 the catch dropped to a little over half a million pounds, and since then it exceeded a million pounds only in 1926, 1928, 1929, 1931, and 1933; in fact, the catch exceeded two million pounds in 1928, 1931, and 1932. However, between 1934–1941 it has fluctuated only from 631,000 pounds in 1935 to 322,800 pounds in 1940, the smallest catch recorded. Although great fluctuations in the catches, and no doubt in abundance, have occurred in the Potomac River since 1896, a definite decline was not indicated by the statistics until 1934. Thereafter, a general decrease in the catches has reached alarming proportions. In 1959 the catch was only 188,000 pounds.

A decline similar to that in the Potomac River has taken place in the entire Chesapeake Bay area, where, exclusive of annual fluctuations in the catch, the general trend has been downward since 1930. According to statistics, this same situation also applies to the South Atlantic states, and perhaps to a somewhat smaller extent to the fisheries of the Middle Atlantic states.

The over-all yield of late has ranged between catches of 8,222,000 and 14,700,000 pounds for the United States (1940, 1945, 1950–1953), and between 1,545,000 and 2,444,000 pounds for Canada (1940, 1945, 1950–1952). The American Shad thus remains very important economically, yielding the fishermen an annual return of over a million dollars.

Formerly, when they were abundant, the market for them more limited, transportation slower, and refrigeration virtually unknown, a considerable portion of the catch was salted. However, now nearly all of it is marketed in the fresh state. Johnson has stated, "During recent years the outstanding problem of wholesale dealers, insofar as shad are concerned usually has been one of obtaining adequate supplies rather than of disposing of the catch" (*68*: 15). In fact, the demand on the Atlantic coast has been so great that the supply is augmented annually by shipments from the Pacific coast. The chief markets on the Atlantic coast are New York, Philadelphia, Baltimore, and Washington.

Shad are caught principally with pound nets, gill nets, and seines. Small quantities are taken with fyke nets, otter trawls, purse seines, traps, and dip nets.

Introductions. In the late 1800's, many introductions of the fry were attempted by the former U. S. Fish Commission and U. S. Bureau of Fisheries, but all failed; large shipments were liberated in the streams tributary to the Gulf of Mexico, in Great Salt Lake, Utah Lake, and Bear Lake, Utah, and in the Colorado River at the Needles, Arizona.

In the 1870's, the New York State Fish Commission introduced numerous fry in streams tributary to Lake Ontario and in some of the smaller lakes connected to it. According to Smith (*118*: 193), 658,000 fry were introduced, and "the appearance of adult shad promptly followed the introduction of young fish in the Genesee River, and from that time on for a number of years the indications pointed to the probable successful acclimatization of the species." These fish distributed themselves over the entire lake and were taken at irregular intervals from 1875 to about 1885; but few, if any, were seen after 1890. Hubbs and Lagler reported: "In the Great Lakes rare, and confined to the Lake Ontario Basin" (*62*: 27).

Remarkable success has resulted from stocking waters of the Pacific coast north of Monterey, California. The first fry, about 12,000, were planted in 1871 in the Sacramento River by the California Fish Commission, and additional shipments were sent there by the United States Fish Commission between 1873–1880. On the northern part of the Pacific coast, fry were introduced in the Willamette, Snake, and Columbia rivers in 1885 and 1886. From these plantings the species has spread from California to Alaska, and it has become important commercially from San Francisco northward; the catch during recent years generally has exceeded two million pounds.[28]

Artificial Propagation. This species received the attention of fish culturists as early as 1848 when eggs were taken artificially and hatched. However, it was not until 1867 that a really successful apparatus was perfected. This contrivance was known as the "Seth Green box," a floating box modified after one used for hatching salmon eggs. However, when used in tidal waters it was subject to accidents. Thereafter various devices were brought forward in rapid succession, and finally (in 1882) the "universal jar" or "McDonald jar," a modification of the "Chase jar" used for hatching whitefish eggs, was adopted by the U. S. Fish Commission and is still in use. Many millions of fry, or newly hatched larvae, have been liberated in the streams along the Atlantic coast.

Range. The regular range of the American Shad extends from the lower St. Lawrence River and Nova Scotian Banks as far south as Indian River City, Florida. The most northerly record is for one taken in Bulls Bay near St. John's, Newfoundland (*1*: 125). On the Pacific coast it now ranges from about San Pedro, California, to southeastern Alaska (*131*: 221).

Synonyms and References:

Clupea sapidissima Wilson *in* Rees's New Cyclopedia, *9*, *ca.* 1811: no pagination (orig. descr.; no local.; probably Philadelphia, Pennsylvania); Jordan and Gilbert, Bull. U. S. nat. Mus., 16, 1882: 267 (descr., range);

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[28] For further details concerning their artificial propagation and distribution, see *A Manual of Fish Culture* (*2*: 133–158).

Smith, Bull. U. S. Fish. Comm. (1890), *10*, 1892: 193, pl. 30 (deposited in small lakes and streams connected to Lake Ontario); Cheney, Rep. Forest Comm. N. Y. (1885), 1896: 125–134, color pl. (commerc. import., statist., artif. culture, local spawn., migr.).

Clupea alosa Mitchill (not of Linnaeus), Trans. Lit. philos. Soc. N. Y., *1*, 1815: 449 (descr., habits, size).

Alosa preastabilis DeKay, New York Fauna, Pt. 4, Fishes, 1842: 255, pl. 15, fig. 41 (orig. descr.; type local. New York; cf. European shad).

Alausa sapidissima Gill, Proc. Acad. nat. Sci. Philad., 1861: 54.

Alosa sapidissima Uhler and Lugger *in* Rep. Comm. Fish. Md., 1876: 157; 1876: 133 (descr., synon., food qualities, Maryland); Ryder, Rep. U. S. Comm. Fish. (1881), 1884: 795 (temp. effects on incub. of eggs); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 427; 47 (4), 1900: fig. 191 (descr., range, synon.); Anonymous, Rep. U. S. Comm. Fish. (1897), 1898: 133, pls. 36–39 (artif. propag. and develop.); Bean, T. H., 7th Rep. Forest Comm. N. Y. (1901), 1902: 305, fig. (synon., range, occur., size, food of young in rivers, spawn.); Bean, T. H., Bull. N. Y. St. Mus., 60, Zool. 9, 1903: 204 (synon., refs., decline due to obstructions, food, migr., growth); Fowler, Rep. N. J. St. Mus. (1905), 1906: 99 (descr., import. as food); Smith, N. C. geol. econ. Surv., *2*, 1907: 125, pl. 5 in color (synon., descr., range, foodfish; rel. size of male and female, migr., statist., etc.); Kendall, Occ. Pap. Boston Soc. nat. Hist., *7*, 1908: 39 (refs., New England); Sumner, Osburn, and Cole, Bull. U. S. Bur. Fish. (1911), *31* (2), 1913: 742 (refs., Woods Hole, Massachusetts, spawn., parasites); Regan, Ann. Mag. nat. Hist., (8) *18*, 1916: 8 (diagn.); Wilson, Proc. U. S. nat. Mus., *53*, 1917: 59 (parasites); Leim, Contr. Canad. Biol., N. S. *2* (1), 1924: 163–284 (life hist., bibliog.); Barney, Trans. Amer. Fish. Soc., *54*, 1924: 168, figs. 1–4 (age from otoliths); Borodin, Trans. Amer. Fish. Soc., *54*, 1924: 178 (age from scales); Bigelow and Welsh, Bull. U. S. Bur. Fish. (1924), *40* (1), 1925: 113, fig. 46 (descr., size, range, Gulf of Maine, migr., food, develop., etc.); Jordan, Fishes, 1925: 276 (relation., quality as food, spawn.); Nichols and Breder, Zoologica, N. Y., *9* (1), 1927: 40, fig. (distr., New York and New England, food, life hist., size); Hildebrand and Schroeder, Bull. U. S. Bur. Fish. (1927), 43 (1), 1928: 93, fig. 53 (descr., growth of young, food, migr., artif. propag., distr., commerc. import., marketing, size, range); Breder, Field Bk. Mar. Fish. Atl. Cst., 1929: 66, fig. (abund., decline, migr., food, spawn.); Jordan, Manual Vert. Anim. NE U. S., ed. 13, 1929: 40 (diagn., range); Truitt, Bean, and Fowler, Bull. Md. Conserv. Dep., 3, 1929: 50, fig. 16 (descr., Maryland); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 42 (range, synon.); Walford, Fish. Bull., Sacramento, 28, 1931: 48 (diagn., distr. Pacific coast, commerc. import.); Greeley and Bishop, 21st Rep. N. Y. Conserv. Dep. (1931), Suppl., 6, 1932: 78 (rare, Oswegatchie and Black R. systems); Greeley and Bishop, 22nd Rep. N. Y. Conserv. Dep. (1932), Suppl., 7, 1933: 91 (extinct, upper Hudson); Greeley, 24th Rep. N. Y. Conserv. Dep. (1934), Suppl., 9, 1935: 90 (Hudson R.); Greeley, 25th Rep. N. Y. Conserv. Dep. (1935), Suppl., 10, 1936: 78 (Delaware R. within New York); Greeley, 26th Rep. N. Y. Conserv. Dep. (1936), Suppl., 11, 1937: 91, pl. 3 in color (abund. Hudson R., spawn.); Vladykov and Wallace, Trans. Amer. Fish. Soc. (1937), *67* (2), 1938: 52–66; also Contr. 17, Chesapeake Biol. Lab. (commerc. import., Chesapeake Bay; var. in populations); Greeley, 28th Rep. N. Y. Conserv. Dep. (1938), Suppl., 15 (1), 1939: 39; 15 (2), 1939: 82 (fresh water, Long Island, New York); Greeley, 29th Rep. N. Y. Conserv. Dep. (1939), Suppl., 16, 1940: 68 (rare, Lake Ontario); Welander, Copeia, 1940: 221 (introd., distr. Pacific coast); Hubbs and Lagler, Bull. Cranbrook Inst. Sci., 18, 1941: 27 (range); Fowler, Monogr. Acad. nat. Sci. Philad., 7, 1945: 45 (synon., refs.); Anonymous, Fish. Resourc. U. S., Senate Doc. No. 51, 1945: iii, 67–68, fig. (migr., fish. management; decline, causes and remedies; range); Warfel and Olsen, Copeia, 1947: 177–183 (var. in no. of vert. and signif.); Bigelow and Schroeder, Fish. Bull. (74) U. S. Fish Wildl. Serv., 53, 1953: 108–112 (descr., life hist., Gulf of Maine).

Shad, Clark, Rep. U. S. Comm. Fish. (1881), 1884: 783 (amount of water needed to keep eggs and young alive); Rice, Rep. U. S. Comm. Fish. (1881), 1884: 787 (retard. develop. of eggs); Willey, Contr. Canad. Biol., N. S. *1* (16), 1923: 313–320 (food); Johnson, Invest. Rep. U. S. Bur. Fish., *2* (38), 1938: 1–42, figs. 1–9 (nat. hist., sources of fishery, capture, wholesale trade, consump. in homes and public eating places, nutr. value, recipes, etc.); Hollis, Science, *108* (2804), 1948: 332 (tagging young; return of mature fish to place of hatch.).

Doubtful References:

Clupea indigena Mitchill, Rep. in part on Fishes of New York, 1814: 22 (orig. descr.; type local. presumably New York; type lost); Mitchill, Trans. lit. philos. Soc. N. Y., *1*, 1815: 454 (descr. inadequate for ident.).

Negative Reference:

Clupea sapidissima Jordan and Gilbert (not of Wilson), Proc. U. S. nat. Mus., 5, 1882: 247 (proportions and counts, showing specimens were *A. alabamae*, not recognized until 1896; Pensacola, Florida).

Alosa alabamae Jordan and Evermann 1896

Alabama Shad, Gulf Shad, Ohio Shad

Figures 70, 75

Study Material. A total of 23 specimens, 175–505 mm TL, 145–395 mm SL, from the Choctawhatchee River, Pensacola, Florida (including two cotypes of *A. alabamae*); tributary of the Flint River, Georgia; Black Warrior River, Tuscaloosa, Alabama (male and female types); Coosa River, and the Alabama River, tributary of the Tombigbee River, Alabama; Washita River, near Hot Springs, Arkansas; Ohio River at the falls, Louisville, Kentucky (including type and several cotypes of *A. ohiensis*); and Fairport, Iowa.

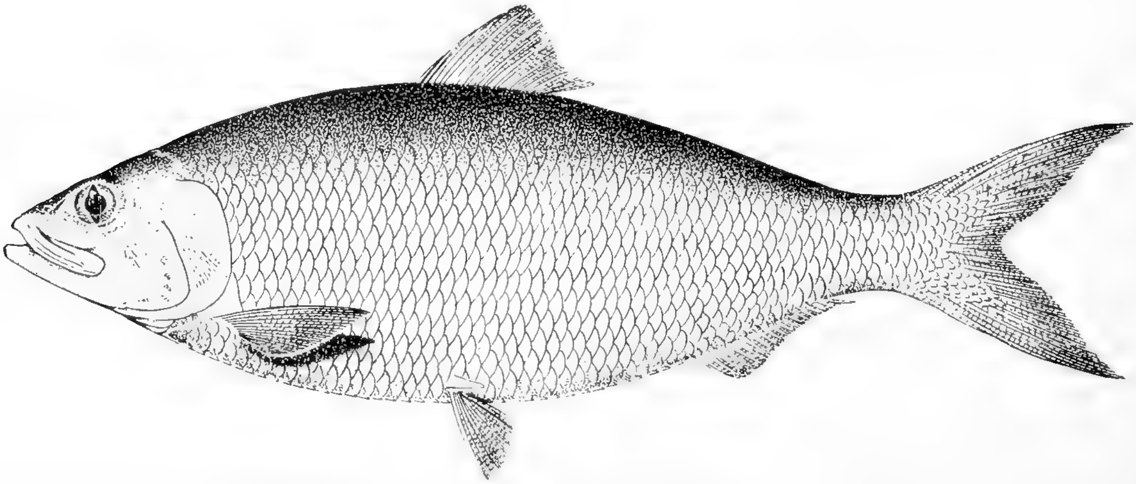

FIGURE 75. *Alosa alabamae*, 380 mm TL, 15 inches, Black Warrior River, Tuscaloosa, Alabama, type, USNM 47689. Drawn by A. H. Baldwin.

Distinctive Characters. See Key to Species, p. 294, and pp. 304, 309, 310.

Description. Proportional dimensions in per cent of standard length, and counts, based on the 23 study specimens, 145–395 mm SL.

Body: depth 25.5–36.
Caudal peduncle: depth 8.0–9.0.
Head: length 23.5–26.5.
Snout: length 5.5–6.9.
Eye: diameter 4.2–6.5.
Interorbital: width 4.5–6.0.
Maxillary: length 11–13.5.
Pelvic fin: length 10–11.5.
Pectoral fin: length 15.3–17.5.

Scales: *ca.* 55–60, often lost in preserved specimens.

Ventral scutes: 35–38.
Gill rakers: 42–48 in adults.
Fin rays: dorsal 16–20, usually 17–19; anal 19–22; pectoral 15–18, usually 16 or 17.
Vertebrae: 55 (1 specimen).

Body shaped as in *A. sapidissima*, the depth in general increasing with age and growth, 2.8–3.9 in SL in adults. Head 3.7–4.25 in SL. Snout 3.8–4.4 in head. Eye 4.2–6.5. Interorbital 4.1–6.0. Maxillary 1.95–2.15. Scales only moderately adherent, about 15 or 16 rows between base of pelvic and anterior rays of dorsal fin. Pelvic fin 2.2–2.5 in head. Pectoral fin 1.4–1.5.

A. alabamae differs from *A. sapidissima* in only the few respects shown in the following comparison:

A. sapidissima	*A. alabamae*
Gill rakers close-set, those at angle of first arch longer than snout, 59–73 on lower limb in adults 300 mm and upward.	Gill rakers less crowded, those at angle of first arch about as long as snout, 42–48 on lower limb in adults 300 mm and upward in length.
Surface of cheek and opercular bones glossy, generally without conspicuous mucous pores and canals.	Surface of cheek and opercular bones not glossy, covered with conspicuous mucous pores and canals.
Axillary scale of pelvic fin generally only a little more than half of length of fin.	Axillary scale of pelvic fin generally about 75 % of length of fin.

Size. The Alabama Shad seems to run smaller in size than the American shad; the largest female seen was 510 mm (20.4 in.) and the largest male 435 mm (17.4 in.) long, both from the Ohio River at Louisville, Kentucky.

Development. Apparently the eggs and young have not been described. Ten small specimens, 48–90 mm TL, 36–73 mm SL, all previously misidentified as *Pomolobus chrysochloris* (USNM 36424, 36620, 36835, and 62225), are no doubt in their first year; they were collected from: the Stone River at Nashville and the Clinch River at Clinton, Tennessee; the Washita River, and the Mulberry River at Mulberry, Arkansas. There is also at hand a specimen 105 mm TL (93 mm SL) taken in brackish water at Grand Isle, Louisiana. The young differ from their adults principally in having a more slender body and in possessing notably fewer gill rakers; the depth is 3.6–4.1 in SL and the gill rakers on the lower limb vary between 27–33. The increase in the number of gill rakers seems to be rapid, as five half-grown examples 175–215 mm TL (145–171 mm SL) from Pensacola already have 38–41 gill rakers.

"Numerous young, 8 or 9 inches in length" were reported for Pensacola, Florida, by Jordan and Gilbert (*73*: 247) as *A. sapidissima*, before *A. alabamae* had been recognized; five of these (USNM 30809) may be part of that material; they are typical of the Alabama Shad and are the only half-grown samples at hand. They, like the smaller American shad, are more slender than their adults and have fewer gill rakers; but the raker count in these is higher than in the smallest examples of *alabamae* reported above.

Spawning and Migrations. A. alabamae, like its close relative *A. sapidissima*, ascends streams in spring and spawns in fresh water. Sexually mature Alabama Shad, observed at Keokuk Dam, Iowa, in 1915 and 1916 from the early part of May to the middle of July, were in upstream migration to spawn but were stopped by the dam, except for a few that might have passed through the lock (*27*: 169). Coker believed there were enough there "to support a substantial fishery." Other runs in the spring of the year have been reported for the Black Warrior River (Tuscaloosa) and at Mobile, Alabama (*32*: 127); the Kanawha River at Montgomery, West Virginia; and the Ohio River at the falls, Louisville, Kentucky (*31*: 275–276). An apparently reliable source reported still other runs to Dr. Evermann—for the Ohio River about 30 miles below Louisville, Kentucky, and for the Mississippi River below Memphis, Tennessee.

In reply to a letter of inquiry addressed to the State Department of Conservation, Montgomery, Alabama, Mr. Ben. C. Morgan, Director of Conservation, replied (June 22, 1946):

> During the months of May and June, and sometimes earlier, we still have enormous quantities of fresh water shad which run or attempt to run up our main streams. I say attempt to run because of the fact that the Coosa, Tallapoosa, Tennessee, and Tombigbee Rivers all have locks and dams which prevent the shad from going further than these dams. Only last year on the Tennessee they banked below the dams by the millions and could be scooped with nets, which we do not allow, of course.

It seems highly probable that the young of this species descend the rivers to salt water at the end of their first summer, and it may be assumed, therefore, that the habits of the Alabama and American shads are very similar.

Food. It is well known that anadromous fishes, while migrating to their spawning grounds, do not feed regularly, if at all. The Alabama or Ohio Shad is no exception to this rule, for Mr. Stringham found that 105 of 163 stomachs examined at Keokuk, Iowa, were empty (*27*: 171). Others contained small quantities of insect and plant remains as well as some unrecognizable debris.

Variations. Although adults of *alabamae* and *sapidissima* differ widely in the number of gill rakers, the number in the very young is so similar in this respect that overlapping definitely occurs (see *Description*).

Examples taken from the Ohio River at the falls, Louisville, Kentucky, differed sufficiently from *alabamae* to be recognized by Evermann as a distinct species, which he named *Alosa ohiensis* (*31*: 277). He described *ohiensis* as differing from *alabamae* principally in a more elongated body and in the greater number of gill rakers on the first arch. However, the seven large specimens from the Ohio now at hand (including the type), though representing the extremes in the two characters mentioned, intergrade with the other 11 sexually mature examples (including the type material of *alabamae* from Tuscaloosa) from the several other localities in the Gulf drainage already listed. Therefore, *ohiensis* at most is only subspecifically distinct. It is herein regarded as a synonym of *alabamae*.

Commercial Importance. This species has never been an important foodfish; only small catches have been recorded a couple of times in the statistical reports of the former U. S. Fish Commission: for 1889, 6,955 pounds from the Ohio River in Indiana and Kentucky (1902: 667); and for 1902, 150 pounds from Alabama (1905: 416). No later catches seem to have been reported. By correspondence with Herman O. Hessen, U. S. Fish and Wildlife Service, Louisville, Kentucky, it was learned that no one now (1946) fishes for the "Ohio Shad" at that place, though a few are taken incidentally each spring. That these Shad were, and perhaps still are, numerous enough in some places to be taken in considerable quantities is evident, but no special effort is apparently made to catch them. In fact, the fish seem to be regarded in some localities as too bony for human use. At least one fisherman interviewed by Mr. Hessen at Louisville, Kentucky, stated that the fish were so bony that fishermen threw them on the bank and made no effort to sell them. Nevertheless, the food qualities of this Shad, tested by those who are familiar with the delicious American shad, have been found not at all inferior (*31*: 275; *27*: 169).

It seems probable that Alabama Shad constitute at least a small unutilized food supply, but their actual abundance remains unknown. Evermann indicated that if proper equipment were used, considerable catches might be taken (*31*: 279); for example, a great increase in the catch resulted at Louisville, Kentucky, when surface-fishing seines were substituted for bottom-fishing seines. However, until people living on the shad streams of the Gulf drainage recognize its delicious food qualities, there will be little demand; hence no special effort to catch them will be made. Because of the many dams constructed across rivers, barring them from the spawning grounds, a decrease in abundance is no doubt taking place.

Despite an unutilized supply of Alabama Shad in streams tributary to the Gulf of Mexico, large shipments of American shad fry, *A. sapidissima*, were liberated in those streams (*2*). However, no American shad are included among the rather numerous specimens examined, nor has any authentic record of their occurrence in those streams been found. Indeed, Alabama Shad seem to be referred to as "Potomac shad" by fishermen who believe they are the progeny of American shad planted by the former U. S. Fish Commission.[29] But it seems quite certain that the introduction failed.

Range. The Alabama Shad is represented by specimens in the National Museum and has been recorded for all the principal streams tributary to the Gulf of Mexico (exclusive of the Pearl River), from the Mississippi eastward to the Choctawhatchee River, about 50 miles east of Pensacola, Florida. A 105-mm specimen from Grand Isle, Louisiana, is also at hand. In the Mississippi Valley it is known from as far west as Hot Springs, Arkansas, and northward to Fairport, Iowa, and Montgomery, West Virginia.

Synonyms and References:

Clupea sapidissima Jordan and Gilbert (not of Wilson), Proc. U. S. nat. Mus., *5*, 1882: 247 (meas., counts

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[29] Fishermen generally do not seem to distinguish Alabama Shad from skipjack herring, *Pomolobus chrysochloris*; according to Coker (*27*: 165) they are referred to as "Government shad" by the fishermen at Keokuk, Iowa, apparently in the belief that they are the result of these plantings.

of half-grown examples from Pensacola, Florida); Bollman, Proc. U. S. nat. Mus., *9*, 1886: 462 (two large ones, Escambia R., Alabama).

Clupea chrysochloris Meek (not of Rafinesque), Bull. U. S. Fish Comm., *14*, 1894: 85 (Mulberry, Arkansas; USNM 62225 *A. alabamae*).

Alosa alabamae Jordan and Evermann *in* Evermann, Rep. U. S. Comm. Fish. (1895), 21, 1896: 203 (orig. descr.; type local. Black Warrior R., Tuscaloosa, Alabama; types USNM 47689 [♀] and 47690 [♂]; cf. *A. sapidissima*); Evermann and Kendall, Bull. U. S. Fish Comm. (1897), *17*, 1898: 127 (distr.); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (3), 1898: 2810, figs. 192, 192a (descr., refs.); Regan, Ann. Mag. nat. Hist., (8) *18*, 1916: 9 (refs., diagn.); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 43 (range, ref.).

Alosa ohiensis Evermann, Rep. U. S. Comm. Fish. (1901), 27, 1902: figs. 1 and 2, ♀ and ♂ *ohiensis*; figs. 3 and 4, ♂ and ♀ *alabamae* (orig. descr.; type local. Ohio R., Louisville, Kentucky; types USNM 50469; cf. *alabamae* and *sapidissima*; distr.); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 42 (range, ref.); Coker, *et al.*, Bull. U. S. Bur. Fish (1929), *45*, 1930: 169 (Keokuk, Iowa 1915, 1916; influence of dam on migr.; an unused food).

Alosa alabamae ohiensis Regan, Ann. Mag. nat. Hist., (8) *18*, 1916: 9 (ref., diagn.).

Genus *Pomolobus* Rafinesque 1820

Alewives, River Herring

Pomolobus Rafinesque, West. Rev. Misc. Mag., *2*, 1820: 170; Ichthyol. Ohiensis, 1820: 38; genotype by monotypy, *Pomolobus chrysochloris* Rafinesque.

Generic Synonym:

Alausella Gill, Proc. Acad. nat. Sci. Philad., Suppl., 1861: 54; Proc. Acad. nat. Sci. Philad., 1861: 36; genotype by monotypy, *Clupea parvula* Mitchill equals probably young of *Clupea pseudoharengus* Wilson.

Characters. BODY oblong, compressed. BONY SCUTES strong, with sharp points; a sharp edge on median line of chest and abdomen. CHEEK generally longer than deep, about as long as deep in *P. mediocris*. MOUTH large. MAXILLARY extending to or beyond middle of eye. UPPER JAW with a more or less definite median notch in adults. LOWER JAW projecting or included, its upper margin within the mouth rising more or less abruptly. TEETH in jaws not entirely wanting in adults; present at least anteriorly in lower jaw, though rudimentary in some species; present on median line of tongue; wanting on vomer. DORSAL with 15–21 rays, the last one not produced, its origin nearer to tip of snout than to base of caudal. ANAL with 16–23 rays, the last one not especially enlarged. PELVIC with 9 rays. VERTEBRAE 46–55.

Remarks. Two members of this genus, *mediocris* and *chrysochloris*, are close to the American species of *Alosa* in the general structures about the head, except that the lower jaw projects beyond the upper one; they differ strongly, however, in having fewer gill rakers, which DO NOT INCREASE IN NUMBER WITH AGE (18–24 on lower limb). The other two species, *aestivalis* and *pseudoharengus*, herein recognized, agree more or less with the species of *Alosa* in the number of gill rakers (38–51 on lower limb) and in having the lower jaw included; they differ, however, in having much shallower cheeks, which are much longer than deep, and in having the upper margin of the lower jaw rising abruptly within the mouth to form a more or less obtuse angle.

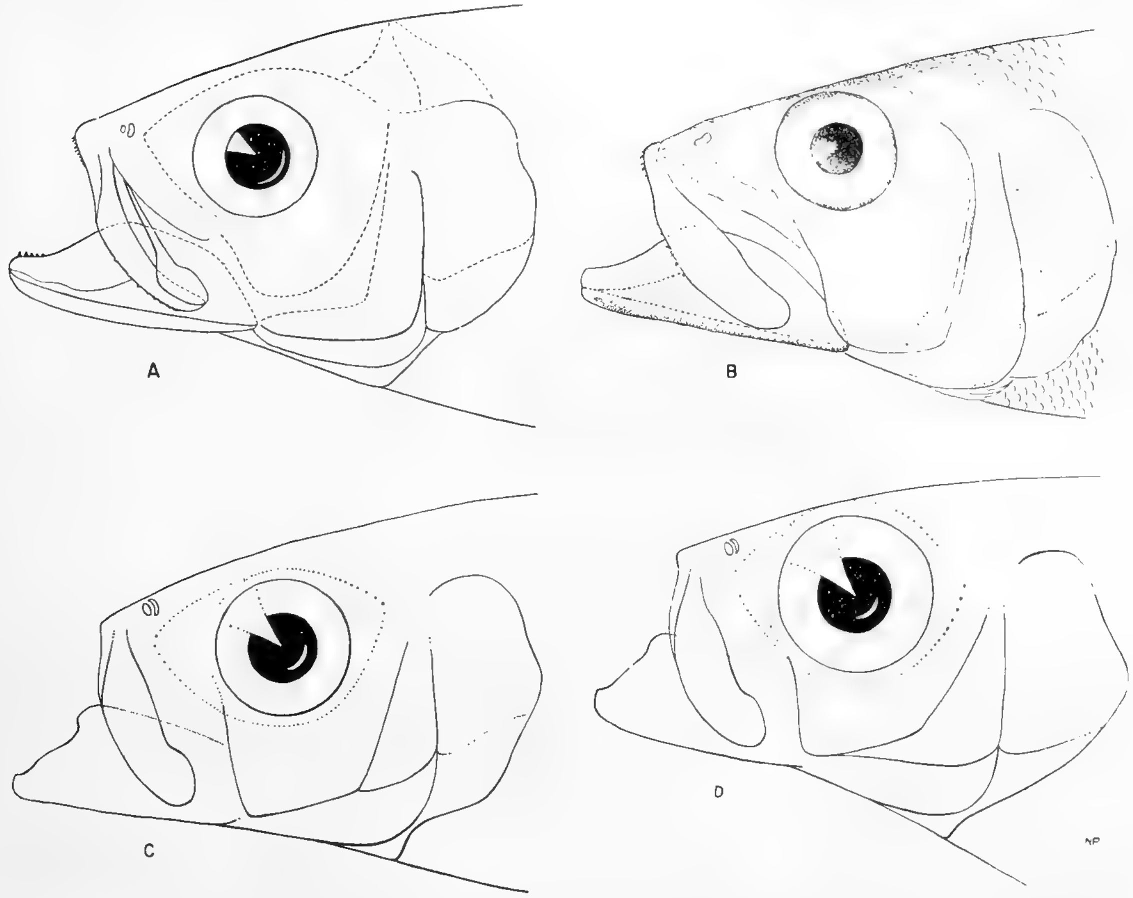

FIGURE 76. *Pomolobus* heads, showing shape of mandible and cheek. A, *chrysochloris*, 54 mm TL, USNM 9424; B, *mediocris*, 122 mm TL (after Hildebrand and Schroeder); C, *aestivalis*, 45 mm TL, USNM 69834; D, *pseudoharengus*, 48 mm TL, USNM 69833. A drawn by Ann S. Green, B by Louise Nash, C, D by Nancy D. Patton.

Range. Three species occur in the Atlantic, from Nova Scotia to northern Florida, and one occurs in the Gulf of Mexico and tributary streams as far west as Corpus Christi, Texas, ranging northward to Minnesota (see Key).

Key to Species

1a. Lower jaw strongly projecting, extending nearly or quite into dorsal outline of head (Fig. 76 A, B); only 18–24 gill rakers on lower limb of first arch, not increasing in number with age.

  2a. Greatest depth of body usually less than length of head, 3.5–4.1 (usually 3.8–4.0) in SL; teeth present in jaws at all ages, those in lower jaw prominent; bluish green color of back ceasing abruptly, not blending into the silvery color of side; no spot at shoulder. *chrysochloris* Rafinesque 1820, p. 315.

2b. Greatest depth of body usually greater than length of head, 3.0–3.75 (usually 3.2–3.6) in SL; teeth missing in upper jaw of adults, those in lower jaw very small (rudimentary); the grayish green color of back blending rather gradually into silvery color of the side; a dark spot at shoulder just behind head, often followed by several smaller spots. *mediocris* (Mitchill) 1814, p. 319.

1b. Lower jaw included or projecting but little, definitely not extending into dorsal outline of head (Fig. 76 C, D); gill rakers 38–41 on lower limb in adults, numerous at all ages.

3a. Diameter of eye generally about equal to length of snout in adults; 41–52 (most frequently 44–50) gill rakers on lower limb in adults; peritoneum usually black, sometimes pale with dusky dots; back in fresh examples bluish. *aestivalis* (Mitchill) 1814, p. 324.

3b. Diameter of eye longer than snout at all ages; 38–44 (most frequently 39–41) gill rakers on lower limb in adults; peritoneum pale, with dusky dots; back in fresh examples grayish green. *pseudoharengus* (Wilson) 1811, p. 332.

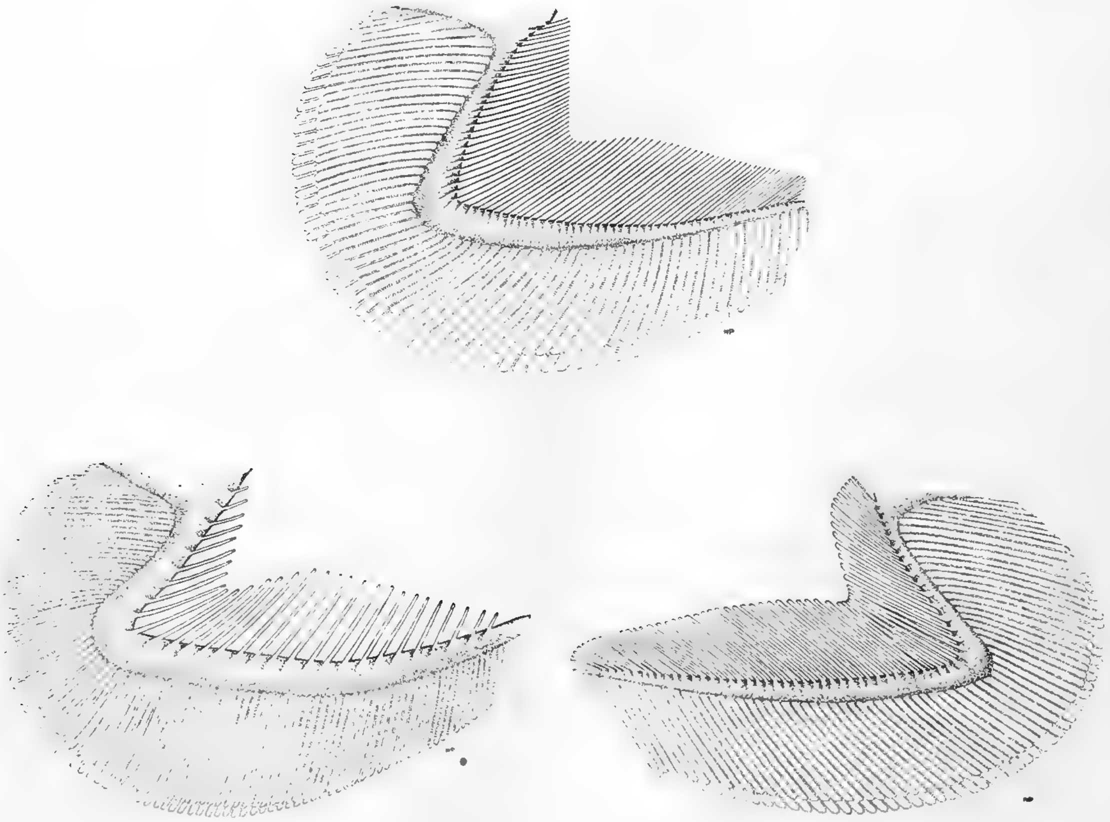

FIGURE 77. *Pomolobus* gill rakers on first branchial arch. TOP, *aestivalis*, 300 mm TL, USNM 125701; LEFT, *mediocris*, 310 mm TL, USNM 118156; RIGHT, *pseudoharengus*, 292 mm TL, USNM 117808. All drawn by Nancy D. Patton.

Pomolobus chrysochloris Rafinesque[30] 1820

Skipjack Herring, Skipjack, Golden Shad, Blue or Green Herring, River Herring

Figures 76, 78

Study Material. A total of 32 or more specimens, 115–420 mm TL, 95–341 mm SL; from Pensacola, Florida; Wetumpka, Montgomery, and Wheeler Reservoir, Alabama; Pascagula, Chickasawhay River, Pearl River, Eagle Lake, and Vicksburg, Mississippi; shrimp grounds (trawl) in Louisiana waters, Pass Manchac, and borrow pits in Mississippi River at Lake Providence, Louisiana; Mustang Island (Gulf side), Texas; St. Francis River, Mississippi River, Miles County, Arkansas; Lexington, Missouri; Mississippi River, Keokuk, and Fairport, Iowa; Cairo and Mississippi River, Victory, Wisconsin; and Fort Snelling, Minnesota; mostly in USNM, but some loaned by Miss Fannye A. Cook, Mississippi Game and Fish Commission, Percy Viosca, Southern Biological Supply Co., and Reeve M. Bailey, University of Michigan.

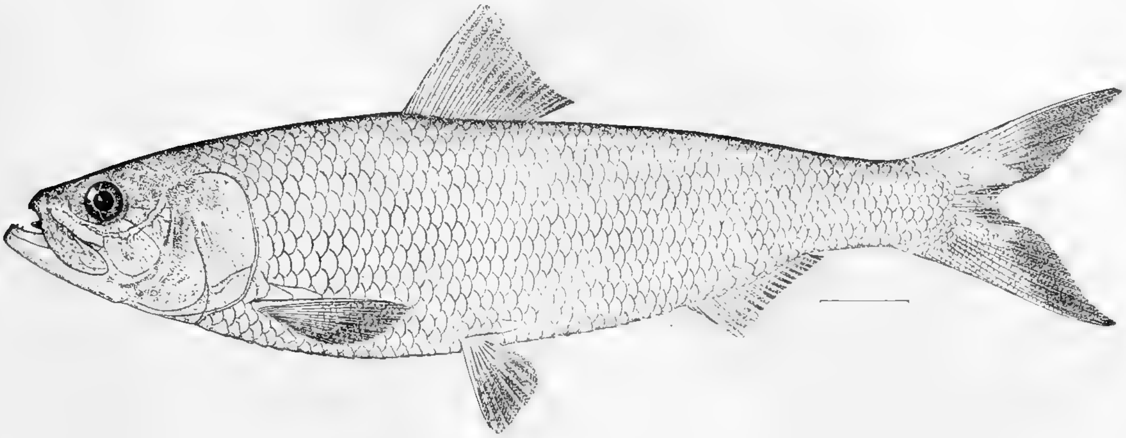

FIGURE 78. *Pomolobus chrysochloris*, 320 mm TL, Pensacola, Florida, USNM 30159. Drawn by S. Stearns.

Distinctive Characters. P. chrysochloris is closely related to *P. mediocris*, the hickory shad, of the Atlantic coast; the principal differences are indicated in the account

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[30] Although this species has long been considered the genotype of *Pomolobus*, it may be questioned with good reason whether Rafinesque's descriptions of the genus and species are based on the Skipjack Herring or the Alabama shad, *Alosa alabamae*, or on both. If Rafinesque had both species, as suggested by his accounts, he confused them. In his generic account he said "Jaws without teeth." This is true of adult Alabama shad but not of the Skipjack. In fact, the latter has such prominent teeth in the lower jaw that they would scarcely be overlooked. Furthermore, in the specific account Rafinesque used the local name, Ohio shad, together with Gold shad and Green herring. Present-day fishermen certainly distinguish the two species and refer to *A. alabamae* as the shad and to *P. chrysochloris* as the herring (generally with a modifier, such as blue, green, or river).

When listing local names, Rafinesque remarked: "A fine fish from twelve to eighteen inches long. Flesh esteemed, white and less bony than the shad." The comparison evidently is with the American shad. The remark concerning the flesh seems to suit the Alabama shad, but not the Skipjack. On the other hand, the size given is more nearly that of the Skipjack than that of the shad; yet an 18-inch Skipjack would be an exceptionally large one. It is evident, then, that one cannot be certain as to the species on which Rafinesque's descriptions were based. Because of the doubt involved, it seems advisable to continue the use of *Pomolobus chrysochloris* for the Skipjack Herring. To do otherwise would lead to great confusion of both generic and specific names.

of *mediocris* (p. 322). Both of these species are at once distinguishable from the other species of *Pomolobus* and from *Alosa* by the much smaller number of gill rakers.

Description. Proportional dimensions in per cent of standard length, and counts, based on study specimens, 95–341 mm SL.

Body: depth 24.2–28.4.
Caudal peduncle: depth 7.8–11.
Head: length 24.6–27.8.
Snout: length 4.8–6.3.
Eye: diameter 4.4–7.0.
Interorbital: width 3.8–4.8.
Maxillary: length 10.5–12.5.
Pelvic fin: length 10–12.6.
Pectoral fin: length 16–19.
Scales: 51–60, often difficult to count accurately.
Ventral scutes: 33–37, most frequently 34 or 35.
Gill rakers: on lower limb of first arch 20–24, most frequently 20–23.
Fin rays: dorsal 16–21, most frequently 18–20; anal 18–21, most frequently 19 or 20; pectoral 16 or 17, rarely 15.
Vertebrae: 53–55 (4 specimens).

Body slender, compressed, its greatest thickness generally somewhat less than half of its depth, its depth increasing with age and growth, usually equal to or less than length of head, 3.5–4.1 in SL.

Scales moderately adherent, with slightly irregular membranous margins, not preceded by striae; 15 or 16 longitudinal rows of scales on body between base of pelvic fin and anterior rays of dorsal. Ventral scutes well developed, 17–21 (most frequently 19 or 20) in advance of pelvics and 14–17 behind them.

Head 3.6–4.0 in SL. Snout 4.2–4.8 in head. Eye 3.8–5.9. Interorbital 5.4–7.5. Cheek, from lower rim of orbit, somewhat longer than deep. Mouth moderately oblique. Upper jaw with a definite median notch in adults. Lower jaw projecting strongly and extending into dorsal profile of head, its upper margin within mouth rising gradually, not forming an angle (Fig. 76 a). Maxillary broad, its width about 0.67 of length of snout, rounded posteriorly, reaching nearly or quite below posterior margin of pupil, 2.25–2.4 in head. Gill rakers not increasing in number with age. Teeth in anterior part of both jaws at all ages, those of lower jaw rather prominent; sockets present if teeth are broken; teeth on tongue prominent, in a rather large elongated patch.

Dorsal fin with slightly concave margin, its origin scarcely an eye's diameter in advance of pelvic and usually equidistant from margin of upper jaw and a vertical from last ray of anal; a scaly sheath on dorsal base, composed of a single row of scales and extending to 4th or 5th ray from end of fin. Caudal deeply forked, the lower lobe rather longer than the upper, about as long as head. Anal low, its margin nearly straight, its origin usually about equidistant between base of pelvic and base of caudal; a scaly sheath present on base. Pelvic fin inserted near ventral edge and usually nearer to base of pectoral than to origin of anal, 2.15–2.4 in head. Pectoral fin placed somewhat higher on side, 1.4–1.6 in head.

Color. Fresh specimens deep bluish green above, this color ceasing abruptly at level of upper margin of gill cover. Sides light green, with strong tinge of gold, especially on head, shading into the white of belly. No dark shoulder spot. Tips of jaws blackish. Dorsal fin yellowish, more or less dusky at base; caudal yellowish, tips of lobes dusky; anal and pelvic pale; pectoral pale, a dusky streak on inner side behind first ray. Peritoneum pale.

Size. Skipjacks are smaller in size than Alabama shad, with which they are more or less associated in the rivers; their length usually ranges between about 300–450 mm (12–18 in.).

Development. Although ovarian eggs 0.08–1.11 mm in diameter were observed, apparently no young under 107 mm (about 4.33 in.) were secured during Dr. Coker's extensive investigations at Keokuk, Iowa (*26*; *27*). Each of the smallest specimens at hand (UMMZ 122510, 128570), from the mouth of Elk River, Wheeler Reservoir, Alabama, and from the Mississippi River, Miles County, Arkansas, is about 40 mm (31 mm SL), apparently the smallest known. They differ from larger examples principally in being more slender, the depth of each being contained 4.75 times in SL. Furthermore, they have minute teeth on the margin of the maxillary, these persisting in examples up to 150 mm or so in length. The gill rakers, unlike those in some other species of the genus *Pomolobus*, do not increase in number with age and growth.

Spawning and Migrations. The spawning place and length of spawning are not fully known. For such information as is available we are indebted to Robert E. Coker, who, with assistants, carried on an extensive investigation at Keokuk, Iowa (*26*: 25, 26; *27*: 94, 165–169). They reported fish with large roe taken there on: April 29 and May 23 in 1914; April 29 and 30, May 24, June 5 and 23, July 1 and 2, and "various other dates" in 1915; and on May 23, June 3 and 17 in 1916. Fully mature fish, ripe for stripping, apparently were not included. Coker concluded his remarks on spawning as follows:

> Many attempts made during several years to find a particular place and time where and when river herring were clearly spawning met with no success, although various methods were tried. The problem proved unexpectedly baffling. Our data suggest only that the spawning season is prolonged, possibly beginning early in May; that the fish do not spawn in large aggregations; that during spawning operations they are not readily captured by ordinary methods of fishery; and that spawning is ended soon after the first of July.

It has not been proven that Skipjack are anadromous like most of the near relatives, even though Jordan said categorically, ". . . migrating from the Gulf of Mexico" (*71*: 40). However, they do enter salt and brackish water. Such a great "run" as was reported at Keokuk, Iowa, in the spring of 1914 as well as smaller runs in successive years and their apparent disappearance in September of each year do suggest extensive migration. However, Coker expressed the opinion that the migrations do not necessarily extend to extreme northern or extreme southern waters. This is in contrast to the strictly anadromous relatives, *Alosa sapidissima*, *Pomolobus aestivalis*, and *P. pseudoharengus* (except where the last species is landlocked), whose young leave the freshwater streams at the end of their first summer and do not return until they are ready to spawn.

Evidence has been set forth that *chrysochloris* reproduced in Lake Pepin after the closing of Keokuk Dam, an almost complete barrier to them. Dr. Coker said that without question there was a decided decline in the number of "River Herring" in this Lake during the three years immediately following the dam's construction, but some commercial catches there in 1926, 12 years after the dam was closed, convinced him that these fish were not rare; and several commercial fishermen stated that "the herring were coming back." On the basis of Dr. Coker's observations, it seems proper to conclude that *P. chrysochloris*, although migratory, does not need to have access to salt water to reproduce, and the species surely is not strictly anadromous. The presence of immature examples in a collection from brackish water as well as from the upper Mississippi also may be of some significance.

Food. Skipjack Herring are carnivorous (*35*: 49); the young feed on insects, the adults on fish. Coker stated that, of about 150 examples examined for food:

> Approximately one-third were empty; a little more than one-third contained fish, chiefly minnows, with some mooneyes, gizzard shad, and other fish not determinable; and less than one-third contained insects and larvae, principally May flies, with some caddis flies and others.

Habits. These are more active fish than most other clupeoids; they frequent rivers with swift currents and often leap from the water, a habit from which they have derived the name Skipjack. They leap in part for sport and in part for the pursuit of prey (*35*: 49). Coker remarked that they have, "a striking habit of leaping from the surface when feeding upon schools of minnows or in mere play."

Parasites. We know only that the larvae (glochidia) of the freshwater mussel *Fusconaia ebena* are parasitic on the Skipjack (see below).

Commercial Importance. The value of this species as a foodfish is negligible, for these fish are bony and not especially well flavored. No catches have been listed in the statistical reports of the U. S. government. However, they represent a very distinct economic asset as a host for the larvae of *Fusconaia ebena*, which has been regarded as the most valuable of all the pearly mussels of the Mississippi Basin because of its abundance in all the larger waters of strong current and because it yields a shell of the best quality for buttons (*27*: 166).

Range. Skipjack Herring range in the Gulf of Mexico from Pensacola, Florida, to Corpus Christi, Texas, and sometimes out into the Gulf, as off Breton Island, Louisiana. They also inhabit larger streams, occasionally lakes, or even borrow pits, of the Gulf drainage. They commonly range as far north in the Mississippi River as Lake Pepin, and occasionally to Fort Snelling, Minnesota, to Hudson, Wisconsin, and in the Ohio River to Pittsburgh, Pennsylvania. Apparently they are landlocked above Keokuk Dam, Iowa. Although Smith (*118*: 214) said that they were abundant in Lake Erie, and Jordan and Evermann (*72*, 1896: 425) as well as several others have stated that they reached Lake Michigan and Lake Erie through canals, Hubbs and Lagler (*62*: 27, ftn.) do not admit them to their list of fishes of the Great Lakes and tributary waters. The species apparently is most common in swift currents of large streams.

Synonyms and References:

Pomolobus chrysochloris Rafinesque, West. Rev. Misc. Mag., *2*, 1820: 171; and Ichthyol. Ohiensis, 1820: 39 (orig. descr.; type local. Ohio R.; type lost; length 12–18 in. attained; seldom ascend to Pittsburgh);[31] Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 425; 47 (4), 1900: fig. 187 (descr., size, distr., habits, value as food); Jordan and Evermann, Amer. Food Game Fishes, 1902: 101 (descr., range; Lakes Erie and Michigan erroneously included); Bean, T. H., 7th Rep. Forest Comm. N. Y. (1901), 1902: 300, fig. (synon., range, habitat; reported to have reached Great Lakes through canals, but occur. there seems doubtful); Bean, T. H., Bull. N. Y. St. Mus., 60, Zool. 9, 1903: 195 (synon., descr., value as food, habits, distr.); Forbes and Richardson, Nat. Hist. Surv. Ill., Ichthyol., *3*, 1908: 48 (refs., descr., range, occur. in Illinois, size, habits); Coker, Rep. U. S. Comm. Fish. (1913), Append. 8, 1914: 25–28 (large schools below Keokuk Dam, Iowa; discus. migr. and ascent up spillways of dam; occur. above dam; spawn.); Regan, Ann. Mag. nat. Hist., (8) *19* (112), 1917: 299 (refs., descr., range); Jordan, Manual Vert. Anim. NE U. S., 1929: 40 (descr., range, habitat); Coker, Bull. U. S. Bur. Fish. (1929), *45*, 1930: 165, fig. 11 (below and above Keokuk Dam, Iowa, migr., spawn., econ. import.); Hubbs and Lagler, Bull. Cranbrook Inst. Sci., 18, 1941: 27 (not in list of Great Lakes fishes though reported there earlier); Gunter, Publ. Inst. mar. Sci. Texas, *1* (1), 1945: 25 (Texas coast, Colorado R. at Austin).

Meletta suoerii Cuvier and Valenciennes, Hist. Nat. Poiss., *20*, 1847: 375 (orig. descr.; type local. Wabash R., tributary of Mississippi R.); Bertin, Bull. Soc. zool. Fr., *66*, 1941: 23 (ident. of type).

Clupea chrysochloris Jordan and Gilbert, Proc. U. S. nat. Mus., *5*, 1882: 247 (descr.; records two specimens; from Galveston, Texas; and Pensacola, Florida); Jordan and Gilbert, Bull. U. S. nat. Mus., *16*, 1882: 266 (descr., range; Lakes Erie and Michigan apparently includ. erroneously); Jordan and Gilbert, Proc. U. S. nat. Mus., *9*, 1886: 11, 14 (Washita R., Arkadelphia, and Saline R., Benton, Arkansas); Bollman, Proc. U. S. nat. Mus., *9*, 1886: 462 (few from Escambia R., Alabama); Gilbert, Bull. U. S. Fish Comm. (1889), *9*, 1891: 158 (near mouth of Escambia R., Alabama); Smith, Bull. U. S. Fish Comm. (1890), *10*, 1892: 214, pl. 31 (Lakes Ontario and Erie); Evermann and Kendall, Bull. U. S. Fish Comm., *12*, 1894: 105 (Red R., Fulton, Arkansas; Galveston, Texas); Meek, Bull. U. S. Fish Comm., *14*, 1894: 78, 82 (White R. at Batesville, Little Red R. at Judsonia, Arkansas).

River herring, Coker, Bull. U. S. Bur. Fish., *45*, 1929: 91–104 (discus. abund. below Keokuk Dam, Iowa, 1914–1916; dam a barrier to fish).

Negative References:

Clupea chrysochloris Meek (not of Rafinesque), Bull. U. S. Fish Comm., *14*, 1894: 85 (Mulberry, Arkansas, but specimen USNM 62225 is *A. alabamae*).

Pomolobus mediocris (Mitchill) 1814

Hickory Shad, Hickory Jack, Bonejack, Fall Herring, Freshwater Taylor, Shad Herring

Figures 76, 77, 79

Study Material. Forty-three specimens, 105–460 mm TL, 82–354 mm SL, from Provincetown, Massachusetts; Noank, Connecticut; Long Island, New York; Beesley's Point, New Jersey; Annapolis, Love Point, Benedict, Barren Island, Lewistown, and Smith Point, all on or near Chesapeake Bay, Maryland; Potomac River, Washington, D. C.; Buckroe Beach and Lynnhaven Roads, on Chesapeake Bay, Virginia; Beaufort, North Carolina; and Brunswick, Georgia.

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[31] The data are from Richard E. Call's Ichthyologia Ohiensis (1899), "A verbatim et literatim reprint of the original, with a Sketch of the Life, the Ichthyologic Work, and the Ichthyologic Bibliography of Rafinesque," the original publications not being available to the author.

Distinctive Characters. See *Relationships* for differences between *mediocris* and *chrysochloris* (p. 322). From species of *Alosa* and other *Pomolobus* species, excepting *chrysochloris*, it is marked by the noticeably smaller number of gill rakers.

Description. Proportional dimensions in per cent of standard length, and counts, based on 43 specimens, 82–354 mm SL.

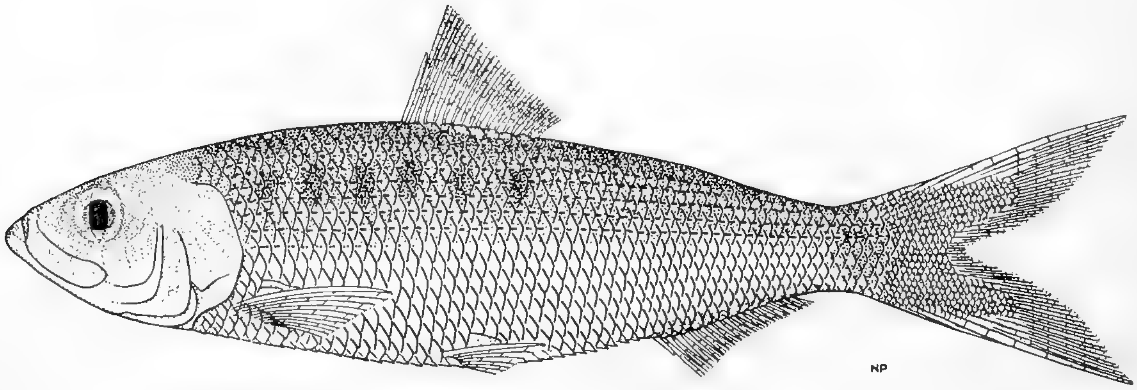

Figure 79. *Pomolobus mediocris*, 309 mm TL, Brunswick, Georgia, USNM 118156. Drawn by Nancy D. Patton.

Body: depth 26.7–32.8.
Caudal peduncle: depth 9.7–12.
Head: length 24.5–29.6.
Snout: length 5.9–7.5.
Eye: diameter 4.9–7.1.
Interorbital: width 3.9–5.4.
Maxillary: length 10.4–13.4.
Pelvic fin: length 10.6–12.4.
Pectoral fin: length 17–21.

Scales: 48–57.
Ventral scutes: 33–38, most frequently 36 or 37.
Gill rakers: on lower limb 18–23, usually 20 or 21.
Fin rays: dorsal 15–20, most frequently 17 or 18; anal 19–23, most frequently 20 or 21; pectoral 15 or 16.
Vertebrae: 54 or 55 (2 specimens).

Body moderately slender, well compressed, its greatest thickness notably less than half of its depth, its depth rather greater in large than in small specimens, usually exceeding length of head, 3.0–3.75 in SL.

Scales only moderately adherent, with definitely crenulate membranous margin, preceded by longitudinal striae; about 16 longitudinal rows of scales on body between base of pelvic and anterior dorsal rays. Ventral scutes moderately developed, 19–23 (usually 20–22) in front of pelvic fins, 12–17 (usually 13–16) behind them.

Head 3.4–4.1 in SL. Snout 3.7–5.0 in head. Eye 3.9–5.3. Interorbital 5.5–7.0. Cheek generally about as deep as long (Fig. 76 b). Mouth oblique. Upper jaw with a definite median notch. Lower jaw projecting strongly and extending into dorsal profile of head (Fig. 76 b), its upper margin within the mouth rising gradually, not forming an angle (Fig. 76 b). Maxillary broad, its width somewhat more than half of length of snout, rounded posteriorly, reaching about to vertical from posterior margin of pupil, 2.0–2.4 in head. GILL RAKERS apparently not increasing in number with age. TEETH in the upper jaw absent in large examples 230 mm SL and upward, but present in smaller ones; present in lower jaw, becoming exceedingly small in large examples; those on tongue minute, in a small elongated patch.

DORSAL with slightly concave margin, its origin rather less than an eye's diameter in advance of pelvic, usually nearer to margin of upper jaw than to vertical from last anal ray; a sheath of scales on its base, consisting for the most part of more than one row of scales and extending nearly or quite to base of last ray. CAUDAL deeply forked, the lower lobe somewhat longer than the upper, fully as long as head. ANAL low, its margin nearly straight, its origin about equidistant between base of pelvic and base of caudal; a sheath of scales on its base. PELVIC fin inserted near ventral edge and about equidistant between base of pectoral and origin of anal, 2.0–2.6 in head. PECTORAL placed somewhat higher on side, 1.3–1.7 in head.

Color. Fresh specimen from Chesapeake Bay grayish green above, shading somewhat gradually into the iridescent silver of sides. Nape green, side of head brassy. Tip of lower jaw dusky. Dorsal and caudal dusky. Anal and pelvic plain, translucent. Pectoral slightly dusky. Narrow dark lines along rows of scales on upper part of side; missing on specimens less than 150 mm SL or so and most distinct in large examples that have lost their scales, the dark pigment being in the skin underneath the scales. A dark spot on shoulder; several obscure dark spots behind it, but missing in some examples. Peritoneum pale, but with scattered dusky punctulations.

Size. Hickory Shad definitely run larger in size than blueback and grayback herrings but smaller than the shad. A maximum length of 600 mm (24 in.) has been reported, but the usual size is much smaller. The commercial catches observed by me at Chesapeake Bay and at Beaufort, North Carolina, consisted mostly of fish varying between about 300–375 mm (12–15 in.) in length.

Reproduction, Development, and Migrations. Next to nothing is known about the breeding habits of Hickory Shad. Although it has been stated that they spawn in North Carolina in the spring, in the headwaters of streams (*119*: 121), spawners have never been seen in either fresh or salt water. In fact, many subsequent authors (*45*: 607; *16*: 106; *20*: 65) have accepted without reservation the opinion that Hickory Shad, like other local members of that genus, are anadromous. However, the only supporting evidence is that there are definite spring and autumn runs; in Chesapeake Bay, only stragglers are seen in the summer; in the spring they are first taken in the lower part of the Bay in March and progressively later farther up the Bay in late March and early April. Also, I have observed adults with well-developed roe in the Potomac above Washington during the spring, but these were not ripe and may have returned to salt water to spawn. The view that this fish does not enter salt water to spawn (*8*: 197; *37*: 95) is supported by Hildebrand and Schroeder (*59*: 84); among thousands of young clupeids collected during many years in Chesapeake Bay and its tributaries, in freshwater streams and estuaries, and in salt water out to 15 fms., they failed to find any Hickory Shad less than 15 mm (6.12 in.) long. Also, in the vicinity of Beaufort, North Carolina, they were absent from extensive collections made by Hildebrand and his associates with gear of various types, though adults were taken in the estuaries there in winter and early spring.

In short, Hickory Shad probably spawn in the spring, but it remains to be learned whether they spawn in fresh or salt water. However this may be, to the north of New York they are the most plentiful during autumn.

Food. Hickory Shad feed chiefly on small fish of various kinds. Their fish diet is supplemented by squid, small crabs, various small crustaceans, and by fish eggs (*59*: 84).

Enemies and Parasites. Little is known about the enemies of this species; but no doubt they are eaten by larger fish and are caught in limited quantities by man. Linton (*85*: 438) found individuals parasitized with nematodes (*Ascaris* sp.), cestodes (larval *Scolex polymorphus*), and trematodes (*Distomum appendiculatum*). Wilson (*136*: 12) found the Hickory Shad to be a host of the copepod *Lernanthropus brevoortiae*.

Relationships. Though closely related to *P. chrysochloris*, Hickory Shad have a heavier and less shapely (less streamlined) body; the depth in adults is greater than the length of the head (measured from margin of upper jaw); in *chrysochloris*, exclusive of very large or very fat specimens, the depth is equal to or less than the head. In *mediocris* the shield of scales on the dorsal fin base consists of more than one row of scales anteriorly and extends nearly or quite to the last ray of the fin, whereas in *chrysochloris* it is composed of only one row of scales throughout and is missing on the last four or five rays. The scales on the side of the Hickory Shad have a pronounced crenulate membranous border preceded by longitudinal striations, while in *chrysochloris* the border is only slightly irregular and the striations not evident. In *mediocris* there is only a slight ridge above the base of the pectoral, which ends at the tip of the axillary process; in *chrysochloris* a more pronounced depression (pocket) is provided for the pectoral fin, and the more prominent ridge above its base extends well beyond the axillary process of the pectoral.

In large Hickory Shad, 300 mm and upward, teeth in the upper jaw are missing, but in specimens at least up to 150 mm long they are present there; however, those in the lower jaw persist, though very small; the patch on the tongue is very small, and the teeth minute. In *chrysochloris* the teeth are consistently larger, persist in the upper jaw among adults, are large in the lower jaw, and the patch on the tongue is notably larger. Although the proportions and counts overlap, it is evident that Hickory Shad have a proportionately deeper body, deeper caudal peduncle, more anal rays, and fewer gill rakers than *P. chrysochloris*.

There are differences in color also, evident in preserved as well as fresh examples. Hickory Shad have a large dark spot behind the upper part of the opercle, often followed by several smaller dark spots, and the adults frequently have dark lines along the rows of scales on the upper part of the side. In *P. chrysochloris* these markings are missing, and the dark blue or grayish color of the back ends very abruptly, not tending to shade into the silvery color of the side, as in Hickory Shad.

Commercial Importance. Hickory Shad are of minor importance as foodfish, mainly because the meat is bony and is considered inferior in flavor. Their value is somewhat higher in North Carolina than elsewhere, because they are taken there during the winter when other fish are scarce. In 1940 or 1941, the following catches were reported: New England (all reports for Rhode Island and Connecticut), 25,800 pounds; the Middle Atlantic States (all reports for New Jersey), 4,400 pounds; the Chesapeake Bay states, 196,200 pounds, of which 22,000 pounds were taken in Maryland and 174,200 pounds in Virginia; and the South Atlantic states (all of which contributed), 371,500 pounds, of which 335,900 pounds were listed for North Carolina. It is evident, then, that the fishery is centered in Virginia and North Carolina. In the United States (1940, 1945, 1950–1953), catches have ranged between 0 and 25,800 pounds for southern New England, 200 and 4,400 pounds for the Middle Atlantic states, 86,000 and 264,000 pounds for Chesapeake Bay, and 273,000 and 970,000 pounds for the South Atlantic states.

Method of Fishing. The commercial fish are caught principally with seines and pound nets, the smaller quantities with gill and fyke nets. The fishery is not intense enough to affect greatly the abundance of these fish in nature. They take the hook occasionally and offer some sport in the spring, at least at Little Falls on the Potomac River. Anglers trolling for striped bass (*Roccus saxatilis*) and mackerel (*Scomber*) landed a number of Hickory Shad off the Merrimack River, Massachusetts, in 1932.

Range. The range of Hickory Shad extends from Florida to Maine. They are recorded for Campobello Island, New Brunswick (*52*: 47), but no record of their occurrence south of the St. Johns River in Florida has been brought to my attention. Though rare north of Cape Cod, they are apparently more numerous in southern New England than in the Middle Atlantic States and are most abundant in Virginia and North Carolina.[32]

Synonyms and References:

Clupea mediocris Mitchill, Rep. in part on Fishes of New York, 1814: 20 (orig. descr.; type local. presumably New York City; type lost); Mitchill, Trans. Lit. philos. Soc. N. Y., *1*, 1815: 450 (descr., New York Bay along Staten Island); McDonald *in* Goode, *et al.*, Fish. Fish. Industr. U. S., 1 (3), 1884: 607, pls. 216A, 216B (discus., names, distr., abund., econ. import., migr.).

Clupea mattowaca Mitchill, Trans. Lit. philos. Soc. N. Y., *1*, 1815: 451 (orig. descr.; type local. Long Island, New York; commonly caught in autumn, size).

Alosa mattowacca DeKay, N. Y. Fauna, Pt. 4, Fishes, 1842: 260, pl. 40, fig. 127 (descr., New York; fig. shows no projecting lower jaw, though descr. says "lower jaw longest").

Alosa lineata Storer, Proc. Boston Soc. nat. Hist., *2*, 1848: 242 (orig. descr.; type local. Massachusetts); Storer, Fish. Mass., 1867: 162, pl. 27, fig. 2 (descr., when and how taken, food value).

Clupea mattowocca Günther, Cat. Fish. Brit. Mus., *7*, 1869: 438 (refs., descr.).

Pomolobus mediocris Uhler and Lugger *in* Rep. Comm. Fish. Md., ed. 1, 1876: 159; ed. 2, 1876: 136 (descr., synon., Potomac R., size); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 425; 47 (4), 1900: fig. 188 (descr., range); 47 (3), 1898: 2810 (correc. of earlier acct.); Smith, Bull. U. S. Fish.

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[32] A listing of this herring among the clupeoid fishes of Brazil (*25*: 190) was based on a specimen 170 mm long from an "ancient collection," without mention of the place of collection. The description offered suits *P. mediocris* quite well. However, as this herring does not seem to occur on the Atlantic coast in semitropical waters, as in southern Florida, one is justified in questioning whether it actually was taken in Brazil.

Comm. (1897), *17*, 1898: 91 (Woods Hole, Massachusetts); Smith and Bean, Bull. U S. Fish Comm. (1898), *18*, 1899: 183 (Potomac R., weight); Evermann and Kendall, Rep. U. S. Comm. Fish. (1899), 1900: 55 (refs., Florida); Linton, Bull. U. S. Fish Comm. (1899), *19*, 1901: 438 (parasites); Bean, T. H., 7th Rep. Forest Comm. N. Y. (1901), 1902: 301, fig., also color pl. (synon., names, size, New York); Jordan and Evermann, Amer. Food Game Fish., 1902: 102, fig. (names, habits, size, descr.); Bean, T. H., Bull. N. Y. St. Mus., 60, Zool. 9, 1903: 197 (synon., descr., local and techn. names, size, habits, range); Fowler, Rep. N. J. St. Mus. (1905), 2, 1906: 95, 2 figs. (descr., habits, size, refs.); Smith, N. C. geol. econ. Surv., *2*, 1907: 121, fig. 40 (refs., descr., range, North Carolina, names, econ. import.); Kendall, Occ. Pap. Boston Soc. nat. Hist., *7*, 1908: 37 (refs., New Engl. locals.); Halkett, Check List Fish. Canada, 1913: 47 (Campobello I., New Brunswick); Regan, Ann. Mag. nat. Hist., (8) *19* (112), 1917, 300 (descr.); Bigelow and Welsh, Bull. U. S. Bur. Fish. (1924), *40* (1), 1925: 105 (descr., size, range, food, Gulf of Maine); Wilson, Proc. U. S. nat. Mus., *64* (17), 1925: 12 (host of parasitic copepod); Hildebrand and Schroeder, Bull. U. S. Bur. Fish. (1927), *43* (1), 1928: 83, figs. 42, 43 (synon., descr., distinct. char., food, migr., other habits, Chesapeake Bay); Jordan, Manual Vert. Anim. NE U. S., ed. 13, 1929: 40 (diagn., range); Truitt, Bean, and Fowler, Bull. Md. Conserv. Dep., 3, 1929: 49 (descr., Maryland); Breder, Field Bk. Mar. Fish. Atl. Cst., 1929: 65 (relation., range, habits, size); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 42 (range, synon.).

Doubtful References:

Clupea pusilla Mitchill, Rep. in part on Fishes of New York, 1814: 20 (orig. descr.; type local. presumably New York; type lost); Mitchill, Trans. Lit. philos. Soc. N. Y., *1*, 1815: 452 (descr.).

Negative Reference:

Pomolobus mediocris Evermann and Hildebrand, young, not of Mitchill, but *P. pseudoharengus* (Wilson), Proc. biol. Soc. Wash., *23*, 1910: 158 (Chesapeake Bay locals.).

Pomolobus aestivalis (Mitchill) 1814

Blueback Herring, Blueback, Glut Herring, Blue Herring, Summer Herring, Blackbelly, Alewife, Kyak

Figures 69, 76, 77, 80, 81

Study Material. A total of 75 or more specimens, 33–295 mm TL, 27–240 mm SL; from off Liverpool, Nova Scotia; Freeport and Portland, Maine; Gloucester, Cape Cod, and Woods Hole, Massachusetts; Noank, Connecticut; New York Bay, N.Y.; Washington, D. C.; Chain Bridge, Bryans Point, Plum Point, Havre de Grace, Patuxent River, Barren Island, and Smith Point, Maryland; Rappahannock River and Buckroe Beach, Virginia; Avoca and Beaufort, North Carolina; and St. Johns River, Florida; in USNM collections.

Distinctive Characters. See *Relationships*, p. 330.

Description. Proportional dimensions in per cent of standard length, and counts, based on study specimens, 27–240 mm SL.

Body: depth 21–33.5.
Caudal peduncle: depth 8.0–10.5.
Head: length 21.5–30.
Snout: length 3.8–5.8.
Eye: diameter 5.0–9.5.

Interorbital: width 3.7–6.0.
Maxillary: length 9.0–13.2.
Pelvic fin: length 9.4–13.6.
Pectoral fin: length 15.5–21.5.

Scales: 46–54.
Ventral scutes: 31–36.
Gill rakers: on lower limb 41–51 in adults, most frequently 45–50.
Fin rays: dorsal 15–20; anal 16–21; pectoral 14–16.
Vertebrae: 49–53 (35 specimens).

BODY rather slender, moderately compressed, its greatest thickness about 2.5 in the depth, its depth 3.0–4.6 in SL.

SCALES only moderately adherent, generally lost in young; with crenulate membranous edge preceded by scarcely visible striae: about 13 or 14 longitudinal rows of scales on body between base of pelvic and base of dorsal. VENTRAL SCUTES rather strong, 18–21 in advance of pelvic fins and 12–16 behind them.

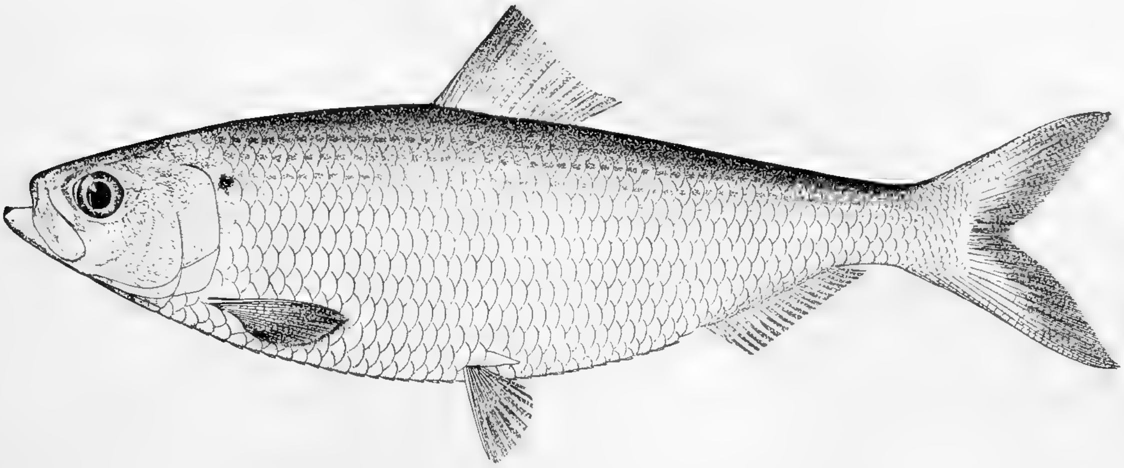

FIGURE 80. *Pomolobus aestivalis*, 265 mm TL, 10.6 inches, USNM 32639.

HEAD frequently equal to depth, 3.33–4.6 in SL. SNOUT 3.6–5.8 in head. EYE small, equal to or shorter than snout in adults, 3.0–6.0. INTERORBITAL 4.0–7.0. CHEEK notably longer than deep (Fig. 76 c). MOUTH oblique. UPPER JAW with a definite notch in adults. LOWER JAW not projecting strongly, partly included, not entering into dorsal profile, its upper margin within the mouth rising abruptly and forming a more or less definite obtuse angle (Fig. 76 c). MAXILLARY broad, its greatest width about 75 % of length of snout, rounded posteriorly, reaching to, or more often somewhat beyond, vertical from middle of eye, 2.0–2.7 in head. GILL RAKERS at angle of first arch fully 0.75 of diameter of eye; increasing in number with age: 28–36 on lower limb in examples 30–49 mm SL, 30–39 in specimens 50–69 mm, 35–41 in specimens 70–89 mm, 38–44 in specimens 90–109 mm, 42–48 in specimens 110–129 mm, 42–50 in specimens 130–149 mm, and 42–52 in examples 190–260 mm (adults). TEETH on premaxillary exceedingly minute in young, missing in adults; those on free rim of maxillary rather prominent in young and often slightly evident posteriorly in adults;

those present on lower jaw persistent anteriorly, though not with free points in adults; a permanent narrow band of granular teeth on median line of tongue.

DORSAL fin with a definitely concave margin, its origin scarcely an eye's diameter in advance of the pelvic fin and usually a little nearer to margin of upper jaw than to vertical from last ray of anal; a narrow sheath of scales at base, incomplete, leaving base of last 4 or 5 rays exposed. CAUDAL deeply forked, the lower lobe the longer, a little longer than head. ANAL low, with straight margin, its origin about equidistant between base of pelvic and base of caudal; a narrow sheath of scales at base. PELVIC fin inserted near ventral edge and about equidistant between base of pectoral and origin of anal, 1.8–2.6 in head. PECTORAL somewhat higher on side, reaching about 0.66 of the distance to base of pelvic, 1.2–1.7 in head.

Color. Fresh fish bluish above and sides silvery. Rows of scales on back and upper part of side with more or less distinct dark lines in adults. Shoulder with a dark spot in the larger examples, generally missing in individuals less than 100 mm long. Fins plain, generally greenish or yellowish in life. Peritoneum usually, though not always, dark.

Size. Bluebacks are known to attain a length of about 380 mm (15 in.) and a weight of approximately 13 ounces. However, the usual size of these fish in commercial catches as observed in the Chesapeake Bay area is under 300 mm (12 in.) and a half pound or less in weight.

Development and Growth. The eggs and early young were described by Kuntz and Radcliffe from material taken at Woods Hole, Massachusetts (*76*: 123–126). The eggs are demersal, somewhat adhesive, semitransparent and yellowish, round, and approximately a millimeter in diameter. The development is rapid; hatching occurs at ordinary laboratory temperature about 50 hours after fertilization.

The newly hatched larvae (Fig. 81 A) are close to 3.5 mm long and quite slender. In about four days the yolk is all absorbed and the larvae have grown to a length of about 5 mm. The vent in these larvae, as in other clupeids, is situated far back, about at the beginning of the posterior fifth of the body.

The smallest specimen at hand, 20.5 mm long (16.5 mm SL), taken June 17 (1873) at Washington, D. C., is still very slender (Fig. 81 B), its depth about 7.5 times in SL. Its eye is rather longer than the snout, the maxillary extends nearly to the pupil, and the fins are all developed, the pelvic being inserted about under the origin of the dorsal. In a 25-mm specimen (20 mm SL), the depth is contained 5.0 times in the length, and the pelvic fin is well behind the origin of the dorsal (Fig. 81 C), as in adults. The 30-mm fish illustrated by Kuntz and Radcliffe (*76*: fig. 100) is much deeper than specimens of somewhat similar size now at hand, its depth being about 3.6 times in SL; in specimens from the Rappahannock River, Virginia, 34, 35, and 38 mm (28, 29, and 30 mm SL), the depth is respectively 4.6, 4.65, and 4.3 times in SL, and specimens even up to 45 and 50 mm long are more slender than the 30-mm one illustrated. If the proportions are correctly shown, it seems highly probable that the illustrated specimen is not this species.

When the young fish reach a length of about 80–90 mm they are usually pro-

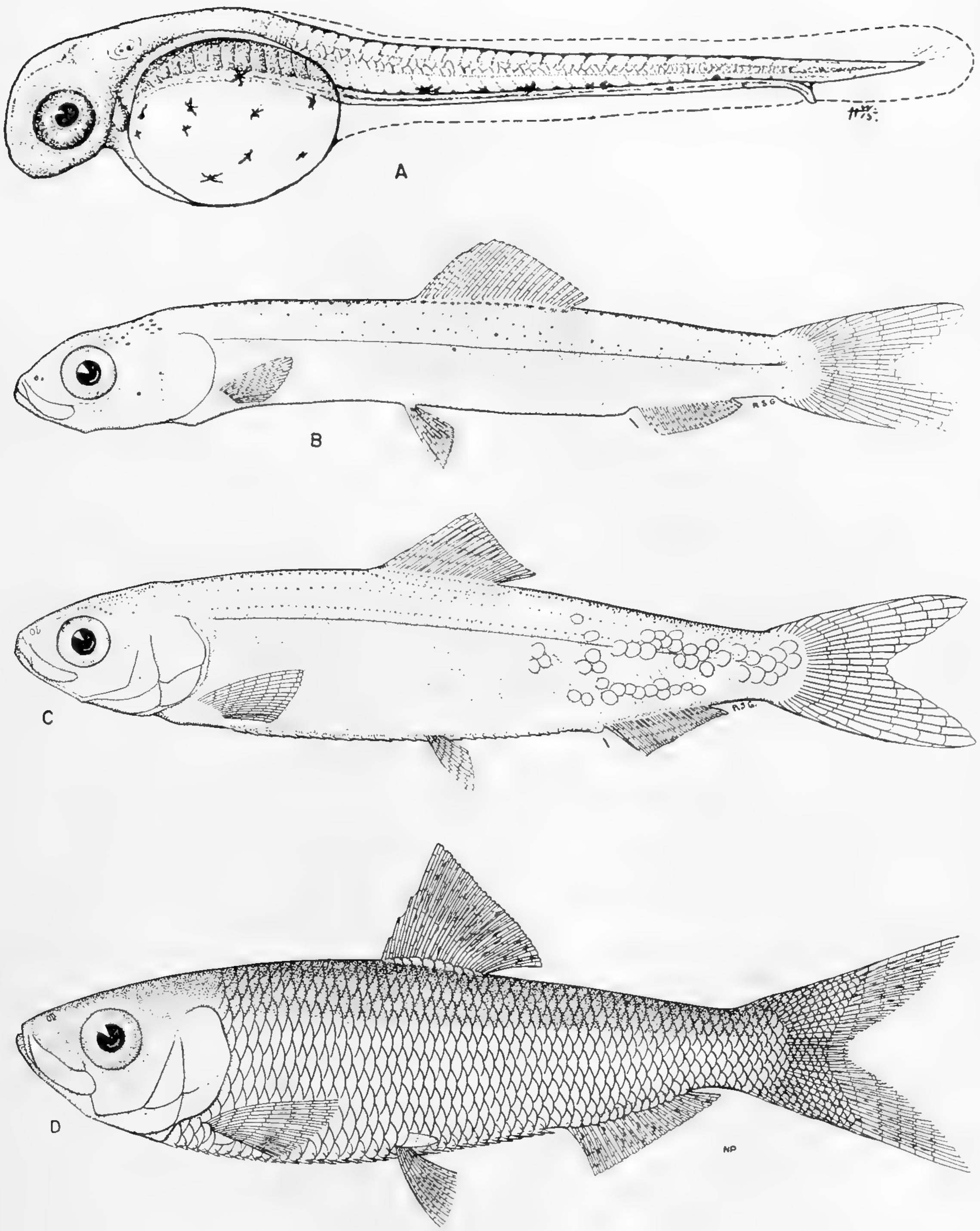

FIGURE 81. *Pomolobus aestivalis* growth stages; all from Potomac River. A, newly hatched larva, 3.5 mm, USNM 12830; B, young, still without scales, 20.5 mm TL, 16.5 mm SL, USNM 12830; C, young with scales developing, 25 mm TL, 20 mm SL, USNM 12830; D, young adult, 45 mm TL, USNM 69834. A drawn by Homer Wheelon; B, C by Ann S. Green; D by Nancy D. Patton.

portionately about as deep as large examples, though the diameter of the eye continues to exceed the length of snout until they are nearly full grown. The gill rakers (see *Description*) increase in number with age, quite rapidly in the young up to about 100 mm SL. It has been indicated also that the teeth are more prominent in the young than in the adult, and that they disappear entirely from the premaxillary with age.

In waters tributary to Chesapeake Bay, in the Potomac River in particular, where most of the young fish were collected and measured, the rate of growth of the young during their first summer and subsequently is shown in a table by Hildebrand and Schroeder (59: 88): 26 taken in June, 30–37 mm; 31 in July, 30–59 mm; 93 in August, 35–64 mm; 101 in September, 40–69 mm; 232 in October, 40–74 mm; and 181 in November, 50–74 mm. Collections of young of the same year-class from Chesapeake Bay consisted of: 276 taken in January, 65–119 mm long; 280 in February, 65–119 mm; 773 in March, 65–115 mm; and 8 in May, 95–120 mm in length. These data suggest that the young grow to a length of about 50–75 mm (2 or 3 in.) while living in fresh water and to a length of 65–120 mm (2.6–4.8 in.) when a year old.

Some older fish were taken in Chesapeake Bay, often in the same otter trawl hauls with the younger ones, but they are not separable into year-classes by the lengths given in the table referred to above. It is highly probable that, with few exceptions, these older and larger fish are approaching an age of two years. The collections consisted of: 8 taken in January, 160–194 mm in length; 15 in February, 150–209 mm; and 8 in March, 140–200 mm. If the six largest examples, which may be about three years old, are excluded, the range for the fish that apparently are two years old is 140–184 mm. If a length of around 200 mm is attained at three years of age, it is reasonable to assume that many individuals will attain a length of 250 mm (10 in.) when four years old. As adult gravid fish often are 250 mm and even less, it is highly probable that many individuals become sexually mature and perform their first migration to the spawning grounds at an age of four years.

Spawning, Migrations, and Habitat. Bluebacks are anadromous, but apparently they do not ascend rivers as far as their near relative, *P. pseudoharengus.* In the vicinity of Woods Hole, spawning takes place in fresh to slightly brackish ponds having an outlet to the sea; also, Bluebacks enter at least the mouths of the larger rivers in New England.

This species usually arrives in the coastal waters a month or so later than *pseudoharengus*—for example, in the lower parts of Chesapeake Bay during the first half of April and in the upper sections of the Bay about two weeks later. Hildebrand and Schroeder (59), in speaking of the migration in Chesapeake Bay, stated: "The peak of the catch of bluebacks is usually taken between April 1 and 20 in the lower bay. The numbers decrease throughout May, until after June 1 only stragglers are caught." The time of arrival varies from year to year by as much as a couple of weeks, depending upon the temperature of the water, which apparently must reach about 70°F before Bluebacks will enter. Northward, of course, the runs take place correspondingly later.

Spawning apparently begins very soon after the fish enter fresh or brackish water. Judging from the size and development of the young and from what is known concerning their migration locally, spawning in the Potomac seems to be confined principally to the last half of April and the first half of May. Ripe fish were taken in July (1915) at Woods Hole, Massachusetts (*76*: 123); while most of the females were spent, considerable numbers of each sex were still unripe.

The spent fish, in the Chesapeake Bay area at least, return to the ocean soon after spawning (*59*: 86). In the Gulf of Maine, "the spent fish, like alewives, return to the sea shortly after spawning. Probably these are the bluebacks taken at Woods Hole and north of Cape Cod in September and October. The winter home of our bluebacks is unknown; probably like their relatives the sea herring, they move out from land and pass the cold season near the bottom" (Bigelow and Welsh, *16*: 113). The capture of seven large Bluebacks, up to 375 mm (15 in.) in length, on March 5 (1931) about 70 miles off Barnegat, New Jersey (*14*: 377), and the acquisition of nine fish by me January 18 (1926) in the market and reported by the dealer to have been taken off Beaufort Inlet, North Carolina, with "sink nets" (often operated in fairly deep water), tend to substantiate the view that they winter near the bottom. The latter fish, one female and eight males, all contained well-developed gonads. Bigelow and Welsh reported that large schools of Bluebacks are often seined off the coast of Maine "outside the islands" during summer and fall and that they consist mostly of "2-year-old fish not yet sexually mature" (*16*).

In the Potomac, where the young are abundant below Little Falls throughout the summer, fish 20 mm long were taken there as early as June 17, and none less than 30 mm was secured in July. Upon the approach of cool water, October and November in the Chesapeake Bay area, the young leave the fresh waters; they are then about five to six months old, and the greater part of them passes through Chesapeake Bay and out to sea in company with graybacks and shad of a similar age. However, some of them stop to spend their first winter in the deeper parts of the Bay, and a few seem to spend their second winter there. However, no young have been listed as occurring offshore, from Chesapeake Bay southward. Pearson did list "*Pomolobus* sp." as having been "observed" in trawl catches off the coast of Virginia and North Carolina (*103*: 18); whether these fish were young or adults was not stated.

Food. The food (*16*: 113) consists of plankton, copepods, pelagic shrimp, and young launce, and no doubt other fish fry.

Enemies. Undoubtedly the principal enemies of young Bluebacks are the predatory fishes inhabiting the fresh and brackish water they occupy the first several months of life. As they school and move into salt water en route to the sea, marine shore fishes undoubtedly take their toll. Welsh and Breder found that weakfish (*Cynoscion regalis*) taken at the head of the Acushnet River, Massachusetts, were gorged with the young of this species (*132*: 159). While the schools migrate from the sea to fresh water, large predatory fishes again must take a toll. Upon arrival in inshore waters and in bays and streams, large numbers are captured by man.

Parasites. The parasitic acanthocephalan *Echinorhynchus acus* and the nematode *Heterakis foveolata* have been listed (*123*: 742). A specimen with a large colonial hydroid, *Obelia commensuralis*, attached to its back has been reported for Beaufort, N. C. (*50*: 1–6).

Relationships. This species and *pseudoharengus* are closely related, but they differ prominently from *chrysochloris* and *mediocris* in the more numerous gill rakers. In general, *aestivalis* has a more slender body and a smaller eye than *pseudoharengus.* However, extensive overlapping occurs in a series of measurements of specimens from various localities, even though specimens of equal size are measured. But in any one area, as in Chesapeake Bay, the separation of the two species by a combination of the two characters mentioned generally is not difficult.

Northward, as in New England, the species run somewhat more slender, and often some northern graybacks are quite as slender as some of the Bluebacks from the southern part of the range. Although the proportionate size of the eye is a somewhat more reliable character than depth of body, some specimens are difficult to distinguish by this character also. Fresh examples generally are distinguishable by the color, the Bluebacks being bluish above, the graybacks grayish green. However, this difference in color disappears in preserved specimens. The Bluebacks usually have more gill rakers and vertebrae than the graybacks, but again intergradation occurs in each instance; and the use of the number of gill rakers is made more complex because of their increase in number with the age of the fish. The range and intergradation of all the proportions and enumerations mentioned are shown in the *Description.*

The peritoneum (lining of abdominal cavity) is said to be black in the Bluebacks and pale or pale gray in the graybacks. Because this character was supposed to be diagnostic, it has been used in keys many times, but in the numerous preserved specimens at hand, it was found unreliable; Herbert E. Warfel, who has worked with *Pomolobus* in Connecticut, has informed me (verbally) that this character is unreliable in fresh material also. It cannot be trusted, because the peritoneum in the Bluebacks varies all the way from black to pale or pearly gray.

It is evident from the foregoing discussion that *aestivalis* and *pseudoharengus* often can be distinguished only by a combination of characters, and that, even then, some troublesome examples occur, with small specimens more difficult to identify than large ones.

Abundance and Commercial Importance. The relative abundance of the Bluebacks and graybacks is not definitely known. Although many fishermen recognize the two species, they are not separated in the market, and the catches are listed merely as "alewives" in the government's statistical reports. It has been stated that the two species are about equally abundant in Chesapeake Bay and that each contributes an equal share to the commercial catch (*59*: 91); also, the Bluebacks are more abundant than the graybacks in the southern states and less numerous northward (*72*, 1896: 426). For the Gulf of Maine, Bigelow and Welsh found it difficult to arrive at a fair idea of the relative abundance of the two (*16*: 112); although it is generally agreed that the graybacks outnumber the Bluebacks in the northern part of their range, these authors were certain that large catches of Bluebacks were taken in the Gulf of Maine from time to time. In Nova Scotia the Bluebacks are rather uncommon and of slight value whereas the graybacks are common and of considerable economic importance (*129*: 55). Some statistics showing the combined catches of the two species, designated "alewives," are given in the account of the grayback (p. 338).

Fluctuations, Methods of Fishing, and Artificial Propagation. The remarks in the account of the grayback concerning fluctuations, effects of fishing, methods of fishing, and artificial culture, also apply in general to the Blueback.

Range. The range of this species extends all the way from Cape Breton, Nova Scotia (*15*: 107, ftn. 92), to the St. Johns River, Florida; it is the most numerous southward.

Synonyms and References:

Clupea aestivalis Mitchill, Rep. in part on Fishes of New York, 1814: 21 (orig. descr.; type local. presumably New York; type lost); Mitchill, Trans. Lit. philos. Soc. N. Y., *1*, 1815: 456 (descr.); Jordan and Gilbert, Bull. U. S. nat. Mus., 16, 1882: 267 (cf. *C. vernalis* Mitchill = *C. pseudoharengus* Wilson; distinct. char., range, synon.); Bean, T. H., Proc. U. S. nat. Mus., 6, 1883: 366 (migr. in Chesapeake Bay); McDonald *in* Goode *et al.*, Fish. Fish. Industr. U. S., *1*, 1884: 579–588, pls. 209, 210 (hist. of nomencl., abund., geogr. distr., food, reprod., size, uses); Goode, Amer. Fishes, 1888: 393 (discus. relation. with *P. pseudoharengus*; names, abund., spawn., etc.).

Pomolobus aestivalis Jordan and Evermann. Bull. U. S. nat. Mus. 47 (1), 1896: 426; 47 (4), 1900: fig. 190 (cf. *P. pseudoharengus*; descr., synon.); Smith, Bull. U. S. Fish. Comm. (1897), *17*, 1898: 91 (Woods Hole, Massachusetts); Evermann and Kendall, Rep. U. S. Comm. Fish. (1899), 1900: 55 (St. Johns R., Welaka, Volusia Bar at Lake George, and Lake Monroe, Florida); Smith, N. C. geol. econ. Surv., *2*, 1907: 124, fig. 42, pl. 4 in color (synon., descr., range, habits, distinct. char.); Kendall, Occ. Pap. Boston Soc. nat. Hist., *7*, 1908: 38 (refs., New England); Evermann and Hildebrand, Proc. biol. Soc. Wash., *23*, 1910: 158 (Bryans Pt., Maryland); Sumner, *et al.*, Bull. U. S. Bur. Fish. (1911), 31 (2), 1913: 742 (refs., Woods Hole, Massachusetts, parasites); Regan, Ann. Mag. nat. Hist., (8) *19*, 1917: 300 (descr.); Kuntz and Radcliffe, Bull. U. S. Bur. Fish., *35*, 1918: 123, figs. 87–100 (develop. of egg and young; fig. 100 apparently not this species); Welsh and Breder, Bull. U. S. Bur. Fish. (1923), *39*, 1924: 159 (eaten by *Cynoscion regalis*); Bigelow and Welsh, Bull. U. S. Bur. Fish. (1924), *40* (1), 1925: 110, fig. 45 (descr., size, range, Gulf of Maine); Nichols and Breder, Zoologica, N. Y., *9* (1), 1927: 39, fig. (distr. New York, s. New England, life hist., develop., size); Hildebrand and Schroeder, Bull. U. S. Bur. Fish. (1927), *43* (1), 1928: 85, figs. 44–50 (synon., descr., cf. *P. pseudoharengus*, habits, growth rate of young, commerc. import., range, Chesapeake Bay); Truitt, Bean, and Fowler, Bull. Md. Conserv. Dep., 3, 1929: 50 (descr., Maryland); Breder, Field Bk. Mar. Fish. Atl. Cst., 1929: 66, fig. (range, migr., spawn., size); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 42 (names, synon., range); Greeley, 24th Rep. N. Y. Conserv. Dep. (1934), Suppl., 9, 1935: 89, pl. 1 color (midsection of Hudson R.; cf. *P. pseudoharengus*); Vladykov and McKenzie, Proc. N. S. Inst. Sci., *19* (1), 1935: 55, fig. 29 (Nova Scotia); Gudger, Amer. Mus. Novit., 945, 1937: 1–6 (colonial hydroid on back); Greeley, 26th Rep. N. Y. Conserv. Dep. (1936), Suppl., 11, 1937: 73 ("summer herring"), 91 (abund. Hudson R., migr. of adults and young); Greeley, 28th Rep. N. Y. Conserv. Dep. (1938), Suppl., 15 (2), 1939: 82 (Long Island, New York); Bigelow and Schroeder, Bull. U. S. Bur. Fish., *48* (20), 1936: 327 (adults captured off Barnegat, New Jersey); Anonymous, Fish. Resourc. U.S., Senate Doc. 51, 1945: iii, 66, fig. (migr., range, commerc. import., methods of capture, causes for decline, remedies; consid. with *P. pseudoharengus*, not separately); Bigelow and Schroeder, Fish. Bull. (74) U. S. Fish Wildlife Serv., *53*, 1953: 106–107 (descr., habits, Gulf of Maine).

Pomolobus cyanonoton Bean, T. H., 7th Rep. Forest Comm. N. Y. (1901), 1902: 305, fig. (synon., migr., time and place of spawn.); Bean, T. H., Bull. N. Y. St. Mus., 60, Zool. 9, 1903: 202 (synon., migr., local occur., common names); Fowler, Rep. N. J. St. Mus., 2, 1905: 98, figs. (male and female fig., dist. char., local occur., synon.).

Pomolobus sp. Pearson, Invest. Reps. U. S. Bur. Fish. (1932), *1* (10), 1936: 18 (in trawl catch).

Doubtful References:

Clupea fasciata LeSueur, J. Acad. nat. Sci. Philad., *1* (2), 1818: 233 (orig. descr.; type local. Sandwich, Massachusetts).

Alosa tyrannus De Kay (not of Latrobe), N. Y. Fauna, Pt. 4: Fishes, 1842: 258, pl. 13, fig. 38 (descr., occur. along coast; plainly not menhaden; descr. and fig. suggest *P. aestivalis*).

Alosa cyanonoton Storer, Proc. Boston Soc. nat. Hist., *2*, 1848: 242 (orig. descr.; type local. presumably Massachusetts); Storer, Fish. Mass., 1867: 161, pl. 27, fig. 1 (descr., names, occur.).

Pomolobus pseudoharengus (Wilson) 1811

Grayback,[33] Gray Herring, White Herring, Branch Herring, Bigeye Herring, Freshwater Herring, Sawbelly, Alewife, Kyak, Gaspereau

Figures 76, 77, 82, 83

Study Material. A total of 65 or more specimens, 30–330 mm TL, 23.5–268 mm SL, from Cape Breton, Nova Scotia; St. Andrews Bay, New Brunswick; Freeport and Portland, Maine; Falmouth and Woods Hole, Massachusetts; Noank, Connecticut; Long Island, New York; off Wildwood, New Jersey; and various localities in the Chesapeake Bay area.

Distinctive Characters. See *Relationships* under *aestivalis*, p. 330.

Description. Proportional dimensions in per cent of standard length, and counts, based on 65 or more specimens, 23.5–268 mm SL.

Body: depth 23.5–35.5.
Caudal peduncle: depth 8.5–12.
Head: length 22.6–34.8.
Snout: length 4.55–7.6.
Eye: diameter 5.0–12.
Interorbital: width 3.45–7.3.
Maxillary: length 10.5–15.
Pelvic fin: length 10.4–15.8.
Pectoral fin: length 14.6–22.6.

Scales: 42–50.
Ventral scutes: 30–36.
Gill rakers: on lower limb 38–43 in adults (occasionally 44).
Fin rays: dorsal 15–19; anal 17–21; pectoral 13–16.
Vertebrae: 46–50 (36 specimens).

Body compressed, its greatest thickness usually about 2.75 in its depth, the depth 2.8–4.25 in SL.

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[33] Grayback has been chosen as the leading name for *P. pseudoharengus* and blueback for *P. aestivalis* because these names in a measure are descriptive, distinctive, and are perhaps understood by more people within the range of the species than any others. Alewife certainly is not distinctive, as it sometimes includes both species mentioned, and in some places it is applied to the menhaden, *Brevoortia*. Branch herring and glut herring are distinctive in the Chesapeake Bay area, but these names are not well known northward. However, alewife is used in subsequent pages to include *both* of these species in citing commercial statistics, for the species are not separated in the market, where they are sold either as alewives or as river herring. [The American Fisheries Society recommends "Alewife" for *pseudoharengus*.—Y. H. O.]

Scales only moderately adherent, often lost in preserved specimens; apparently not different from those of *P. aestivalis*; 14 longitudinal rows between base of pelvic and base of dorsal. Ventral scutes strong, 18–21 in advance of pelvics, 12–16 behind them.

Head less than depth, often fully by diameter of eye, 2.8–4.2. Snout 4.1–6.0. Eye large, longer than snout at all ages, 2.5–4.0. Interorbital 4.0–7.3. Mouth oblique, as in *P. aestivalis*; margin of lower jaw within mouth with a somewhat broader angle (Fig. 76 D); other characters about the mouth, including Teeth, as in *P. aestivalis*. Maxillary 1.8–2.8 in head. Gill rakers at angle of first arch about 0.66 of diameter of eye, increasing in number with age; 25–33 on lower limb in examples 30–49 mm SL, 32–36 in specimens 50–69 mm, 30–39 in specimens 70–89 mm, 35–38 in specimens 90–109 mm, 36–40 in specimens 110–129 mm, 36–40 in specimens 130–149 mm, and 38–44 in examples 210–270 mm (adults).

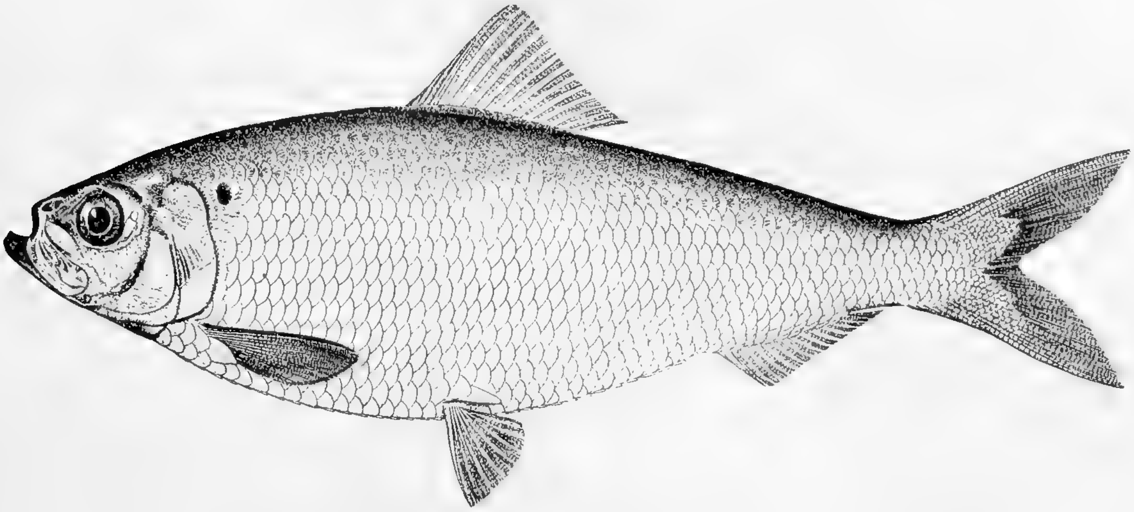

Figure 82. *Pomolobus pseudoharengus*, 300 mm TL, from a market in Washington, D. C., USNM 25197.

Dorsal fin with a straight to slightly concave margin, its origin definitely less than an eye's diameter in advance of pelvic fin and usually nearer to margin of upper jaw than to vertical from last ray of anal. Caudal deeply forked, the lower lobe a little longer than upper lobe, often exceeding head length by nearly the diameter of eye. Anal low, with an almost straight margin, its origin about equidistant between base of pelvic and base of caudal. Pelvic fin inserted near ventral edge and usually equidistant between base of pectoral and origin of anal, 1.75–2.5 in head. Pectoral fin somewhat higher on side, reaching about 0.66 of the distance to pelvic in adults and nearly to pelvic in some small examples, 1.1–2.0 in head.

Color. Fresh specimens, grayish green above. Sides silvery. Rows of scales on upper part of side sometimes with more or less definite dusky lines in adults. A small dark spot at shoulder, often missing in specimens less than 100 mm long. Fins all plain, slightly yellowish to green in life. Peritoneum generally pale or silvery, often with dark punctulations, and sometimes quite dusky.

Size. The Graybacks, like the bluebacks (*aestivalis*), attain a length of about 380 mm (15 in.) and a weight of about 14 ounces; the usual length of market fish, as observed in the Chesapeake Bay area, averaged only about 275 mm (11 in.) in length and about a half pound in weight.

Although Graybacks generally grow to a length of 275–300 mm (11–12 in.) in salt water along the Atlantic coast, their usual length in Lake Ontario (*118*: 188) is less than 150 mm (6 in.). The same writer mentioned fish only 100–125 mm (4–5 in.) long with roe as further evidence of stunted growth resulting from the local conditions under which the fish were living.

Development and Growth. The eggs are 1.25 mm in diameter and very glutinous when first laid, adhering to brush, rope, stones, piling, and other objects (*119*: 123). The incubation period extends over six days at a mean water temperature of 60° F.

Recently hatched larvae are very slender and extremely transparent, and have only a row of pigment spots on the side of the tail (*113*: 506, pl. 1, fig. 8). A two-day-old fish is about 5.0 mm long, and Ryder's figure shows the greatest depth, including the fin folds, to be about 10 times in TL, with the vent (as usual in clupeoid fishes) situated very far back at about the beginning of the posterior fifth of the body. This agrees very well with a larva of similar age and size described as *P. aestivalis* (*76*: 126).[34] The appendages (pyloric caeca), connected to the intestine near the stomach, are very small or wanting in the young but become greatly developed with age (*59*: 90).

The young reach a length of 15 mm when a month old (*16*: 109). On the smallest specimen at hand, 29 mm (22 mm SL), taken on June 18 (1873) at Washington, D. C., the depth is 4.0 times in SL; in other respects it already resembles the adult; the eye is notably longer than the snout and remains so throughout life. When the fish reach a length of about 100 mm, the proportionate depth is more or less the same as in adult fish.

The gill rakers (see *Description*) increase in number with age, this increase being especially rapid in the young up to about 100 mm SL. In this species, as in *P. aestivalis*, the teeth are more prominent in the young than in the adults and disappear from the premaxillary with age.

The young reach a length of 50–100 mm (2–4 in.) by autumn in streams tributary to the Gulf of Maine (*16*). This rate of growth is about the same as that shown by Hildebrand and Schroeder (*59*: 91) in a table based on collections made in streams tributary to Chesapeake Bay (especially the Potomac River). This table includes: 26 young for June, 45–74 mm; 105 for August, 50–84 mm; 134 for Sep-

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[34] Early larvae and some young adults, supposedly of *P. pseudoharengus*, were described and figured by Prince (*105*: 103–108, pls. 8, 10, in part). It seems doubtful whether his identifications were correct, for his drawings of young adults, compared with young adults from the Potomac, now before me, show the body to be much deeper and the mouth nearly vertical.

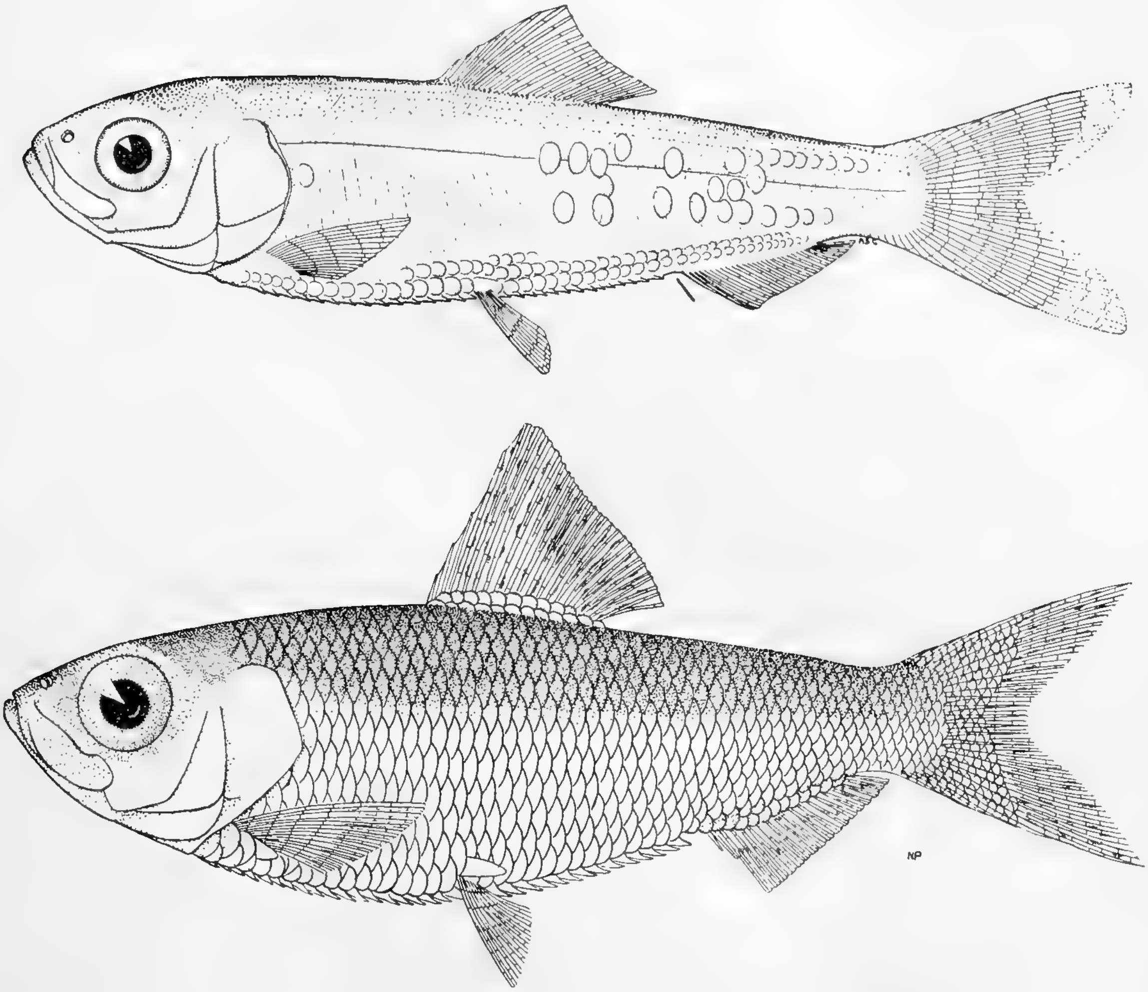

FIGURE 83. *Pomolobus pseudoharengus*, from Potomac River. TOP, young, showing scales developing, 29 mm TL, 22 mm SL, USNM 85668; BOTTOM, young adult, 47.5 mm TL, USNM 69833. UPPER drawn by Ann S. Green; LOWER by Nancy D. Patton.

tember, 50–79 mm;[35] 138 for October, 55–94 mm; 221 for November, 55–109 mm; and 19 for early in December, 60–79 mm TL. In Chesapeake Bay, young that appeared to be in their first winter, as judged from their small size, were 75–140 mm in January, 80–114 mm in February, and 80–145 mm in March. The young fry taken in the Bay during the winter varied so widely in length that it is clear they represented more than one year-class. The 262 older fish taken during the winter ranged between 115–224 mm, or 115–194 mm, if the three largest examples are excluded.

The foregoing data seem to show that the young of this species grow to a length of 55–109 mm (2.20–4.36 in.) while in fresh water, to about 65–145 mm (2.6–5.8 in.) at one year of age, and to about 115–195 mm (4.6–7.8 in.) at two years of

[35] The largest young of the season evidently are not represented in this collection.

age. Mature gravid fish often are only 250 mm (10 in.), or even less, and if a length of 200 mm (8 in.) or more is attained at three years of age, it is probable that many become sexually mature and perform their first migration to the spawning grounds when four years old. However, Bigelow and Welsh (*16*: 110) have reasoned that at least some of the fish in the Gulf of Maine area reach maturity at three years of age. This conclusion was reached because the "progeny" of adults used in restocking streams returned in the third year after the streams were restocked.

Spawning. This species is very prolific; a total of 644 females from the Potomac River yielded an average of 102,800 eggs per fish (*119*: 123). The time of spawning varies from some time in March in Chesapeake Bay to late April or May in Maine. They may spawn in running water or in ponds. Ripe fish have been taken many times in the Potomac, near Washington, where the eggs have been found adhering to fish traps and where young occur throughout the summer. Greeley has described their spawning in dense schools in fast water approximately two feet deep over a bottom of coarse stones, some sand, and gravel in the Poestenkill, at Troy, New York (*47*: 89). Around the Gulf of Maine, however, they spawn more commonly in ponds (including those behind barrier beaches), though probably not so exclusively as Bigelow and Welsh believed (*16*: 109).

According to Greeley (*47*: 89):

> The act of spawning is characterized by the whirling of a pair of fish in a close spiral, usually ending as they reach the surface with a splash and separate. The whirling is done rapidly and often only a flash of silver is to be seen. A number of spawning pairs were observed here [presumably the Hudson] by Dr. C. W. Greene and the writer. The sexes of the fish cannot be determined from the appearance of the fish in the water, but it was assumed that the fish seen whirling were mated pairs. It is probable that the male is on the outside of the spiral during the act of spawning and that the rapid circling is adopted for maintenance of contact as the eggs are shed and fertilized. Many eggs were scattered over the bottom and had drifted downstream where they were deposited by the current in slack water areas behind obstructions. The temperatures here May 16 (11 A.M.) were: air, 57 degrees; water 52 degrees.

Migrations and Habitat. This species is strictly anadromous. It has been common knowledge since colonial times that they run

> indifferently up rivers as large as the St. John (New Brunswick), the Merrimac and Potomac, or streams so small one can almost leap across, and only a few inches deep. In large rivers they may run far upstream . . . or their journey may be only a few yards, as it is in the artificial cuts that are kept open through barrier beaches to allow the fish access to fresh water ponds behind the latter (*15*: 103).

The Graybacks arrive in inshore waters a month or so ahead of the bluebacks and a week or two ahead of the shad. In Chesapeake Bay the first catches are made in late February or early March. In southern New England (Woods Hole, Massachusetts) they arrive sometime during March and are caught through March and April (*120*: 91). However, they do not reach the rivers of Maine until late April or early May and, as shown by the commercial catches, they are most numerous there during the last half of May (*16*: 109).

That the young return to the stream of their birth (the so-called "parent stream theory") was confirmed when the progeny of gravid adults planted in depopulated streams returned to these rivers three years after hatching (*16*: 110). This incident is also cited in a subsequent paragraph as a successful method of restocking streams. But a much more intensive study of this interesting question is needed before any categorical statement can be made as to how generally the parent stream theory applies in the case of the Graybacks (*15*: 103).

As in the case of bluebacks and shad, relatively little is known about the home of Graybacks in the sea. The capture of 18 adult Graybacks 70 odd miles off Barnegat, New Jersey, on March 5, 1931 (*14*: 327), suggests that the home may be some distance offshore. Since these adults were taken in March, they may have been en route to some nearby stream, hence it should not be assumed that the fish actually were taken from their usual abode in the sea. It has been surmised for some time that the Graybacks, as well as blueback herring and American shad, live quite a distance offshore from the rivers of their origin and that their migrations consist of inshore and offshore movements. This theory finds slight support in the discovery that different races spawn in different river systems. However, further study is needed.

The young, often with bluebacks and American shad of similar age, have been seen descending as early as June 15 in the more southerly streams fringing the Gulf of Maine. Successive companies of fry move out of the places where they were hatched, run down with the current throughout the summer and are at sea by autumn. In the Potomac, which the fish cannot ascend beyond Little Falls, the young remain abundant in the vicinity of Washington, D. C. Here they may be taken in the same seine hauls with bluebacks and American shad until October, when the main seaward migration takes place; however, some young remain in the river until November and a few linger until December. Most of the young apparently pass directly through Chesapeake Bay and out to sea, but some stop to spend their first winter in the deeper parts of the Bay, a few seem to remain for their second winter, and very few apparently stay there for their third winter.

The fish in the freshwater lakes endeavor to carry out the same spawning migration as those that inhabit the Atlantic coast, for the fish enter the shallow parts of the lakes and ascend the tributary streams to spawn.

Food. The food of the young while in fresh water apparently consists principally of diatoms, copepods, and ostracods. After they enter salt water, their chief diet seems to be shrimps and fish. Young 50–70 mm long, taken in fresh water, had fed principally on copepods and ostracods; and larger young, 83–178 mm long, caught in Chesapeake Bay, had continued to feed on copepods, though the larger ones had ingested principally mysids and fish (*59*: 90). Copepods, shrimps, and young squid were listed as the food of the young by Sumner, *et al.* (*123*: 72). Bigelow and Welsh (*16*: 110) have described their chief food as copepods, amphipods, shrimps, and appendicularians, small fish (such as herring, eel, launce, and cunner) as well as fish eggs and young of their own. Alewives often contain diatoms, even when adult. It is conceivable that diatoms could be screened from the water by the rather numerous, close-set gill rakers of adults.

It has long been known that anadromous fishes, as a rule, feed sparingly or not at all while ascending streams, and Graybacks are no exception to this rule. However, the spent fish feed ravenously on shrimp on entering brackish water along the coast, where anglers often hook them on an artificial fly (*16*).

Enemies. The young are undoubtedly preyed upon by various predatory fishes, turtles, snakes, and birds while they live in fresh water. When they begin to school and migrate out to sea, marine fishes and numerous other sea inhabitants very probably destroy many. When they re-enter shallow shore water as adults in great schools, large marine fishes of many kinds, finback whales, birds, and turtles, take a further toll. Upon arriving inshore and in the rivers, man—who captures great quantities for food —must be their chief enemy.

Parasites. The following have been listed by Sumner, *et al.* (*123*: 742): Acanthocephala (*Echinorhynchus acus*); cestodes (*Rhynchobothrium imparispine*); trematodes (*Distomum appendiculatum*, *D. bothryophoron*, *D. vitellosum*, and *Monostomum* sp.); and copepods (*Argulus alosae*, *Caligus rapax*, and *Lepeophtheirus edwardsi*).

Variations. Specimens from various localities within the range of this species along the coast (*Study Material*, p. 332) show a tendency toward a more slender body and a proportionately larger head toward the northern part of the range; and a limited number of specimens from fresh water, Cayuga Lake and Lake Ontario (proportions not used in *Description*), show this tendency to be even more pronounced there. In general, the fish from the northern part of the range (especially from Casco Bay, Maine), and more particularly those from fresh water, have the appearance of being more or less emaciated. However, insufficient specimens have been studied to determine the significance of the apparent differences mentioned. These differences may be of subspecific value, but more likely they are of only racial importance. The decrease in body depth in northern specimens makes their separation from *P. aestivalis* more difficult than identification of specimens from the southern part of the range.

Abundance and Commercial Importance. The relative abundance of *pseudoharengus* and *aestivalis* is discussed in the account of the latter (p. 330). It has been claimed by various writers that Graybacks are far less numerous now than during colonial days, or even a half century ago. The matter was summed up for the Gulf of Maine by Bigelow and Welsh (*16*: 108) in these words:

> During the past two centuries . . . its numbers have declined, and its range has been restricted, both by actual extirpation from certain streams by overfishing, by the pollution of river waters by manufacturing wastes, and by the erection of dams that it cannot pass. However, the alewife is still a familiar fish all along our coast, and yields an abundant catch in many of our streams.

These remarks also apply in a measure to fish in the more southern part of the range, though the decline apparently has been less pronounced southward.

The following statistics give the catches of Graybacks and bluebacks combined, under the name "Alewives." These records show in part the decline in their abundance during the past 50 years or so, but they also show that these fish are still abundant and of great economic importance. There has been no compensation for any variations in the "fishing effort"—the number of men, vessels, and amount and efficiency of the gear used—but it may be assumed that there was no decrease in this respect. Federal Government statistics, which have been taken at irregular intervals, report total catches in round numbers for the Atlantic coast of the United States as follows: 62,067,000 pounds in 1896, 52,061,000 in 1905, 35,809,000 in 1921, 35,290,000 in 1929, and 29,542,000 in 1941. The greatest proportionate decline took place in New England, for which the following catches are listed: 12,116,000 pounds in 1896, 8,429,000 in 1905, and 3,975,000 in 1924; however, from 1924 to 1941 the catch there remained fairly even.

South of New England the decline in abundance began later and was more gradual and less pronounced. For example, the Chesapeake Bay states (Maryland and Virginia), which have furnished a larger part of the total catch of "Alewives" than any other section of the coast since the beginning of this century, yielded a fairly even catch until about 1925. Thereafter a decline has been indicated by the statistics: 25,611,000 pounds in 1925, 21,129,000 in 1930, 18,884,000 in 1937, and 17,012,000 in 1941. The catch in the South Atlantic states, from North Carolina to Florida, is also very large, has fluctuated greatly, and has shown a slight downward trend: 15,857,000 pounds for 1897, 11,601,000 for 1902, 15,186,000 for 1918, 7,571,000 for 1923, 11,176,000 for 1929, 6,218,000 for 1937, 11,611,000 for 1938, and 9,116,000 for 1940. The over-all catch of the two species combined has ranged between 47,300,000 and 57,700,000 pounds for the United States (1940, 1945, 1950–1953), and between 6,250,000 and 41,000,000 pounds for Canada (1940, 1945, 1950–1952).

The Graybacks and blueback herring are still abundant. In fact, every state along the Atlantic coast exclusive of Pennsylvania, South Carolina, and Georgia, make substantial contributions to the catch, as do Nova Scotia and New Brunswick, Canada. Although these species are among the cheapest fish on the market, they furnish a substantial income because of their abundance. During recent years the annual yield to the fishermen from this fishery alone has been $ 400,000–800,000 in the United States, and $ 33,000–350,000 in Canada.

Most of the "Alewives" caught are salted, but an increasingly large part of the catch is sold in the fresh state. Although the flesh is quite bony, as in other herrings, it is delicious and is in demand whether fresh, salted, or smoked. At the salting houses the roe generally is separated for canning and the offal is made into fish meal and oil.

Although these fish have become common to abundant in some freshwater lakes, as in Lakes Ontario and Erie, they are of little economic importance there because of their small size. However, in 1892 Smith said that they were of more economic importance in Lake Ontario than is generally realized (*118*: 189). He pointed out that they had replaced more important foodfishes (young ciscoes and suckers) as bait for sturgeon and lake trout in the trawl-line fishery, that the young were used as bait in extensive sport fishing, and that many tons of those that wash ashore annually are used as fertilizer.

Fluctuations. Overfishing, pollution, and impassable dams in streams have been the chief factors in diminishing the abundance of "Alewives" in many localities, but all of these causes can be remedied at least in some measure by restocking suitable streams with gravid fish (*16*: 110; *et al.*). This has been done in Massachusetts localities, where, in the third year after the ripe fish were introduced, the progeny appeared in those streams.

It is not always easy to determine whether an increase or decrease in catch is due to the amount of fishing, to special conditions created by man, to successful or unsuccessful spawning, or to general conditions obtaining in nature. However, if the increase or decrease extends over a period of several years, reasonable conclusions may be reached. For example, the tremendous abundance of "Alewives" in the Chesapeake Bay area in 1908 and 1909, when the catches were about twice those in preceding and successive censuses (66,690,000 and 51,425,000 pounds), may be ascribed to especially favorable conditions during and probably after the spawning season. On the other hand, the general decline in the fishery in New England (discussed above), despite some fluctuations, quite surely was the result of adverse conditions created by man. Therefore, frequent censuses are necessary to show the status of this as well as other fisheries for the guidance of those entrusted with the promulgation of regulations for the conservation of the fishery.

Artificial Cultivation. "Alewives" have not been artificially propagated regularly because it has not been deemed necessary. However, in 1882 two million fry hatched by fish culturists were transported to the Colorado River, Texas (*45*: 586), an introduction that apparently was not successful. As already stated, another method of "planting" was successfully used in Massachusetts. Some depopulated streams in that state, which had been reconditioned and made suitable, were successfully restocked merely by releasing gravid fish. Graybacks apparently were unintentionally introduced into Lake Ontario when shad fry were planted there (*45*: 588; *118*: 188).

Methods of Fishing. "Alewives" are easily caught, chiefly with dip nets in New England. Pools are constructed about the mouths of rivers and the gravid fish are led into them by means of nets and stone diversions. Southward, as in the Chesapeake Bay area and in North Carolina, they are caught chiefly with pound nets. However, they are taken also with weirs, seines, gill nets, fyke nets, and a few with otter trawls.

Range and Distribution. The range of *pseudoharengus* extends from the Gulf of St. Lawrence and Nova Scotia, where it is common (*129*: 54), to North Carolina. It has been recorded for the St. Johns River, Florida, but the first report (*45*: 336), as *Clupea vernalis*, was apparently based on a *P. aestivalis* (USNM 17929, collected by Spencer F. Baird), now before me; and the second report, so far as known, by Lönnberg (*88*: 114), may be disregarded, for this species is too difficult to distinguish from *P. aestivalis* by a simple "observation." According to Smith, "extensive collections of fishes in the St. Johns River, in Florida, have failed to disclose its presence" (*119*: 122). Indeed, no specimens of this species from south of the Albemarle Sound area (where *aestivalis* is plentiful) have been found in the National Museum, and it was only sparingly represented among many specimens of *P. aestivalis* collected over a period of years in the Newport River and its estuary near Beaufort, N. C. Possibly this species does not occur south of North Carolina.

This species, as stated above under *Artificial Cultivation*, apparently was unintentionally introduced into Lake Ontario, whence it has spread to Lake Erie and to Lake Huron. It also inhabits Lakes Seneca and Cayuga, which it probably reached by natural means from the ocean (*45*: 116), and the Oswego River system in New York State (*46*: 95). It has remained common in Lake Ontario, has become common in Lake Erie, and has penetrated Lake Huron, where it is still rare (*62*: 27).

Synonyms and References:

Clupea pseudoharengus Wilson, in Rees' New Cyclopedia (Art. *Clupea*), *9*, undated, *ca.* 1811: no pages (orig. descr.; no local.; probably Philadelphia, Pennsylvania); Smith, Bull. U.S. Fish Comm. (1890), *10*, 1892: 187, pl. 29 (unintent. introd. in Lake Ontario, abund. there, diseases, mortal., uses).

Clupea vernalis Mitchill, Trans. Lit. philos. Soc. N. Y., *1*, 1815: 454 (orig. descr.; type local. New York; effects of mill dams on migr. to spawn); Jordan and Gilbert, Bull. U. S. nat. Mus., 16, 1882: 267 (descr., range, synon.); McDonald *in* Goode, *et al.*, Fish. Fish. Industr. U. S., 1, 1884: 579–588, pls. 207, 208 (hist. of nomencl., abund., geogr. distr., migr., food, reprod., size, uses); Bean *in* Goode, *et al.*, Fish. Fish. Industr. U. S., 1, 1884: 588–593 (Lakes Cayuga, Seneca, and Ontario, origin in lakes, movements, enemies, fatal., capture); Ryder, Rep. U. S. Comm. Fish. (1885), 1887: 506, pl. 1, fig. 8 (descr. of egg and newly hatched young); Goode, Amer. Fishes, 1888: 393 (discus. with *P. aestivalis*, names, abund., spawn.).

Clupea megalops Rafinesque, Amer. Mon. Mag. (1817–1818), *2* (3), 1818: 206 (orig. descr.; type local. Delaware R.).

Meletta venosa Cuvier and Valenciennes, Hist. Nat. Poiss., *20*, 1847: 374 (orig. descr.; type local. New York); Bertin, Bull. Soc. zool. Fr., 66, 1941: 23 (ident. of types).

Pomolobus pseudoharengus Gill, Rep. U. S. Comm. Fish. (1871–72), 1873: 811 (names, range); Uhler and Lugger, Rep. Comm. Fish. Md., ed. 1, 1876: 158; ed. 2, 1876: 135 (descr., synon., habits, Maryland; *pseudoharengus* and *aestivalis* not distingu.); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 426; 47 (*4*), 1900: fig. 189 (descr., range, habits, synon.); Smith, Bull. U. S. Fish Comm. (1897), *17*, 1898: 91 (Woods Hole, Massachusetts); Bean, T. H., 7th Rep. Forest Comm. N. Y. (1901), 1902: 302, with fig. (synon., names, occur. in lakes, migr., size, methods of capture); Bean, T. H., Bull. N. Y. St. Mus., *60*, Zool. 9, 1903: 199 (synon., descr., names, range, migr., size, growth of young, econ. value, methods of capture); Fowler, Rep. N. J. St. Mus., 2, 1905: 95 (figs. of male and female, descr., migr., synon.); Smith, N. C. geol. econ. Surv., *2*, 1907: 122, fig. 44, pl. 3 in color (synon., descr., range, migr., reprod., commerc. import., North Carolina, methods of capture); Kendall, Occ. Pap. Boston Soc. nat. Hist., 7, 1908: 38 (refs., New England); Sumner, Osburn, and Cole, Bull. U.S. Bur. Fish. (1911), *31*, 1913: 742 (refs., Woods Hole, Mass., food, parasites); Regan, Ann. Mag. nat. Hist., (8) *19*, 1917: 300 (descr.); Bigelow and Welsh, Bull. U. S. Bur. Fish. (1924), *40*, 1925: 107, fig. 44 (descr., size, range, Gulf of Maine, habits, food, commerc. import.); Nichols and Breder, Zoologica, N.Y., *9* (1), 1927: 38, fig. (distr. New York, s. New England, food, life hist., size); Hildebrand and Schroeder, Bull. U. S. Fish Comm. (1927), *43* (1), 1928: 89, figs. 51–52 (synon., descr., relation., growth of young, food, habits, commerc. import., range, Chesapeake Bay); Greeley, 17th Rep. N. Y. St. Conserv. Dep. (1927), Suppl., 1928: 95 pl. 3 in color (Oswego R. watershed); Jordan, Manual Vert. Anim. NE U. S., ed. 13, 1929: 40 (diagn., range); Truitt, Bean, and Fowler, Bull. Md. Conserv. Dep., 3, 1929: 49, fig. 15 (descr., Maryland); Breder, Field Bk. Mar. Fish. Atl. Cst., 1929: 65 (food, spawn., size); Greeley, 18th Rep. N. Y. Conserv. Dep. (1928), Suppl., 1929: 167 (common Lake Ontario, enters Niagara R.); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 42 (names, synon., range); Greeley and Greene, 20th Rep. N. Y. Conserv. Dep. (1930), Suppl., 5, 1931: 82 (St. Lawrence watershed); Greeley and Bishop, 21st Rep. N. Y. Conserv. Dep. (1931), Suppl., 6, 1932: 78 (common Lake Ontario, St. Lawrence R., annu. mortal.); McKay, Copeia, 1934: 97 (first rec. for Lake Huron); Vladykov and McKenzie, Proc. N. S. Inst. Sci., *19* (1), 1935: 54, fig. 28 (Nova Scotia); Greeley, 24th Rep. N. Y. Conserv. Dep.

(1934), Suppl., 9, 1935: 89 (Mohawk-Hudson watershed, descr. of spawn.); Bigelow and Schroeder, Bull. U. S. Bur. Fish., *48* (20), 1936: 327 (adults off Barnegat, New Jersey); Greeley, 26th Rep. N. Y. Conserv. Dep. (1936), Suppl., 11, 1937: 90 (abund. Hudson R.; landlocked in reservoir and lake); Greeley, 26th Rep. N. Y. Conserv. Dep. (1937), Suppl., 12, 1938: 62 (Allegheny and Chemung watersheds); Greeley, 28th Rep. N. Y. Conserv. Dep. (1938), 13, 1939: 39 (in fresh water, Long Island, New York); Greeley, 28th Rep. N. Y. Conserv. Dep. (1938), Suppl., 15 (2), 1939: 82 (salt water, Long Island, New York); Greeley, 29th Rep. N. Y. Conserv. Dep. (1939), Suppl., 16, 1940: 68 (notes on alewife), 59–61 (abund. Lake Ontario; stunted growth in fresh water; annu. mortal., spawn.); Hubbs and Lagler, Bull. Cranbrook Inst. Sci., 18, 1941: 27 (range, Lakes Ontario, Erie, and Huron, where introd.); Anonymous, Fish. Resourc., U. S. Senate Doc., 51, 1945: iii, 66, fig. (migr. range, commerc. import., methods of capture, causes for decline, remedies, consid. with *P. aestivalis*); Bigelow and Schroeder, Fish. Bull. (74) U. S. Fish Wildl. Serv., *53*, 1953: 101 (descr., habits, Gulf of Maine).

Pomolobus pseudoharengus lacustris Jordan, Manual Vert. Anim. NE U. S., ed. 1, 1876: 265 (orig. descr.; type local. Cayuga Lake, New York; landlocked form subspecif. distinct from anadromous one).

Pomolobus mediocris Evermann and Hildebrand (not of Mitchill), Proc. biol. Soc. Wash., *23*, 1910: 158 (notes on young; found later to be *pseudoharengus*).

Pomolobus sp., Pearson, Invest. Rep. U. S. Bur. Fish., *1* (10), 1932: 18 (in trawl catch, off Virginia capes).

Doubtful References:

Clupea parvula Mitchill, Rep. in part on Fishes of New York, 1814: 21 (orig. descr.; type local. presumably New York; type lost); Mitchill, Trans. Lit. philos. Soc. N. Y., *1*, 1815: 452 (descr.).

Clupea virescens De Kay, New York Fauna, Pt. 4, Fishes, 1842: 252, pl. 13, fig. 37 (orig. descr.; type local. New York Bay; type lost).

Clupea pseudoharengus Lönnberg, Ofvers. Svensk. Vet. Akad. Forh., *51* (3), 1894: 114 (observed enter. St. Johns R., Florida in spring; probably *P. aestivalis*).

Pomolobus pseudoharengus Evermann and Kendall, Rep. U. S. Comm. Fish. (1899), 1900: 55 (St. Johns R., after Bean 1883 and Lönnberg 1894).

Genus *Brevoortia* Gill 1861

Menhaden

Brevoortia Gill, Proc. Acad. nat. Sci. Philad., 1861: 37; genotype by original designation, *Brevoortia menhaden* Gill equals *B. tyrannus* (Latrobe).

Characters. Body oblong, compressed. Bony scutes present, the median line of chest and abdomen with a sharp edge. Scales adherent, the exposed part much deeper than long, the margin serrate or pectinate in adults; a series of modified scales present next to median line on back in front of dorsal fin. Cheek deeper than long. Mouth large. Maxillary extending to or beyond middle of eye. Upper jaw with a distinct median notch. Lower jaw included in the upper one, not projecting, its upper margin (within mouth) nearly straight. Teeth wanting in adults. Lower limb of first Gill arch with an obtuse angle. Gill rakers long and numerous, increasing in number with age, those on upper limb of first arch extending downward and over those on upper part of lower limb. Dorsal with 17–22 rays, the last one not greatly produced; its origin about equidistant between rim of snout and base of caudal. Anal with 17–25 rays, the last one little enlarged. Pelvic small, with 7 rays. Vertebrae about 42–50. Intestine very long. Peritoneum black.

Remarks. The species of this genus generally are recognizable by the strongly serrate or pectinate adherent scales, the exposed part of which is much deeper than long; the modified series of scales next to the median line of the back in front of the dorsal fin; the very long gill rakers on the upper limb, which project downward over the equally long rakers of the lower limb; the very deep cheek; and the rather small pelvic, composed of only seven rays.

The young, about 60 mm TL and less, of North American representatives at least, have minute teeth on the margin of the maxillary, but these disappear with age. The gill rakers on the upper limb do not yet extend downward over those on the lower limb, as in larger fish; the number, as already indicated, increases greatly with age. Furthermore, until the fish reach about 100–125 mm TL, the two series of scales, one on each side of the median line of the back in front of the dorsal fin, do not become fully differentiated or modified. Though the exposed margin of the scales on young may be somewhat uneven, the scales are not definitely serrate; the serrae become somewhat developed when the fish attain a length of about 100 mm and continue development until they are comparatively large, but these serrations are not developed uniformly on all parts of the fish. For some species the length and shape of these serrations or pectinations are diagnostic characters, but fish of nearly equal size must be compared and scales from the same part of the body must be used.

The species of Menhaden included in this work fall into two closely related pairs: *tyrannus* from the Atlantic and *patronus* from the Gulf; *smithi* from the Atlantic and *gunteri* from the Gulf—and one odd species, *brevicaudata*, from Noank, Connecticut, related to *tyrannus*. Such a close relationship between species exists in other groups as well.[36]

In each pair of fishes named, the range probably was once continuous but became discontinuous when the last passageway for marine fishes across the Florida peninsula was closed. At least these fishes do not now occur on the coasts of southern Florida, indicating that suitable conditions do not exist there. Therefore, the separation between Atlantic and Gulf representatives is complete. Under this separation, and apparently under the influence of differences in environment, these fishes have become sufficiently differentiated to constitute distinct species.

Range. The Atlantic and Gulf coasts of the United States northward to Nova Scotia; southern Brazil to Argentina; and western Africa.

Measurements and Counts for Brevoortia. For measurements and counts not discussed below, see p. 258.

HEAD DEPTH: for this genus, measured from the slight crossgroove at occiput to the keel of the first ventral scute. Although this is not an exact vertical, it does provide definite and uniform points for measuring.

SCALES: the number in a lateral series represents the number of oblique series (running upward and slightly backward) across the middle of the side; these should

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[36] Among the shad, *Alosa sapidissima* of the Atlantic and *A. alabamae* of the Gulf; also the hickory shad, *Pomolobus mediocris*, of the Atlantic and the skipjack herring, *P. chrysochloris*, of the Gulf and Mississippi Valley. In the family Sciaenidae, the weakfish, *Cynoscion regalis*, of the Atlantic and the sand seatrout, *C. arenarius*, of the Gulf (Ginsburg, *41*: 83); and another pair occurs in the genus *Menticirrhus* (Ginsburg, unpublished).

be counted uniformly, since they tend to become reduced in size on the back and larger on the lower part of the side. The comparisons and figures given on these pages are based on scales from the middle of the side below the anterior dorsal rays.

CAUDAL FIN: lower lobe measured from middle of caudal base.

PECTORAL FIN: axillary appendage measured from base of upper pectoral ray.

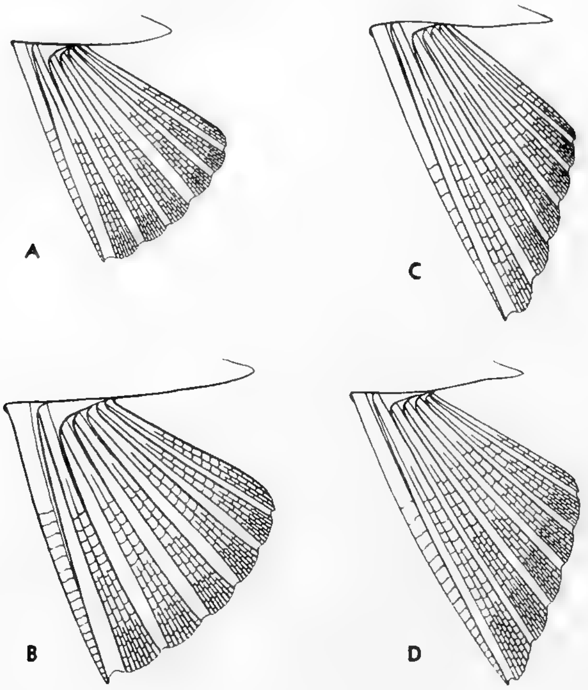

FIGURE 84. *Brevoortia* pelvic fins: A, *patronus*, 215 mm TL, off Galveston, Texas, USNM 129810, see Fig. 91; B, *tyrannus*, 320 mm TL, Chesapeake Bay, USNM 129809, see Fig. 86; C, *gunteri*, 270 mm TL, Rockport, Texas, USNM 129798, see Fig. 93; D, *smithi*, 295 mm TL, USNM 118723, see Fig. 92; all equally enlarged. Drawn by Ann S. Green.

Species. Five species fall within the scope of this work (see Key to Species), and two others, *aurea* and *pectinata*, occur in southern Brazil, Uruguay, and Argentina. Still another one, sometimes identified with *tyrannus*, has been reported for western Africa. I have seen no specimens of the latter and cannot add any information as regards its relationship to American forms. In general, the scales of South American representatives are scarcely reduced in size on the back and on the base of caudal, whereas in North American species they are greatly reduced there.

Key to Species of the Western Atlantic

1 a. Scales fairly regularly placed, 35–36 oblique series crossing middle of side; greatest depth of body 30–40 % of SL.

2 a. Scales on back and at base of caudal much smaller than those along middle

of side; pelvic fin with a definitely convex margin, the innermost ray more than 67% of the length of the outermost one, the fin not pointed when folded (Fig. 84 A, B); upper part of opercle with prominent radiating striae; shoulder spot followed by a variable number of smaller dark spots in adults.

3a. Ventral outline of body only moderately convex anteriorly, usually only about half of greatest depth below a straight line extending through lower margin of eye to middle of base of caudal; sheath of scales at base of dorsal fin composed for the most part of a single row of scales covering only the basal third of the longest rays when standing erect; pectoral fin falling far short of base of pelvic fin, 3–7 vertical series of scales between its tip and base of pelvic, the fin with 16–18 (rarely 15) rays.

4a. Maxillary reaching well beyond vertical from posterior margin of pupil, 13–16% of SL; mandible 16–19% of SL; pectoral fin failing to reach base of pelvic fin by less than diameter of eye, 3 or 4 vertical rows of scales between tip of pectoral and base of pelvic, its length 17–21% of SL; caudal fin with lower lobe about as long as head, 25–35.5% of SL. *tyrannus* (Latrobe) 1802, p. 346.

4b. Maxillary reaching only to a vertical from posterior margin of pupil, 12–13% of SL; mandible 15.5–16.5% of SL; pectoral fin failing to reach base of pelvic fin by a distance exceeding diameter of eye, 5–7 vertical series of scales between its tip and base of pelvic, its length 15.5–16% of SL; caudal fin with lower lobe shorter than head, 22.5–25% of SL. *brevicaudata* Goode 1879, p. 363.

3b. Ventral outline of body strongly convex anteriorly, much more than half of greatest depth below a straight line extending through lower margin of eye to middle of base of caudal; sheath of scales at base of dorsal fin composed for the most part of two rows of scales covering basal two-thirds of shortest rays when standing erect; pectoral fin often reaching nearly to base of pelvic fin, seldom more than 1 or 2 vertical series of scales between its tip and base of pelvic, the fin with 14–17 (usually 15 or 16) rays. *patronus* Goode 1879, p. 365.

2b. Scales on back and at base of caudal not much smaller than those along middle of side; pelvic fin with a nearly straight oblique margin, the innermost ray not more than 67% of the length of the outermost one, the fin pointed when folded (Fig. 84 C, D); upper part of opercle with feeble radiating striae, if any; shoulder spot not followed by smaller dark spots.

5a. Scales in only 35–46 oblique series crossing middle of side; five longitudinal rows on side of caudal peduncle; pectoral fin sometimes reaching base of pelvic fin, occasionally falling short of this point by diameter of pupil, its length 17.5–21% of SL, 0–3 vertical series of scales between its tip and base of pelvic. *pectinata* Jenyns 1842.

Rio Grande of Brazil to Bahia
Blanca, Argentina.

5b. Scales in 48–56 oblique series crossing middle of side: seven longitudinal rows on side of caudal peduncle; pectoral fin failing to reach base of pelvic fin by a space varying from half to a full diameter of eye, its length 16.7–18 % of SL, 3–6 vertical series of scales between its tip and base of pelvic. *aurea* Agassiz 1829.
Bahia (Baía), Brazil, probably to the Rio de la Plata.

1b. Scales small, irregularly placed, about 60–75 oblique series crossing middle of side (difficult to count); greatest depth of body 36–45.5 % of SL.

6a. Length of head 29–31.5 % of SL; maxillary reaching from below middle of eye to vertical from posterior margin of pupil, 2.0–2.4 in head; pectoral fin generally failing to reach base of pelvic fin by somewhat more than half of diameter of eye, 5–8 vertical series of scales between its tip and base of pelvic, its length 18.5–21 % of SL; total number of ventral scutes 30–32 (usually 30); vertebrae 45–47. *smithi* Hildebrand 1941, p. 372.

6b. Length of head 31–35.5 % (usually 32–34 %) of SL; maxillary reaching to, or a little beyond, vertical from posterior margin of pupil, 1.8–2.2 in head; pectoral fin generally failing to reach base of pelvic fin by less than diameter of pupil, 2–4 vertical series of scales between its tip and base of pelvic, its length 19–23.5 % (usually 20–22 %) of SL; total number of ventral scutes 27–30 (usually 28 or 29); vertebrae 42–44.
gunteri Hildebrand 1948, p. 376.

Brevoortia tyrannus (Latrobe) 1802

Atlantic Menhaden, Menhaden, Mossbunker, Bunker, Fatback, Shad, Pogy, Bugfish

Figures 84–89

Study Material. At least 150 specimens, sometimes many more, 70–430 mm TL, 55–355 mm SL, collected at many localities from Massachusetts Bay to Fernandina, Florida. Some of the data used were accumulated by me over a period of 33 years; in addition, unpublished data from Dr. A. Bascom Hardcastle and some gathered by the late William W. Welsh; also juveniles from Woods Hole, Massachusetts; Chesapeake Bay; and Beaufort, North Carolina.

Distinctive Characters. The close relationship of *Brevoortia tyrannus* to *B. patronus* of the Gulf of Mexico is shown in the account of the latter (p. 370). From *B. smithi*, which occupies the same range as the Atlantic Menhaden from North Carolina southward, *tyrannus* differs prominently in having larger scales with notably longer pectinations; these species also differ in several other respects as shown in the account of *B. smithi* (p. 374).

Description. Proportional dimensions in per cent of standard length, and counts, based on at least 150 study specimens, 55–355 mm SL.

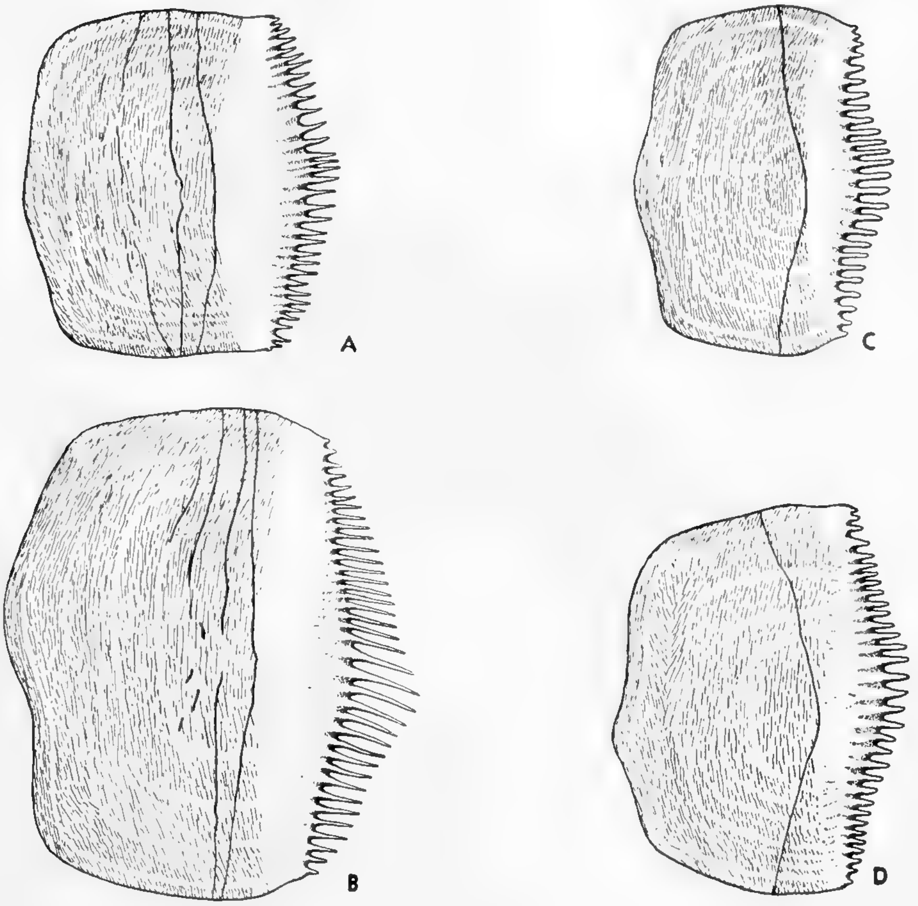

FIGURE 85. *Brevoortia* scales from middle of side below anterior dorsal rays. A, *patronus*, 215 mm TL, see Fig. 91; B, *tyrannus*, 320 mm TL, see Fig. 86; C, *gunteri*, 270 mm TL, see Fig. 93; D, *smithi*, 295 mm TL, see Fig. 92; all equally enlarged.

Body: depth 30–40, usually 32–37.
Caudal peduncle: depth 8.5–11.
Head: length 29–36, most frequently 31–34.
Snout: length 5.5–9.0, usually 6.0–8.0.
Eye: diameter *ca.* 5.0–8.0.
Interorbital: width 6.2–8.2.
Maxillary: length 13–16.
Mandible: length 16–19.
Anal fin: length of base 14–19, usually 15–18.
Pelvic fin: length 8.0–10.
Pectoral fin: length 17–21; usually 18–20.
Scales: oblique series along middle of side, 41–55, most frequently 45–52.
Modified scales: in a series in front of dorsal 31–43, most frequently 33–39.
Ventral scutes: 30–35, usually 32 or 33.
Fin rays: dorsal 18–22, usually 19–21; anal 18–24, usually 20–23; pectoral 16–18, rarely 15.
Vertebrae: 47–49, very rarely 45, 46, or 50 (194 specimens).

Body elongate, compressed, its greatest thickness varying greatly, from nearly half of depth in large fat fish in spawning condition to only about a third of depth in lean half-grown examples; greatest depth generally at, or slightly in advance of, vertical from tip of pectoral, 2.5–3.3 in SL in specimens 100 mm and upward; ventral outline moderately convex anteriorly, usually only half of greatest depth below a straight line through lower margin of eye to middle of base of caudal. Caudal peduncle rather slender, 2.9–4.0, usually 3.2–3.8, in head, and 3.2–4.1, but usually 3.5–4.0, in greatest depth of body.

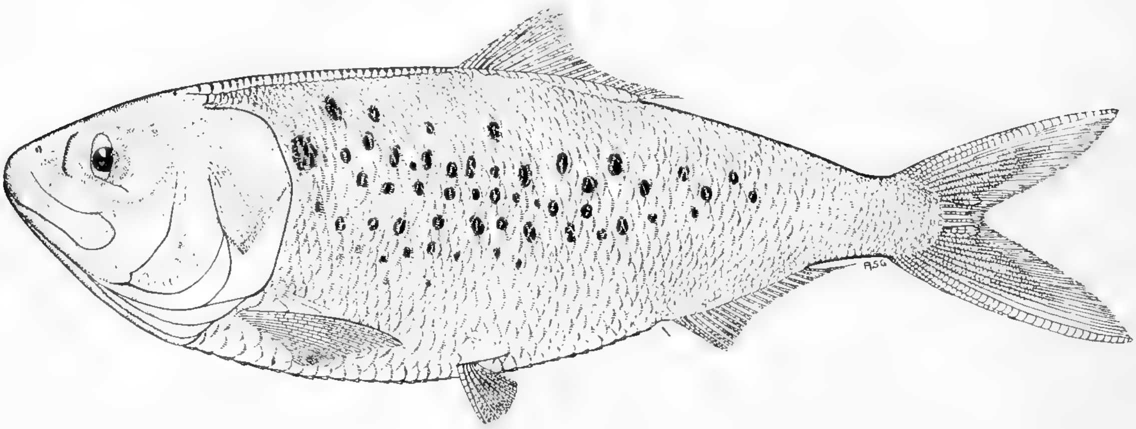

Figure 86. *Brevoortia tyrannus*, 320 mm TL, 247 mm SL, Chesapeake Bay, USNM 129809. Drawn by Ann S. Green.

Scales adherent, the exposed part notably deeper than long, the scale itself somewhat deeper than long (Fig. 85 b); margin irregular in young about 60 mm long; short blunt serrae on margin in examples of about 100 mm, the serrae increasing in length with age, becoming slender hair-like appendages, often extending nearly across the exposed portion of the next scale in large specimens; scales greatly reduced in size on upper part of side, on back, and at base of caudal; in rather regular series on lower half or so of side; most frequently 3 or 4 vertical rows of scales exposed between tip of pectoral and base of pelvic. A row of large modified scales on each side of median line of back in front of dorsal fin, these scales not fully modified in specimens under about 125 mm TL, rather variable in number, most frequently 34–38 in each series. Ventral scutes rather strong, 17–22, usually 18–21, in front of pelvic fins; 10–15, usually 12–14, behind these fins.

Head 2.8–3.5, usually 2.9–3.2, in SL, its depth 3.1–4.0, usually 3.3–3.8. Snout only moderately blunt, with a prominent median notch in adults, the length 3.9–5.5, usually 4.0–4.7, in head. Eye difficult to measure accurately in adults because of much adipose tissue, about 4.4–6.2. Interorbital 4.2–5.3, usually 4.4–5.0. Cheek deeper than long except in young. Maxillary rounded, generally scarcely reaching below posterior rim of eye, the length 1.9–2.7, usually 2.1–2.5, in head. Mandible included in upper jaw, its upper margin (within mouth) nearly straight, its length to joint 1.7–2.0 in head. Upper section of OPERCLE with prominent radiating ridges. GILL RAKERS very numerous; those on upper limb extending down and over those on lower limb, the longest about as long as snout in adults; increasing in number with age and growth, the greatest increase occurring before a 100-mm length is attained: about 60 on lower limb in 60-mm specimens, about 100 in 100-mm fish, about 140 in 200–250-mm examples, and 150–160 in large adults 330–360 mm long. TEETH absent except for minute ones on margin of maxillary in young about 60 mm and less.

DORSAL fin moderately elevated anteriorly, its margin definitely concave, its longest rays as long as snout and fully half of eye, the last ray somewhat longer than the preceding ones; origin of fin generally slightly nearer to base of caudal than to margin of snout; a low sheath on base of fin, composed for the most part of a single series of scales not extending above the basal third of shortest rays when standing erect. CAUDAL rather deeply forked, the middle rays about as long as eye; the lobes rather short, the lower one the longer, about as long as head, 2.8–4.0, usually 3.0–3.8, in SL. ANAL low, little elevated anteriorly, the margin nearly straight; its origin under or somewhat behind vertical from tip of last dorsal ray, its base 5.2–7.0, usually 5.5–6.6, in SL; a very narrow sheath of scales at base. PELVIC fin small, with a very gently convex margin, the outermost ray only a little longer than the innermost (Fig. 84 B), the fin inserted slightly behind vertical from origin of dorsal, the length 3.1–3.8 in head. PECTORAL fin slightly falcate, its length 5.0–5.9 in SL in adults, 1.6–1.9 in head, the longest ray about four times the length of the shortest one, the fin generally failing to reach base of pelvic in adults by a distance somewhat greater than diameter of pupil. AXILLARY APPENDAGE of pectoral variable in length, about 75 % of the length of fin in large examples, only about half of length of fin in examples about 100 mm long, and little developed in young of 50 mm.

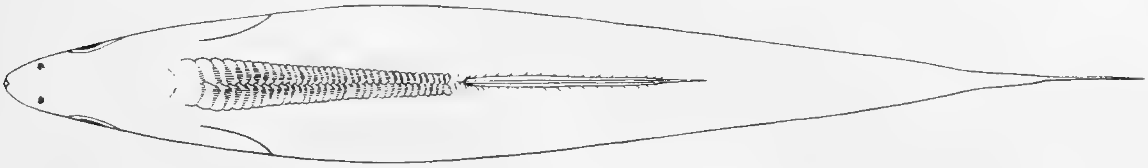

FIGURE 87. *Brevoortia tyrannus,* modified scales in front of dorsal fin, from same specimen shown in Fig. 86. Drawn by Ann S. Green.

Color. In fresh specimens, back dark green to bluish. Sides generally brassy and sides of head bright silvery to slightly brassy. A large black spot at shoulder a very short distance behind margin of opercle and well above middle of side, variable in size and shape among specimens, generally roundish but sometimes vertically elongate, and about as large as pupil. This spot develops first and is generally evident when the fish reach a length of about 75 mm (3 in.). The shoulder spot usually followed among half-grown and large examples, from about 150 mm (6 in.) upward, by a variable

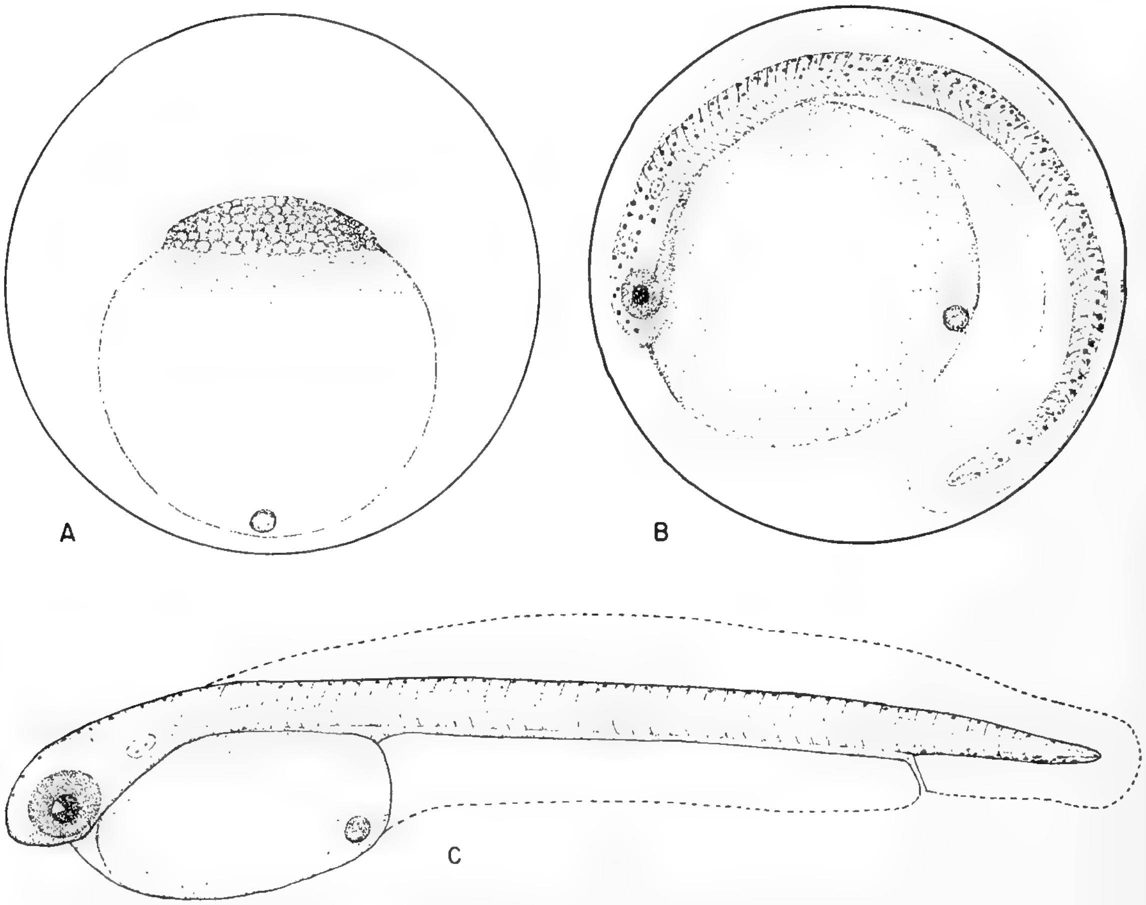

FIGURE 88. *Brevoortia tyrannus*. A, newly laid egg in advanced stage of cleavage; B, egg with advanced stage of embryo; C, newly hatched larva, 4.5 mm long. After Kuntz and Radcliffe.

number of smaller dark spots, sometimes only a few small ones and sometimes many, differing greatly in number, size, and intensity of darkness, these spots sometimes arranged in two, three, or more indefinite horizontal series on anterior part of side, seldom extending far beyond vertical from origin of anal; a profusely spotted example illustrated in Fig. 86. Fins pale yellow to brassy, sometimes with dusky punctulations; caudal generally dusky at base and often with a dusky margin. Peritoneum black.

Variation in color, especially in the dark spots on the side, is very great.

Size. The usual size of adult fish at Beaufort, North Carolina, is about 300–350 mm (12–14 in.) TL. It is generally accepted that the fish grow rather larger in the northern part of the range than in the southern part. The largest specimen in the U. S. National Museum, from Long Branch, New Jersey, is 430 mm (17 in.) long, but a larger one, 480 mm (18 in.), has been reported as taken at Woods Hole, Massachusetts (*120*: 91), and one of 500 mm (20 in.) was reported to the writer by Dr. H. F. Prytherch verbally. The last mentioned specimen was taken at Beaufort, North Carolina, and weighed 3.5 pounds.

Development and Growth. The eggs and larvae have been described by Kuntz and Radcliffe from material collected at Woods Hole, Massachusetts (*76*: 119). The eggs are buoyant and spherical, have a diameter of 1.4–1.6 mm, and are highly transparent; they contain a small oil globule, and are covered with a thin horny membrane; the perivitelline space is broad. Incubation occupied "not more than 48 hours."

The newly hatched fish are "relatively slender" and about 4.5 mm long. The vent, as usual in clupeoid fishes, is "less than one-fifth the length of the body from the posterior end." At four days of age the larvae were 5.7 mm long, and black chromatophores were present in a series along the entire digestive tract. At 9.0 mm the dorsal and caudal fins were at least partly developed, and posteriorly the intestine was convoluted. At 23 mm all the fins had become well differentiated, and the body remained "relatively slender"; black chromatophores were present on the nape, along the margin of the opercle, near the base of the dorsal, anal, and caudal fins, and in groups posterior to the dorsal fin and ventral to the pectoral fin; internal black areas could be seen along the dorsal wall of the abdominal cavity, and a series of dark spots was present above the notochord.

Compared to the Woods Hole larvae, specimens from Beaufort, North Carolina, of comparable size agree with them fairly well in development, but in each phase they are notably more slender. Beaufort examples 9.0 mm long are little compressed and scarcely thicker than a number-60 sewing thread; the depth is contained about 30 times in TL. Specimens 18 mm long are fully as well developed as those of 23 mm described and illustrated by Kuntz and Radcliffe, and the 23-mm examples are rather more advanced than the northern ones of equal length; the body continues to be more slender; the depth is contained about 21 times in TL. In 25-mm preserved examples from Beaufort, the convoluted intestine noted in younger fish is scarcely discernible, and the vent is now situated slightly behind a vertical from the base of the last dorsal ray, about as in the adult. Some examples, at a length of 30 mm, or even up to 35 mm, remain very slender, their depth being contained about 13 times in TL; and in these slender examples the ventral surface of the chest and abdomen remains round to slightly flat, with indications of a row of bony points along each lateral edge. Juvenile pigment spots remain about as described for examples of 23 mm or so, but other specimens of the same length are much more compressed and notably deeper; their greatest depth is contained only about 7.7 times in TL, or only about 6.7 in SL. In these deeper and older fish, the two series of lateral bony points noted in the slender fish have become coalesced to form definite ventral scutes on the median line of the chest and abdomen; also, the fish are rather fully pigmented, the sides of the head are bright silvery, a silvery lateral band is evident, and a sheen of the same color is present on the sides of the abdomen. It seems, then, that when the fish reach a length of about 30 mm the increase in length is retarded during metamorphosis from the somewhat roundish slender larvae to the deeper and more compressed young adults.

Schools of young Atlantic Menhaden were observed repeatedly at Beaufort in winter and spring, and specimens 24–35 mm, caught from a school on April 23,

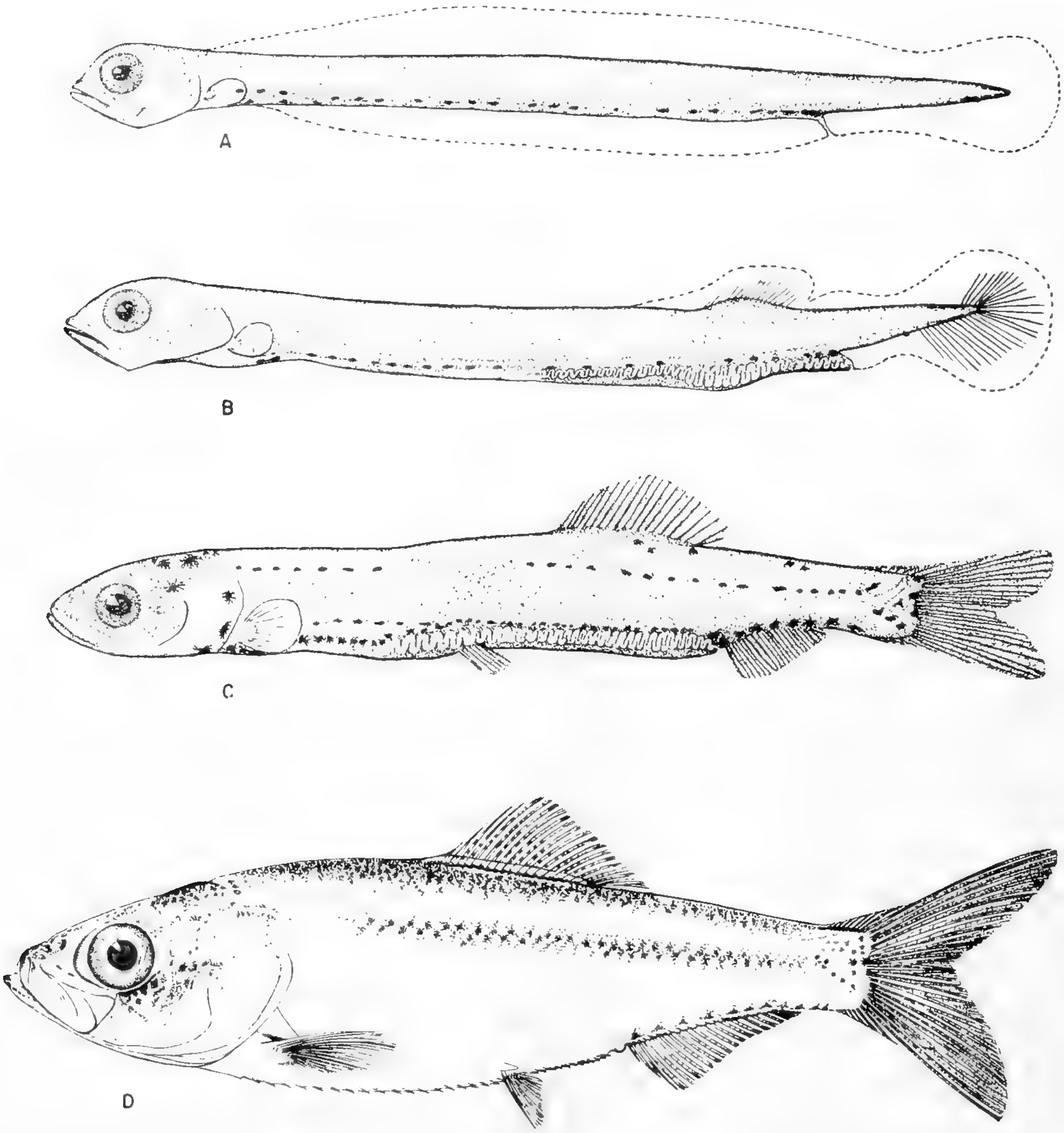

Figure 89. *Brevoortia tyrannus.* A, larva four days after hatching, 5.7 mm; B, young, 9 mm; C, 23 mm; D, 33 mm. A, B, C drawn by Albert Kuntz, D by E. B. Decker.

1926, differed little in development; all had remained slender and were more or less in the larval stage. As seen in the water they were almost transparent, but when removed from the water, dark pigment spots were evident along the middle of the side in a more or less definite lateral band.

Specimens 40–45 mm long are shaped very much like large fish, although they remain rather more slender; their greatest depth of body is contained about 3.6–4.0 in

SL. The obtuse angle in the lower limb of the first gill arch is evident, and the gill rakers on the upper limb of this arch now definitely extend down and over the upper ones on the lower limb. Striations on the upper plate of the gill covers are evident, but the cheek remains about as long as deep. Scalation is about complete. The silvery lateral band of smaller specimens has blended with the silvery abdomen; the dark shoulder spot, always present in adults, is evident though small; and in some specimens suggestions of supplementary spots are already present.

The gill rakers increase in number and in proportionate length with age (see *Description*). Therefore, if their number is to be usable at all for differentiating species, specimens of equal size must be compared.

In the Gulf of Maine, the fish hatched during the summer reach a length of 60–80 mm during their first winter and average slightly more than 160 mm the second winter, and those hatched in the fall are 30 mm long the first winter and 130 mm the second winter, with every gradation in size between the two (*16*: 122).

In Chesapeake Bay, where the fish apparently spawn only during the autumn, the young are only about 27 mm long the following January and 46 mm the following April (*59*: 103). These data, though not complete, are in general agreement with more extensive data collected by me at Beaufort, where spawning quite certainly occurs only during late fall and early winter. Seventy-nine larvae, collected there from the last half of November to and including the first half of March, were between 4.0–20 mm, and the average increase in length in each month was about 12 mm, excluding December, when only three larvae were taken (5.0, 5.0, and 7.0 mm). Thereafter, more rapid growth was indicated: seven specimens taken the last half of March were between 22–31 mm and averaged 27 mm; 110 collected in April were 30–40 mm and averaged about 35 mm; 50 collected during May were 30–41 mm and averaged about 35 mm; and 48 examples taken in June ranged between 38–56 mm and had an average length of 45 mm. Lengths of 85–150 mm (3.4–6.0 in.) were attained during their second winter; the average was about 110 mm (4.4 in.); measurements were based on 167 fresh examples.

"Sexual maturity is apparently attained in the season following the third winter, and a few of the older fish Welsh examined showed as many as 9–10 winter rings on their scales" (Bigelow and Schroeder, *15*: 116).

Spawning. The Atlantic Menhaden spawn at sea in saline waters. Many large fat fish with well-developed roe were observed by me off Beaufort, North Carolina, during autumn only. Such fish were seen also in the fall in the Chesapeake Bay area (*59*: 103) and in December off Fernandina, Florida (from unpublished notes by William W. Welsh). However, off New England, spawning takes place in late spring and throughout the summer, the height of the spawning season occurring in June; and in 1915 off Woods Hole, Massachusetts, eggs were taken as late as the last week of October (*76*: 119).

At Beaufort, spawning apparently takes place only off Beaufort Inlet, for all of the small ones, 16 mm and less, were taken at sea. This would be expected, for the large mature fish in that vicinity seldom enter the harbor or other inshore waters. Northward, however, as at Woods Hole, Massachusetts, the eggs and larvae were collected in the harbor (*76*: 119). The place and season of spawning, then, seem to vary according to locality.

Habits. Both young and adults, acccording to Bigelow and Schroeder, feed and travel in compact schools at the surface, swimming close together side by side and tier above tier (*15*: 114):

> In calm weather they often come to the surface when their identity can be recognized by the ripple they make, for pogies, like herring, make a much more compact disturbance than mackerel do... Also, pogies as they feed frequently lift their snouts out of water, which we have never seen herring do, while they break the water with their dorsal fins, also with their tails. And the brassy hue of their sides catches the eye.

The larvae appear to be more or less solitary, for only one specimen or at most a few were generally taken in a haul, off Beaufort. They do not stay at or near the surface as strictly as older ones do, for most of the larvae at hand were taken in nets towed along the bottom. However, schooling and surface swimming begin early in life, for many schools of young 25–35 mm long (some just reaching the adult stage) were observed many times on windy days near shore on the leeward side of Pivers Island at Beaufort.

Migrations. These fish are present principally in the Gulf of Maine from July to September, off Woods Hole, Massachusetts, from June to September, and off the coasts of New York, New Jersey, and Delaware from May to September, being most numerous during midsummer; in Chesapeake Bay small to medium-sized fish are numerous throughout the summer, and large ones are taken off the mouth of the Bay (or off the Capes) during October and November; in North Carolina, small and medium-sized fish are present all summer, the large ones from October to December; and on the east coast of Florida the fish are numerous from early spring to late fall.

Small to medium-sized specimens are present in Chesapeake Bay throughout the year but in greatly reduced numbers during the winter. Adults off Beaufort, though most numerous during late fall, sometimes remain in the nearby offshore waters until January if the winter is mild. Schools composed of fish that are generally 150 mm (6 in.) and less are present in Beaufort Harbor and connecting estuaries all winter, and schools of young, generally under 50 mm in length, ascend freshwater creeks or enter small drainage ditches in the spring. Unlike adults in northern waters that come close inshore, into the bays and harbors (*16*: 122), large fish in North Carolina very rarely cross Beaufort Inlet to enter the Harbor and adjacent waters.

It is still much of a mystery where the schools of adults go after the fish leave the waters within 10–15 miles of shore, the usual operating range of the fishing schooners. Sufficient taxonomic work has been done, however, to indicate that each section of the coast, that is the New England, Middle Atlantic, and South Atlantic states, has a more or less distinct population. Therefore, if a north-south migration does take place, then the fish from each section return to the general vicinity from which they migrated originally. It seems more probable now that the principal migration is offshore and inshore.[37] No doubt temperature is an important factor in the movements of the fish; it certainly affects the supply of plankton upon which they feed. In years when inshore runs fail, it is even probable that the fish remain so far offshore that they are beyond the usual range of the fishing vessels. In slight confirmation of this theory, I recall that one autumn, when the usual inshore runs failed at Beaufort, a progressive operator, upon my suggestion, induced one of his boat captains to go farther offshore than usual in search of a catch. Fish, indeed, were found, at a considerable distance offshore, apparently too far off for practical fishing with the crews and schooners available.

Food. Menhaden feed on small organisms strained from the water by their numerous long, slender, close-set gill rakers, which form an effective strainer. While feeding, the fish generally swim near the surface and often "break water"; they whirl around, sound a short distance, come out of the whirl, and swim up and straight ahead at a considerable speed for a rather short distance. During this time the mouth is wide open and the gill covers are lifted, thus making it possible for a fish to filter a great amount of water with minimum effort. The food that is ingested depends in large measure upon the organisms that are present where the fish are feeding. Even a considerable amount of mud and general debris is often swallowed. Included in the stomach contents examined by various investigators were: numerous small crustaceans, especially copepods; small annelid worms; rotifers; and unicellular plants, particularly diatoms and peridinians. The plant organisms, as a rule, constitute the chief food.

This species has a very thick-walled stomach, and a long intestine, as is usual among fish that feed on vegetable matter. Among 64 fish taken at Beaufort, ranging between 65–214 mm, the intestinal tract increased more or less proportionately with the length of the fish; generally it remained between 400 and 450 % of the standard length, according to A. Bascom Hardcastle (unpublished data).

Enemies. Most predatory animals associated with the sea feed on Atlantic Menhaden—an easy prey because of their habit of schooling. Their fiercest enemy probably is the bluefish (*Pomatomus*), which, it is said, kills many more than it eats. Among the other fish that feed on them extensively are the cod, pollock, hakes, weakfish, swordfish, tuna, dolphin, amberjacks, and sharks. Whales and porpoises, as well as birds, also devour many of them.

Parasites. Atlantic Menhaden so often have a large crustacean parasite in the mouth that they are sometimes referred to as "bugfish." It is said that in some schools nearly every fish has a parasite in its mouth. This "bug," an isopod listed as *Olencira praegustator* (Latrobe) (*107*: 231), has a robust body, generally fully half an inch long and occasionally approaching an inch in length. Sometimes the mouth of the fish is deformed because of its presence; thus the amount of water screened for food must be considerably reduced in fish so infected.

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[37] According to Rose (*110*: 104, 105), the recent investigations by the U. S. Fish and Wildlife Service make it likely that the north-south migrations of the Menhaden are more regular and extensive than Dr. Hildebrand supposed. —H. B. B.

Another large parasite, the copepod *Lernaeenicus radiatus* (LeSueur), buries its horns in the flesh on various parts of the fish's body, most commonly along the back (*137*: 480). This parasite sometimes approaches a length of two inches and has a predominant reddish color, which makes it very conspicuous. Other copepods listed by Wilson as parasitic on *B. tyrannus* are: *Bomolochus teres* Wilson, *Caligus schistonyx* Wilson, *Caligus chelifer* Wilson, *Pandarus sinuatus* Say, *Lernanthropus brevoortiae* Rathbun, and *Clavellisa spinosa* Wilson.

The following have been listed by Linton (*85*: 440): *Scolex polymorphus* Dujardin, a cestode, small and free in the intestine; cysts and blastocysts of *Synbothrium* on the viscera; and the trematodes *Distomum appendiculatum* Rudolphi and *D. vitellosum* Linton; later he added *Dactylocotyle* sp., and *Distomum pyriforme* Linton (*86*: 352).

Hardcastle has reported a sporozoan parasite of the genus *Eimeria* for the testes of specimens taken at Beaufort; he stated that a "study of over a hundred individuals [Menhaden] showed an infection of nearly 50 per cent" (*54*: 214).

Diseases. No report of a specific disease has been found in the literature, but there are records of many fish having become stranded along the shore. It has been suggested that their enemies at times drive them ashore, but my observation is that the fish make no special effort to flee from enemies. In fact, when caught in a net they make little effort to escape. It seems more probable, therefore, that the stranded fish died of a disease. An epidemic has indeed been reported (*123*: 742).

Variations. Large fish generally are proportionately deeper than small ones, and those from the southern part of the range are proportionately deeper than northern ones. However, the variation in depth among fish from any one general region is great enough to obscure any definite distinctions. Southern fish have a somewhat larger head and longer fins (especially the pectoral) than those from the northern part of the range, but the gap is fully bridged by examples from intermediate areas. Contrary to expectation, data at hand show that the vertebrae do not average fewer in southern specimens. But further detailed studies are needed to determine the exact characteristics of populations inhabiting the different general sections of the coast; even now specimens from the Gulf of Maine are too few in the collections at hand to determine their finer characteristics.

As shown in the *Description*, the number of gill rakers increases greatly with age, with the principal increase occurring before the fish reach a length of about 100 mm (4 in.). Also, the scales in small specimens have only irregular margins while those in larger fish are pectinate. In using scales to differentiate species (their development in all species being similar), it is necessary to compare scales from examples of about equal size; and it is preferable to use large specimens, for in them the differences are most pronounced.

See *Color* for variations in color.

Commercial Importance. These fish, though exceedingly valuable, are not used very extensively as food by man, mainly because of their bony nature and oiliness. However, some find the flesh delicious, and those living along the coast, especially the fishermen, eat them in season as a common article of diet. Considerable quantities are often "corned" (salted) for home use during winter, and the writer knows from first-hand experience that these fish are delicious when smoked. They were canned to a limited extent for export during the last war, and a small quantity is still canned for home consumption.

Because of their abundance, large numbers are available for reduction to oil, fish meal, and fish scrap; the Atlantic Menhaden fishery is one of the most valuable of our fish industries. The catch for 1945 amounted to 759,073,820 pounds, valued at $ 11,202,127 (Canned Fish and Byproducts, U. S. Fish Wildl. Serv., 1945: 15); of this amount, 120,493,920 pounds were credited to Florida, 142,209,510 to North Carolina, 77,232,910 to Virginia, 280,463,340 to Delaware, and 138,584,140 to New Jersey. For 1950 through 1953, the approximate catches have been as follows: between 9,304,000 and 39,900,000 pounds for New England, mostly taken south and west of Cape Cod; between 372,950,000 and 857,584,000 pounds for the Middle Atlantic states; 92,374,000 for Chesapeake Bay; and between 147,125,000 and 314,841,000 pounds for the South Atlantic states. In 1953 the total catch was 1,259,031,000 pounds.

Because of the great fluctuations in catch from year to year, the catch for a single year, or even for many successive years, may not indicate their actual abundance. Furthermore, since the fish are not equally fat every year, or at all times when available, equal quantities of fish (pounds) do not always yield equal quantities of oil (gallons), the most valuable product obtained from these fish. Thus the value of a given catch depends to a large extent upon the amount of oil it yields. In general, large fish yield more oil than small ones. For example, at Beaufort, North Carolina, the summer "runs," consisting of small to medium-sized fish, yield so little oil that they are considered scarcely worth handling, but the fall runs, consisting of large and fat gravid fish, make the industry profitable.

In discussing this subject, Greer (*48*: 24)[38] wrote as follows in 1915:

> The yield of oil varies greatly on different parts of the coast, and also from year to year and at different seasons. The fish are always larger and fatter during the fall than at any other season, consequently there is a greater yield of oil during that period. The fish taken from northern waters produce more than those taken from southern waters; the writer visited one of the northern factories during August 1913, and was told that a short time previous to his visit they had made 20 gallons, and that the average yield for July had been 16.5 gallons per 1,000 fish.[39] The maximum for the Middle Atlantic States is about 15 gallons, though it usually is less; in the early part of the season it is very much less than that amount. The South Atlantic fish rarely produce more than 8 gallons per 1,000 fish, and frequently it is less than 1 gallon during the early spring fishing. The average number of gallons of oil made from 1,000 fish during the season of 1912 was as follows: Connecticut 11.73; New York 11.36; New Jersey 5.08; Delaware 7.72; Virginia 3.72; and North Carolina 1.98.

[38] This paper, entitled "The Menhaden Industry on the Atlantic Coast," although written before the manufacture of fish meal for stock and poultry feed, contains much valuable information concerning the history of the industry, the construction of factories, the machinery used in these reduction plants, the vessels employed, the methods of fishing, their reduction, men employed, etc.

[39] The fish generally are measured, and the measure used is said to contain 1,000 fish, no account being taken of the size of fish. Thus, the measure arbitrarily contains 1,000 fish regardless of whether they are 6 or 12 inches long. In converting the number of fish to pounds, the factor 0.67 is used in the statistical division of the U. S. Fish and Wildlife Service. That is, the number of fish is multiplied by 0.67.

As further evidence of the great value of this extensive fishery, additional data from Greer show that the total catch for 1912, a near banner year, was 1,061,483,750 fish (711,435,312 pounds); this catch yielded 6,651,203 gallons of oil valued at $ 1,551,990 and 88,520 tons of scrap worth $ 2,138,165; 48 factories, valued at $ 3,625,983, were in operation; the vessels engaged in the fishery numbered 147, valued at $ 3,456,792; and there were 2,159 employees in the factories and 3,735 fishermen, drawing a combined wage of $ 1,579,984.

The value of the fish scrap, now that most of it is used as fish meal for poultry and livestock feed instead of as fertilizer, is considerably greater than it was; this change in turn produced other changes, for this processing requires quicker and more sanitary handling of the fish, including cooking before decomposition sets in; some changes at the factories were also required, for apparatus had to be installed for drying the residue quickly after the oil had been extracted.

Fluctuations in Abundance. No species has been more erratic in its appearances along the coast than *B. tyrannus.* For example, in 1911 and in 1912 large catches were made at Beaufort, the center of this fluctuating industry in North Carolina, but then these near banner years were followed by several exceptionally lean years, which forced some of the local operators into bankruptcy. However, in 1918 the fish were back again. Even though the annual catches (without adjustment for variations in fishing effort) have fluctuated since that time from 54,476,000 pounds in 1932 to 181,968,000 pounds in 1939, there has been no complete failure in any year since the period 1913–1916.

Although at least some of the reasons for the fluctuations in abundance of certain species of fish are known, no explanations have been given for the fluctuations in Atlantic Menhaden. For the Gulf of Maine, Bigelow and others have stated that these fluctuations date back to the early history of the fishery and have continued since then (*15*: 116, 117; *16*: 120). Thus, in 1845 they were abundant and in 1847 scarce. Then, for some years prior to 1875, they were tremendously abundant off the coasts of Massachusetts and Maine every summer, and a considerable fishery for them grew up on the Maine coast. However, during the cold summer of 1877 few were taken in the Gulf until September and October, when they were reported as "about as abundant as normal." So few of these fish appeared north of Cape Cod from 1879 through 1885 that the capture of one caused comment, and many people thought that the fish would never return. However, in 1886 the fish reappeared and in 1888 they were so abundant that the fishery was revived. The period of abundance was short, however, for in 1891 the catch was less than half of that taken the year before, and in 1892 few were seen north of Cape Cod. Similar periods of scarcity and abundance followed each other until 1904, when a 20-year period of scarcity began. Then in 1922 the fish returned in such abundance that 18 steamers fished successfully in Massachusetts Bay; further, "upward of 1,500,000 pounds were landed by the larger fishing vessels besides what the small boats brought in." From the middle 1920's until the middle 1940's there were not enough of them in the Gulf of Maine to be of any commercial importance there.

Although they were plentiful again in the Gulf from 1946 through 1949, fewer were present from 1950 through 1956.

Comparison of statistics for the past 20 years or so shows no correlation as to the quantity taken along different sections of the coast. If North Carolina, for example, has a good run in a given year, it does not follow that Florida, New York, or New Jersey will have a good run that same year. For example, in 1929 the fishery in North Carolina yielded 173,490,000 pounds of Atlantic Menhaden—considered an unusually large catch. But in that same year the catch credited to Florida was rather less than average, 50,532,000 pounds, and the combined catch for New York and New Jersey was a near failure with only 11,092,000 pounds. Again in 1937, when the catch in North Carolina amounted to only 61,706,000 pounds (next to the smallest during about 20 years), the catch for Florida was 139,788,000 pounds and the combined catch for New York and New Jersey was 99,684,000 pounds, both well above the average for the 20-year period.

It seems improbable that the commercial catches taken by the fisheries in the western Atlantic have made any serious inroads on Atlantic Menhaden populations in any general area. If it is true that the handiwork of man has had no important effect on the abundance of this species, then the fluctuations must be attributed to natural phenomena that occur in their enviroment.

Successful and unsuccessful spawning seasons are known to profoundly affect the abundance of some species and this is probably so in the case of this species also. However, it does not explain why a fish that may attain an age of 9–10 years (as concluded from the number of winter rings on the scales) may be abundant one year in a certain locality but very scarce or even absent there the next year. Furthermore, since the fish caught during a fishing season in any one area are not all of the same age and size, the failure of one or even several successive spawning seasons would not cause an abrupt diminution from one year to the next. The theory that these fish follow their food and therefore remain in water having an abundant growth of plankton of suitable size has been advanced. It would follow then that if sufficient food is not available near the shore, the fish will remain offshore, perhaps beyond the range of the vessels employed in the fishery. This theory seems to be the most plausible one advanced to date. It has been suggested also that the temperature of the water is a factor, which no doubt is true, particularly insofar as it affects the growth of the planktonic food required by these fish. It is obvious that further study is needed to determine more specifically the reason or reasons for the exceedingly great fluctuations in the runs of Atlantic Menhaden.

Methods of Fishing. These fish are caught chiefly with purse seines, though smaller quantities are taken with long haul seines and in pound nets; and minor quantities are caught with ordinary seines or drag nets and with gill nets.

The vessels employed in the operation of this large industry are a very familiar sight to those living near the fishing centers, and in some localities, for example Beaufort and Moorehead City, North Carolina, the economic life of the communities is so dependent upon the fishery that nearly everyone watches the incoming vessels to see what kind of a catch has been made. If the catch is good, the operator's flag is flown from the "crow's nest" (see below), thus notifying the factory to get up steam and for hands to stand by to take care of the catch. It is a common saying among people of these communities that the stench from the factories "smells like bread and butter" to them.

Formerly, sailing vessels were used in this fishery. These were superseded by auxiliary schooners, which in turn were replaced by power-driven vessels equipped with diesel engines. All of those used in North Carolina and southward are of nearly the same design and are capable of carrying 400,000 fish or more. They are ruggedly built wooden vessels, most of them less than 100 feet long, with a broad beam and a high bow to make them seaworthy. A tall mast is set in the forepart of the vessel, and near the top of it is a small platform, generally surrounded by a rail and often partly enclosed by canvas. This is the crow's nest from which one or two men watch for schools of fish.

Each vessel carries two "purse seine boats" which, when not in use, are suspended from derricks on each side of the mother ship. When a school of fish is sighted, the vessel approaches it, the purse seine boats with seine aboard are lowered, and the school of fish, or at least part of it, is surrounded as quickly as possible with the seine. Next the seine is "pursed" by drawing in a line (at the bottom of the net) that runs through rings. After the fish have been concentrated into a more or less compact mass they are loaded aboard the vessel with a large dip net, generally operated by means of block and tackle.

Steamers are also used in pursuing these fish, though less so than formerly. They are larger than the vessels driven by diesel engine, hence they can go farther and stay out longer. This was advantageous in former days when the scrap was used only as a fertilizer, but now that it is used mostly as poultry and stock feed and since the fish preferably should be processed on the day they are caught, the advantage of these larger vessels has diminished.

General Range. Continental waters of North America, from Nova Scotia to Florida; taken commercially from eastern Maine to northern Florida, as far south as Mayport. Stragglers have been taken as far northeastward as St. John Harbor, New Brunswick (*64*: 11), and St. Mary Bay, Nova Scotia (*16*: 120), and as far south as Indian River City, Florida (*33*: 56); and large schools have been reported as seen during the winter off Cape Canaveral and Mosquito Inlet (*43*: 36). This species has often been reported for the coasts of the Gulf of Mexico, Brazil, Uruguay, and Argentina, but these reports are for another species (p. 344; *58*: 1–39). Fowler reported it for the "Senegal region" of Africa but had no specimens from there (*39*: 174); also, there are earlier reports of a *Brevoortia* from Africa; whether it is *tyrannus* needs verification.

Details of Occurrence. As discussed under *Fluctuations in Abundance* (p. 358), it is well known that Atlantic Menhaden fluctuate widely from year to year and over periods of years. Prior to 1850 they were reported as plentiful at the mouth of the

Bay of Fundy on the New Brunswick side; though they have not frequented these waters subsequently, except for occasional strays (see above), they have been plentiful off and on westward. In years when these fish were plentiful, their chief centers of abundance north of Cape Cod have been the Massachusetts Bay region, the region of Casco Bay, and among the islands thence eastward to Penobscot Bay, where they may congregate as much as 40–50 miles out from the land. But they have never been reported for the central part of the Gulf or for the off-lying fishing banks.

Although the Atlantic Menhaden's appearances and disappearances are unpredictable for any given locality, they are far more regularly and uniformly numerous southward from Cape Cod than northward, not only along the open coast but within the larger bays and sounds as well. Landings southward from New York for 1954, the most recent year for which pertinent catch statistics are at hand, were as follows: 136 million pounds for New York and New Jersey, 306 million for Delaware, 160 million for North Carolina, 42 million for northeastern Florida, but only four million pounds for Maryland and Virginia combined, and about the same amount for South Carolina. While these data might suggest centers of greatest abundance at some areas along the American coast compared to others, it seems more likely that they reflect not only the economic laws of supply and demand, but the wide and varied patterns of distribution that have been discussed under *Fluctuations in Abundance* (p. 358).

Synonyms and References:

Clupea tyrannus Latrobe, Trans. Amer. philos. Soc., *5*, 1802: 77, pl. 1 (drawn without dorsal; no descr.; type local. Chesapeake Bay; notes probably applicable to some species of *Pomolobus*; an isopod, *Olencira praegustator*, from mouth descr.).

Clupea menhaden Mitchill, Rep. in part on Fishes of New York, 1814: 21 (orig. descr.; type local. presumably New York); Mitchill, Trans. Lit. philos. Soc. N. Y., *1*, 1815: 453 (descr.; New York; use as fertilizer); Günther, Cat. Fish. Brit. Mus., *7*, 1868: 436 (synon., descr.).

Clupea neglecta Rafinesque, Amer. Month. Mag., *2* (3), 1818: 206 (orig. descr.; type local. Long Island, New York).

Alosa menhaden De Kay, New York Fauna, Pt. 4: Fishes, 1842: 259, pl. 21, fig. 60 (descr., import., New York); Storer, Fishes Mass., 1867: 158, pl. 26, fig. 4 (descr., abund., how caught, uses, Massachusetts Bay).

Alosa sadina De Kay (not of Mitchill), New York Fauna, Pt. 4: Fishes, 1842: 263, pl. 40, fig. 129 (descr., fig. clearly shows *B. tyrannus*).

Clupea carolinensis Gronow *in* Gray, Cat. Fish. Brit. Mus., 1854: 140 (orig. descr.; type local. S. Carolina).

Brevoortia menhaden Gill, Rep. U. S. Comm. Fish. (1871–1872), 1873: 811 (how and where used, range); Uhler and Lugger, Rept. Comm. Fish. Md., ed. 1, 1876: 156; ed. 2, 1876: 133 (descr., synon., use, Maryland).

Brevoortia tyrannus Goode, Proc. U. S. nat. Mus., *1*, 1879: 5 (establ. validity of Latrobe's specific name, *tyrannus*), 31 (descr.; cf. "var. *aurea*" and *B. patronus*; varieties *menhaden* and *aurea* reognized; new variety *brevicaudata* named and defined); Goode, Rep. U. S. Comm. Fish. (1877), 1879: iii–xii, 1–529, pls. 1–31 (complete hist. of American menhaden; discus. species and varieties, includ. S. American ones; full descr. of industry); Jordan and Gilbert, Bull. U. S. nat. Mus., 16, 1882: 269 (descr., synon.); Good *in* Goode, *et al.*, Fish. Fish. Industr. U. S., 1 (3), 1884: 569, pl. 205 (common names, migr., distr., food, reprod., enemies, uses); Goode, Amer. Fishes, 1888: 385, fig. (migr., food, etc.); Smith, Bull. U. S. Fish Comm. (1890), *10*, 1892: 64 (behavior in lower Potomac R.); Smith, Bull. U. S. Fish Comm. (1891), *11*, 1893: 191, 195 (small ones enter brackish and fresh water); Peck, Bull. U.S. Fish Comm. (1893), *13*, 1894: 113–126, pls. 1–8 (food and feed.); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 433, fig. 195 (descr., size, range, synon.); Evermann and Kendall, Rep. U. S. Comm.

Fish. (1899), 1900: 56 (refs.); Linton, Bull. U. S. Fish Comm. (1899), *19*, 1901: 277, 440 (food, cestode and trematode parasites); Bean, T. H., 7th Rep. Forest Comm. N. Y. (1901), 1902: 309, fig. (synon., local names, size, range, commerc. uses, migr.); Bean, T. H., Bull. N. Y. St. Mus., 60, Zool. 9, 1903: 211 (synon., descr., size, range, uses, New York); Linton, Bull. U. S. Bur. Fish. (1904), *24*, 1905: 352 (nematode, trematode, and copepod parasites); Richardson, Bull. U. S. nat. Mus., 54, 1905: 231 (isopod parasite); Fowler, Rep. N. J. St. Mus. (1905), 1906: 103, pl. 6 (descr., New Jersey); Smith, N. C. geol. econ. Surv., *2*, 1907: 130, figs. 44, 45 (diagn., range, size, common names, spawn., econ. import., North Carolina); Kendall, Occ. Pap. Boston Soc. nat. Hist., *7*, 1908: 40 (refs., New England); Sumner, Osburn, and Cole, Bull. U. S. Bur. Fish. (1911), *31*, 1913: 742 (reprod., food, parasites, epidemic, Woods Hole, Massachusetts); Regan (in part of Latrobe), Ann. Mag. nat. Hist., (8) *19*, 1917: 301 (*B. patronus* and *B. aurea* in synon., diagn., range); Kuntz and Radcliffe, Bull. U. S. Bur. Fish. (1915–1916), *35*, 1918: 119–123, figs. 76–86 (eggs, larval develop.); Hildebrand, Rep. U. S. Comm. Fish. (1918), Append. 6, 1919: 3, 2 figs., 1 pl. (photos of scales, descr., uses, spawn., food, Beaufort, North Carolina); Huntsman, Contr. Canad. Biol. (1921), 1922: 11 (St. John Harbor, New Brunswick); Bigelow and Welsh, Bull. U. S. Bur. Fish. (1924), *40* (1), 1925: 118, fig. 48 (descr., size, range, breed., food, enemies, commerc. import., Gulf of Maine); Jordan, Fishes, 1925: 277, fig. 211 (econ. import., habitat); Fish, Bull. U. S. Bur. Fish (1925), 1926: 165–167, 170, 172 (surface catches, Woods Hole, Massachusetts); Nichols and Breder, Zoologica, N. Y., *9* (1), 1927: 41, fig. (distr., food, life hist., size, New York and s. New England); Hildebrand and Schroeder, Bull. U. S. Bur. Fish. (1927), *43*, 1928: 102, figs. 55–59 (refs., descr., var., food, spawn., econ. import., range, Chesapeake Bay); Jordan, Manual Vert. Anim. NE U. S., ed. 13, 1929: 4 (diagn., range, uses, food); Truitt, Bean, and Fowler, Bull. Md. Conserv. Dep., 3, 1929: 51, fig. 17 (descr., Maryland); Breder, Field Bk. Mar. Fish. Atl. Cst., 1929: 69, fig. (range, uses, spawn., habits, "races"); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 44 (range, synon.); Wilson, Bull. U. S. nat. Mus., 158, 1932: 381, 401, 404, 437, 451, 480 and 517 (copepod parasites); Greeley, 26th Rep. N. Y. Conserv. Dep. (1936), Suppl., 11, 1937: 91 (brackish water Hudson R.; numerous at mouth of Mamaroneck R.); Perlmutter, 28th Rep. N. Y. Conserv. Dep. (1938), Suppl., 15 (2), 1939: 17, tab. 4 and 15 (time of occur., Long Island; spawn.); Greeley, 28th Rep. N. Y. Conserv. Dep., Suppl., 15 (2), 1939: 82 (young at Long Island, New York; prey of other fish); Anonymous, Fish. Resourc., U. S. Senate Doc. 51, 1945: 71, figs. (habits, biol., econ. import.); Hildebrand, Smithson. misc. Coll., *107* (18), 1948: 7, fig. 1 (synon., relation., descr., var., range); Bigelow and Schroeder, Fish. Bull. (74) U. S. Fish Wildl. Serv., *53*, 1953: 113 (descr., life hist., Gulf of Maine).

Brevoortia tyrannus Fowler, Monogr. Acad. nat. Sci. Philad., 7, 1945: 45, 74, 165 and 266 (refs., occur.).

Menhaden, Greer, Rep. U. S. Comm. Fish. (1914), 1915: 5–27, pls. 1–7 (complete acct. of industry); Hardcastle, J. E. Mitchell Sci. Soc., *57* (2), 1941: 214 (sporozoan parasite); Anonymous, Canned Fish and Byproducts, Fish and Wildlife Service, CFS 304, 1945: 15 (statist. for 1945).

Doubtful Reference:

Brevoortia tyrannus Fowler, Bull. Amer. Mus. nat. Hist., *70* (1), 1936: 174 (refs. part African; descr. of Amer. specimens).

Negative References:

Alosa tyrannus De Kay (not of Latrobe), New York Fauna, Pt. 4, Fishes, 1842: 252, pl. 13, fig. 38 (descr., probably *Pomolobus aestivalis*).

Brevoortia tyrannus Henshall (not of Latrobe), Bull. U. S. Fish Comm., *14*, 1895: 211 (Tampa, Florida; presumably *B. patronus*); Evermann and Kendall, Proc. U. S. nat. Mus., *31*, 1906: 74 (synon., lit. on *Brevoortia*; cf. specimens from various localities, includ. two from Argentina; presumably *B. patronus*); von Ihering, Rev. Industr. Anim., 1 (3), 1930: 229 (N. and S. Amer. representatives compared from lit., econ. import.); Gunter, Publ. Inst. mar. Sci. Texas, *1* (1), 1945: 29 (habitat, Texas; this is *B. patronus*).

Brevoortia brevicaudata Goode 1879

Figure 90

Study Material. Eight specimens, 165–180 mm TL, 126–147 mm SL, all from Noank, Connecticut, USNM 14044, 14846. This species, as herein understood, is known only from the above specimens.

Distinctive Characters. See *Relationship* (p. 364).

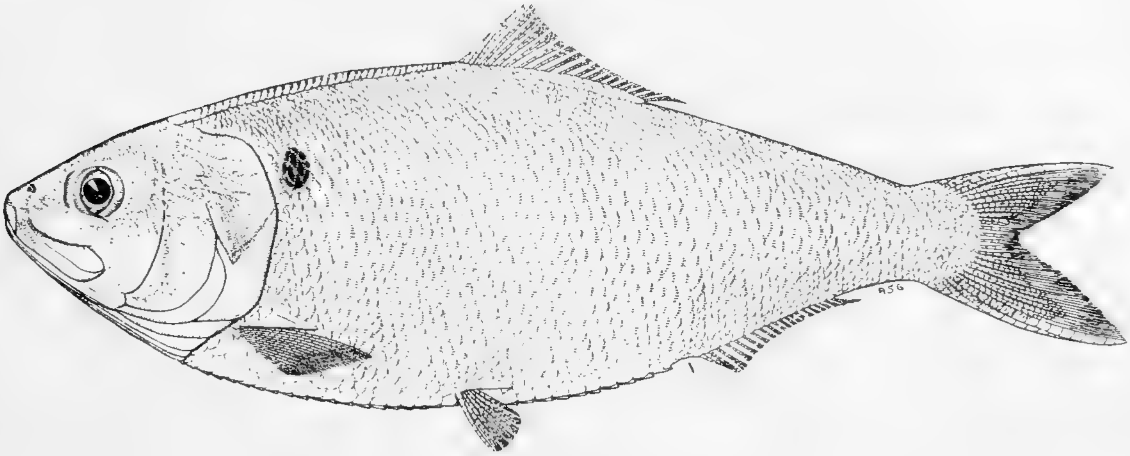

FIGURE 90. *Brevoortia brevicaudata,* 180 mm TL, 145 mm SL, Noank, Connecticut, type, USNM 129797. Drawn by Ann S. Green.

Description. Proportional dimensions in per cent of standard length, and counts, based on specimens 126–147 mm SL.

Body: depth 35–38.
Caudal peduncle: depth, 9.6–10.5.
Head: length 29–30.
Snout: length 6.4–7.3.
Eye: diameter 5.4–6.
Interorbital: width 6.2–7.0.
Maxillary: length 12–13.
Mandible: length 15.5–16.5.
Anal fin: length of base 17.5–19.
Pelvic fin: length 8.2–8.6.
Pectoral fin: length 13.5–16.

Scales: oblique series along middle of side 47–53.
Modified scales: in a series in front of dorsal fin, 35–39.
Ventral scutes: 31–33.
Fin rays: dorsal 19–22; anal 21 or 22; pectoral 17.
Vertebrae: 48 (1 specimen).

BODY deep and robust, its greatest thickness about a third of its depth, its greatest depth near midpoint between tip of pectoral and insertion of pelvic, 2.6–2.85 in SL. CAUDAL PEDUNCLE rather deep, 2.8–3.0 in head or 3.4–3.7 in greatest depth of body.

SCALES adherent, much deeper than long, with rather short pectinations as in *B.*

tyrannus of similar size, greatly reduced on back and at base of caudal; 5 or 6 vertical rows of scales exposed between tip of pectoral and base of pelvic fin. A row of large modified scales on each side of median line in advance of dorsal. VENTRAL SCUTES moderate, 18–20 in advance of pelvic fins and 12–14 behind them.

HEAD small, 3.3–3.85 in SL, its depth 3.6–3.8. SNOUT with a definite median notch, its length 3.9–4.6 in head. EYE small, 4.7–5.4. INTERORBITAL 4.1–4.7. CHEEK notably deeper than long. MAXILLARY rather short, reaching about to vertical from posterior margin of pupil, 2.2–2.4 in head. MANDIBLE short and included, its upper margin (within mouth) nearly straight, its length to joint 1.8–1.9 in head. Upper section of OPERCLE with prominent radiating ridges. GILL RAKERS long, and numerous, the longest ones about as long as snout and half of eye, about 115–125 on lower limb.

DORSAL fin low, its longest rays scarcely longer than the snout, its origin nearer to margin of snout than to base of caudal by a distance nearly equal to diameter of eye; its base with a low sheath composed for the most part of a single series of scales, not extending above the basal third of the rays. CAUDAL fin very short, the middle rays about as long as eye; lower lobe somewhat longer than upper one, more or less damaged, but shorter than head, about 3.7–4.4 in SL. ANAL very low, its origin under, or a little behind, vertical from tip of last dorsal ray, its base 5.25–5.7 in SL; a very narrow sheath of scales at base. PELVIC fin small, with a gently convex margin, its outermost ray not much longer than innermost ray; the fin inserted about under origin of dorsal; the length 3.4–3.6 in head. PECTORAL fin very short, not falcate, its length 7.25–8.25 in SL, or 1.8–2.2 in head, its longest ray about three times longer than the shortest one, failing to reach base of pelvic by a distance notably greater than diameter of eye. AXILLARY appendage of pectoral short and broad, only a little more than half of length of fin, 3.0–3.8 in head.

Color. Old preserved specimens dark greenish on back and upper part of side. Lower parts silvery to brassy. Sides of head silvery. A roundish dark spot at shoulder, about the size of pupil of eye; only one specimen at hand with suggestions of auxiliary dark spots on side behind shoulder spot. Fins all uniform brownish.

Relationship. It is strange that no additional specimens like the ones herein described, collected in 1874, are among the many in the U. S. National Museum from the general vicinity of Long Island and northward to Woods Hole, Massachusetts. These specimens differ in so many respects from the more or less typical *B. tyrannus* in the same general vicinity (Noank, Conn.) that it seems necessary to recognize them as representing a distinct species. The apparent distinctions are shown in a comparison with specimens of *B. tyrannus* of equal size from the same general vicinity of Noank (p. 365). It is evident from this comparison that *brevicaudata* is not a geographical variant.

The eight specimens in the *Study Material* are, in part at least, those studied by Goode, who gave measurements of two specimens from USNM 14846 and an accurate description (*44*: 33, 37); although he gave them the "variety" name *brevicaudata*, he did not designate a type. Therefore Goode's variety has been elevated to specific

Comparison of *B. brevicaudata* with *B. tyrannus*
(in per cent of standard length)

	brevicaudata	*tyrannus*		*brevicaudata*	*tyrannus*
Head: length	29–30.5	30.5–33	Mandible: length	15.5–16.5	17.5–18.5
Eye: diameter	5.5– 6.0	6.2– 6.9	Caudal fin: lower lobe	22.5–27	30–33
Maxillary: length	12–13	14–15	Pectoral fin: length	13.5–16	19.5–20

rank, with the designation of a lectotype approximately 180 mm TL (caudal somewhat damaged) and 145 mm SL, USNM 129797 (*58*: 10).

Thus the characters in all respects are smaller in *brevicaudata* than in *tyrannus*. The maxillary in the former reaches about to a vertical from the posterior margin of the pupil instead of well behind it; the caudal's lower lobe in *brevicaudata*, if measured from the middle of the caudal base, is shorter than the head instead of about equal to it in length; the pectoral in *brevicaudata* fails to reach the base of the pelvic by a distance exceeding the eye's diameter instead of less than its diameter, and it leaves 5–7 vertical series of scales exposed instead of 3 or 4, as in *tyrannus*.

If the specimens of *brevicaudata* are compared with examples from the southern part of the range of *tyrannus*, as from Fernandina, Florida, the differences are even more pronounced, for the head and eye in such material are relatively larger than those in northern specimens of *tyrannus*, and the fins are still longer.

Nothing distinctive is known about the life history of this species.

Range. Known only from Noank, Connecticut.

Synonyms and References:

Brevoortia tyrannus var. *brevicaudata* Goode, Proc. U. S. nat. Mus., *1*, 1879: 34, 37 (orig. descr.; type local. Noank, Connecticut; cotypes USNM 14846; cf. "normal" *tyrannus* and *aurea*).

Brevoortia tyrannus brevicaudata Goode, Rep. U. S. Comm. Fish. (1877), Append. A, 1879: 22 (said to vary from "normal type" with shorter maxillary and mandible, lower anal, and shorter caudal; Noank, Conn.); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 634 (cf. *aurea*, after Goode); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 44 (range, synon.).

Brevoortia brevicaudata Hildebrand, Smithson. misc. Coll., *107* (18), 1948: 10, fig. 2 (synon., descr., range, lectotype USNM 129797).

Brevoortia patronus Goode 1879

Largescale Menhaden, Gulf Menhaden, Alewife, Shad

Figures 84, 85, 91

Study Material. At least 110 specimens, 60–265 mm TL, 45–207 mm SL, collected at many places along the Gulf coast from Apalachicola, Florida, to Brazos Santiago, Texas, including the types of *B. patronus* Goode, USNM 892. Some of the data used were extracted from unpublished tables prepared by the late William W. Welsh; also a few lots of juveniles.

Distinctive Characters. See *Relationship* (p. 370).

Description. Proportional dimensions in per cent of standard length, and counts, based on at least 110 specimens, 45–207 mm SL.

Body: depth 33–45, usually 35–42.
Caudal peduncle: depth, 8.5–12.
Head: length 31–38, usually 32–35.
Snout: length 6.0–9.0, most frequently 7.0–8.0.
Eye: diameter 7.0–9.2.
Interorbital: width 6.5–8.0.
Maxillary: length 14–17, usually 15–16.
Mandible: length 17–20, most frequently 18 or 19.
Anal fin: length of base 17–21.
Pelvic fin: length 8.5–10.5.

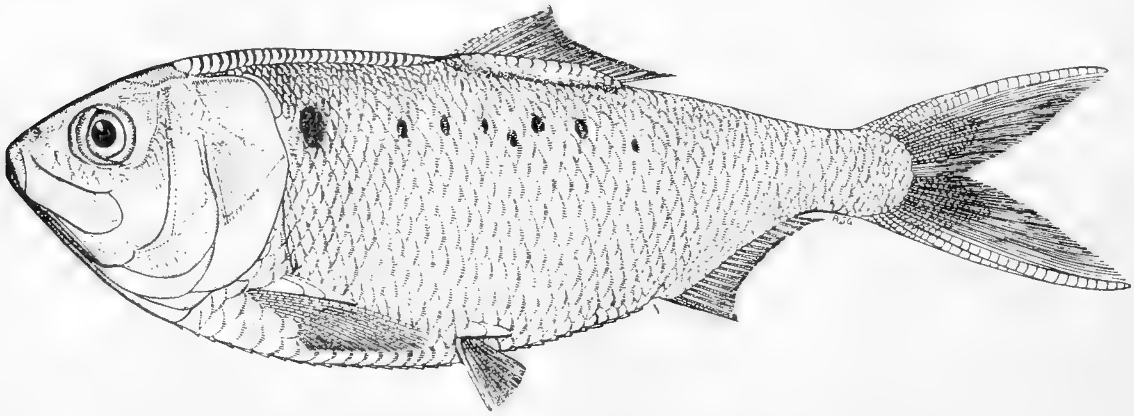

FIGURE 91. *Brevoortia patronus*, 215 mm TL, 164 mm SL, off Galveston, Texas, USNM 129810. Drawn by Ann S. Green.

Pectoral fin: length 19–23, most frequently 20–21.

Scales: oblique series along middle of side 36–50, usually 38–46.
Modified scales: in a series in front of dorsal 24–33, generally 25–31.
Ventral scutes: 28–32, most frequently 29–31.
Fin rays: dorsal 17–21, most frequently 19 or 20; anal 20–23; pectoral 14–17, most frequently 15 or 16.
Vertebrae: usually 45–47, rarely 42, 43, 44, or 48 (117 specimens).

BODY rather deep, strongly compressed, its greatest thickness about a third of its depth, the greatest depth well in advance of tip of pectoral and often only about an eye's diameter behind margin of opercle, 2.2–3.0, usually 2.4–2.8, in SL; ventral outline very strongly convex anteriorly, notably more than half of greatest depth of body below a line extending through lower margin of eye to middle of base of caudal. CAUDAL PEDUNCLE rather slender, 3.0–3.9, usually 3.2–3.7, in head.

SCALES adherent; the exposed part much deeper than long, the scale itself somewhat deeper than long (Fig. 85 A), the margin definitely serrate in young of about 60 mm, the serrae gradually increasing in length with age, becoming definitely pectinate, the pectinations reaching the full length of the otherwise exposed portion of the succeeding scale in specimens 200 mm TL and upward; scales greatly reduced in size on back and at base of caudal; rarely more than two rows of scales exposed between tip of pectoral and base of pelvic. A row of large modified scales on each side of median line of back in advance of dorsal fin, these scales not fully modified in examples less than about 100 mm TL, rather variable in number, generally about 25–31 in each series, therefore usually fewer than in *tyrannus*. VENTRAL SCUTES quite strong, more prominent in young than in adults, 18 or 19, rarely 16 or 17, in advance of pelvic fins, and 12 or 13, occasionally 11, behind them.

HEAD rather large, 2.6–3.2, usually 2.9–3.1, in SL, its depth 2.7–3.4, most frequently 2.8–3.2. SNOUT blunt, with a prominent median notch, its length 3.9–5.0, most frequently 4.2–4.6, in head. EYE with comparatively little adipose tissue, 4.1–5.0, usually 4.3–4.8. INTERORBITAL 4.1–5.0, usually 4.3–4.7. CHEEK much deeper than long in adults. MAXILLARY generally reaching vertical from posterior margin of pupil, 2.0–2.4, usually 2.1–2.2, in head. MANDIBLE included in upper jaw, its upper margin (within mouth) straight, its length to joint 1.75–1.9 in head. Upper section of OPERCLE with strong radiating ridges. GILL RAKERS very numerous, those on upper limb extending down and over those on lower limb, the longest ones rather longer than snout; increasing in number with age, about 40–50 in specimens 25–40 mm TL, 80–85 in specimens 45–60 mm, 125–130 in specimens 100–130 mm, and 135–150 in examples 200 mm and upward. TEETH wanting, except for minute ones on margin of maxillary in small specimens under about 60 mm.

DORSAL fin rather high anteriorly, its margin definitely concave, its longest rays nearly as long as snout and eye, the last two rays considerably longer than the preceding ones, its origin about equidistant between margin of snout and base of caudal; a broad scaly sheath on the base of fin, almost covering the fin except for the last produced rays if the fin is deflexed, extending well above basal third of the shortest rays when standing erect. CAUDAL moderately forked, the middle rays exceeding length of eye by nearly diameter of pupil, the lobes rather long, the lower one often longer than head, 2.5–3.2, most frequently 2.8–3.1, in SL. ANAL moderately low, somewhat elevated anteriorly, its margin definitely concave, its origin under, or a little in advance of, tip of last dorsal ray, its base 4.75–5.9 in SL; a low scaly sheath at base. PELVIC fin small, with a gently convex margin, its length 3.1–3.7 in head, its outermost ray only a little longer than the innermost ray (Fig. 84 A); the fin inserted well behind vertical from dorsal origin. PECTORAL long, somewhat falcate in adults, its length 4.35–5.25, usually 4.75–5.0, in SL, 1.5–1.9, most frequently 1.5–1.7, in head, its longest rays about four times longer than the shortest one, sometimes nearly reaching base of pelvic. AXILLARY SCALE of pectoral variable, generally scarcely more than half of length of fin in large examples, little developed in young.

Color. Back bluish-gray. Sides brassy-green. Sides of head silvery. A large black shoulder spot, often followed by a single series (rarely by a double series) of smaller and less definite spots, these being roundish in some and vertically elongate in others; the shoulder spot generally appearing in specimens between a length of 50 and 75 mm, the auxiliary spots usually appearing later. Fins mostly plain yellowish green; the caudal with a dusky margin. Peritoneum jet black.

Size. A small size seems to be normal. An example 265 mm (10.6 in.) TL is the largest now at hand. Goode (*44*) quoted Silas Stearns as having seen examples 11, 12, and 13 inches long, but these may have been *gunteri.*

Development and Growth. The postlarvae, 19–24 mm TL and 16–19 mm SL, are relatively slender, though deeper than young of *tyrannus* of the same length, their greatest depth being about 7.4–10.5 in TL and 4.75–8.0 in SL. Also, these young fish are more advanced in development, for even the smallest ones have all fins (exclusive of the pectoral) well enough developed to show rays; however, the pelvic fin is still well in advance of the dorsal. The convoluted intestine, characteristic of young clupeoids generally, remains evident in the smaller examples but has become fully invaginated in the larger ones. The snout seems to be rather more pointed in the postlarvae than in larger fish, and the large rounded maxillary scarcely reaches beyond the anterior margin of the pupil. The gill rakers of the upper limb do not yet extend down and over those of the lower limb, and the filaments on the posterior rim of the gill arches are little developed at this size. The ventral scutes in front of the pelvics are well developed in the largest specimens, but not those behind them. The smallest specimens have a series of dark chromatophores along the lateral edge of the abdomen and another along the anal base; also, few dark chromatophores are present on the opercle, on the base of caudal, and on the chest; some of these markings have become obscure in the larger specimens of this lot. Dark specks, present on the caudal and dorsal fins, are decidedly more numerous in the larger specimens than in the smaller ones.

Specimens of about 30 mm already are shaped much like adults. Scales in part are developed, and general pigmentation has taken place, the lower part of the sides already being silvery in some specimens. The dark specks on the dorsal and caudal fins have increased greatly in number, but the chromatophores along the base of anal of juveniles remain faintly visible. The gill rakers have increased considerably in proportionate length, and those of the upper limb now extend downward across those of the lower limb; the filaments, too, are much better developed. The maxillary remains shorter than in adults, for it scarcely reaches below the middle of the eye. Striations are faintly visible on the upper part of the opercle, the ventral scutes are fully developed, and the pelvic fin now is situated under the anterior rays of the dorsal, as in adults. The dark peritoneum is plainly visible through the abdominal walls at this stage of development.

Little is known about the rate of growth. Length frequencies, based on 186 fish, suggest that a maximum length of about 100 mm (4 in.) is attained at one year of age, probably 150 mm (6 in.) at two years. However, some of the fish in each year-class are much smaller, some being only about 80 mm long at one year of age and about 125 mm at two years. The rate of growth seems to be about the same as that of *tyrannus* at Beaufort, North Carolina.

Reproduction. As in the case of their growth, little is known about reproduction in the Largescale Menhaden. Goode (*45*: 577) quoted Silas Stearns as follows:

> The first traces of spawn are found in May. But by July it has become sufficiently developed to be noticed by any person unaccustomed to the examination of such objects. In the latter part of September or first of October, at which time they are seen in abundance, the ovaries are sufficiently grown to distend the fish's abdomen, yet not fully ripe. When they are next caught, in November and December, on the sea-beach, they are without ovaries and show signs of having spawned.

Since the Gulf species, *patronus* and *gunteri*, were not distinguished until recently, one cannot be sure which species Silas Stearns observed. Even now it is not known whether the spawning seasons of the two are different.

The large examples at hand were all taken in February and March, and in these the gonads are in a collapsed state, as though the fish had spawned recently. Furthermore, the juveniles at hand, 28–60 mm TL, were taken in late winter and during the spring. In fact, there are some postlarvae, 19–24 mm TL, taken at Dead Man's Island, Corpus Christi, Texas, March 31, 1926, which are believed to be this species. Thus it is indicated that spawning takes place during the winter, that is, rather later in the year than the time suggested by Silas Stearns.

Migrations and Habitat. These Menhaden, like *tyrannus*, travel in schools while they feed on plankton at the surface. However, at times they apparently live at or near the bottom also, for the Bureau of Fisheries schooner, GRAMPUS, took many specimens with an otter trawl in February and March 1917 off Corpus Christi and Galveston, Texas. Gunter also reported their capture in the Gulf with an otter trawl (*51*: 29).

According to Gunter (*51*), this species was not taken in water having salinities below 25.0, which agrees in general with the places of collection of the specimens now at hand. At least all of the larger specimens of *patronus* were taken either offshore or in localities where the salinity would be expected to run rather high. However, small to half-grown examples are at hand that were caught where the water must have been nearly fresh, as at Manchac Pass on the Illinois Central Railroad, north of New Orleans, Louisiana, and in Grand Plains Bayou, near Baldwin Lodge, Mississippi. Such a habitat, for both young and adults, would correspond to that of *tyrannus*.

It was stated by Silas Stearns that the fish are not seen in shallow water during winter but appear in the spring and remain until late fall (*in* Goode, *45*). He said that in fine weather the fish could be seen approaching the coast in great schools, and that, once they had reached the inside waters, a large school would break up into smaller schools. He also said that quiet bayous, creeks, and nooks in the bay were favorite "feeding or playing grounds." Furthermore, he noted that small schools feed at the mouths of rivers, and that upon becoming "accustomed to the fresh water," they move upstream to quiet places. Again, one does not know whether Stearns observed one or both species inhabiting the Gulf.

Food. There is every reason to believe that the food of *patronus* is essentially the same as that of *tyrannus*. Both species feed at the surface in dense schools, have a gizzard-like stomach, and a long intestine, which suggest a vegetable diet. The presence of mud in the stomach suggests that they also feed on the bottom. Stearns said, "The Gulf menhaden are a bottom-feeding fish, as their stomachs always contain soft brown mud, from which I suppose they extract microscopic animal and plant matter" (*45*).

Parasites. As in Atlantic menhaden, the isopod *Olencira praegustator* (Latrobe) is frequently found in the mouth of Largescale Menhaden (*107*: 231). Stearns (*45*) likewise reported it, saying:

> When the Gulf Menhaden arrive in spring, each one has a parasite in its mouth, a crustacean called *Cymothoa praegustator*. This is found always in one position, clinging with its claws to the roof of the fish's mouth, with its head looking forward and very near to the jaws of the fish. The parasites remain with the menhaden as long as the latter is in salt water; in brackish water they are less frequently observed, disappearing altogether in fresh water. With all the fall fish of this species which I have examined there were no parasites.

Once more it is possible that Stearn's observations may have been based on one or both species inhabiting the Gulf.

Two species of copepods, *Bomolochus teres* Wilson and *Lernanthropus brevoortiae* Rathbun, have been reported as parasitic on Gulf *Brevoortia* (*12*: 582, 588), but it is not known whether one or both species served as host.

Relationship. This species, closely related to *tyrannus* of the Atlantic coast, generally has been considered identical to it or only subspecifically distinct. However, it differs in so many respects from *tyrannus* that it apparently must be recognized as a distinct species. Furthermore, the range of the two species is discontinuous, for neither occurs in southern Florida, south of the Indian River on the Atlantic or south of Tampa on the Gulf.

The body depth in *patronus* compared with *tyrannus* is a bit greater, the shape is different, the head and body are deeper anteriorly, and the ventral outline is notably more strongly convex. The deepest part of *patronus*' body is well in advance of the tips of the pectoral fin and only about an eye's diameter behind the margin of the opercle, whereas in *tyrannus* it usually is over the tip of the pectoral and notably more than an eye's diameter behind the margin of the opercle. The differences in shape are plainly evident in Figs. 86 and 91. Also, in *patronus* the fins generally are longer, the scaly sheath on the base of the dorsal is broader, the axillary process of the pectoral usually is shorter, and the modified scales in front of the dorsal are larger and have shorter pectinations; in fact, overlapping in the number of modified scales is slight, occurring in only some of the rather numerous specimens examined.

The extremes of variation, as well as the usual variation, are given in the *Description*, and from those data it is evident that some overlapping occurs in every proportion and count. Nevertheless, the average differences are great in some of them. The more outstanding ones are the following, with those for *patronus* given first (in per cent of standard length): depth 38.8, 34.2; head (length) 33.6, 32.2; head (depth) 33.5, 27.8; pectoral fin 20.9, 18.7; lower lobe of caudal 34.3, 29.4; vertebrae 45.8, 48.0; scales along middle of side 41.7, 48.2; modified scales on back in advance of dorsal fin 28.0, 36.0; and ventral scutes 29.8, 32.5.

The differences in shape and depth of body, already mentioned, are more outstanding in young adults than in mature individuals. In fact, the depth in *patronus* is already about as great in fish 40–60 mm TL as in large ones; in examples of *tyrannus* of similar size the body is notably more slender; for example, in 34 specimens of *patronus* falling within the range mentioned, the depth is 36.4–45.0 % of SL, whereas in 60 examples of *tyrannus* the range is 25.8–35.8.

Variation. It is not evident at present that specimens vary between different areas, as in those from Florida at one extreme of the range and those from Texas at the other. Sufficient specimens for a thorough study of variation are at hand from Texas only. The young, as stated elsewhere, acquire the shape of the adult very early in life, and the pronounced variation in depth of body is therefore an individual variation rather than one of age. There is also considerable variation in the number and intensity of the dark spots on the side, with some specimens, including large ones, having only a shoulder spot (p. 367).

Commercial Importance. Commercial utilization of *patronus* is a recent development. Statistics at hand show for 1940 a catch of menhaden for Mississippi only, this being 25,194,000 pounds. For 1950–1953, however, the following catches (probably *patronus* for the most part but including some *gunteri*) were reported for the Gulf coast (in pounds): 326,030,100 for 1950, 351,965,100 for 1951, 459,983,900 for 1952, and 437,045,000 pounds, valued at $ 5,189,000, for 1953.

Range. Gulf coast of Florida to Texas. It was recorded once for as far south on the western Florida coast as Tampa (55: 211), but at present there are no specimens in the National Museum collection from farther south than Apalachicola, Florida. There are many from as far west and south as Corpus Christi, and the types (USNM 892) are from Brazos Santiago, Texas.

Synonyms and References:

Brevoortia patronus Goode, Proc. U. S. nat. Mus., *1*, 1879: 39 (orig. descr.; "descr." based on specimens from Brazos Santiago, Texas [USNM 892]; "diagnosis" based in part on specimens from "Mouth of Rio Grande" [USNM 891], which are *B. gunteri*; "table of measurements" includes both species); Goode, Rep. U. S. Comm. Fish. (1877), 1879: 26 (after Goode, 1879); Jordan and Gilbert, Bull. U. S. nat. Mus., 16, 1882: 269 (descr., may be based in part on *B. gunteri*); Goode *in* Goode *et al.*, Fish. Fish. Industr. U. S., 1 (3), 1884: 575, pl. 206 (movements, parasites, reprod., food); Richardson, Bull. U. S. nat. Mus., 54, 1905: 21 (isopod parasite); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 44 (range, synon.); Gunter, Ecol. Monogr., *8*, 1938: 355 (season. var. in abund., Louisiana); Hildebrand, Smithson. misc. Coll., *107* (18), 1948: 13, fig. 3 (synon., relation., descr., range).

Brevoortia tyrannus patronus Evermann and Kendall, Bull. U. S. Fish Comm. (1892), *12*, 1894: 105, pl. 21 (Galveston, Texas; differences between Atlantic and Gulf specimens slight); Evermann, Rep. U.S. Comm. Fish. (1898), 1899: 309 (many young at Grand Plains Bayou, Mississippi); Weymouth, Proc. U. S. nat. Mus., *38*, 1911: 136 (Cameron, Louisiana); Fowler, Monogr. Acad. nat. Sci. Philad., 7, 1945: 365, 372 (refs., occur.).

Brevoortia tyrannus Henshall (not of Latrobe), Bull. U. S. Fish Comm. (1894), *14*, 1895: 211 (Tampa, Florida); Evermann and Kendall, Proc. U. S. nat. Mus., *31*, 1906: 74 (synon., discus. lit. on *Brevoortia*; cf. specimens from various locals.; descr. of two from Argentina); Bere, Amer. Midl. Nat., 17 (3), 1936: 582, 598 (copepods); Gunter, Publ. Inst. mar. Sci. Texas, *1* (1), 1945: 29 (Texas coast habitat).

Brevoortia smithi Hildebrand 1941

Yellowfin Shad

Figures 84, 85, 92

Study Material. A total of 18 specimens, 120–315 mm TL, 91–240 mm SL, collected at Beaufort, North Carolina; Cumberland Sound, Georgia; and at the "mouth of St. Johns River" and in the "Indian River," Florida; the type, 295 mm TL, 225 mm SL, included among the material from Beaufort, USNM 118723. Also, specimens from Boca Ciega, Pinella County, and off Englewood, coast of western Florida, that are intermediate in some respects between *B. smithi* and *B. gunteri*, received through the kindness of William Gosline.

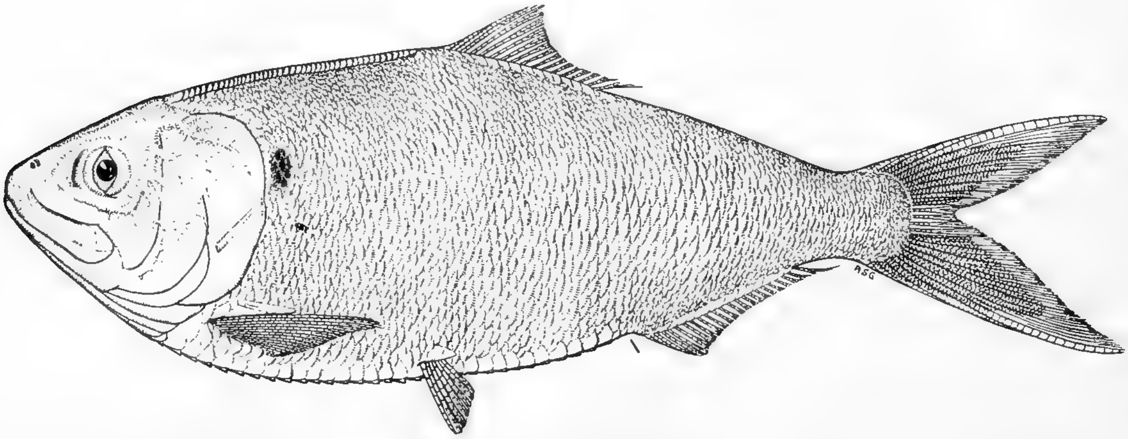

FIGURE 92. *Brevoortia smithi*, 295 mm TL, 225 mm SL, Beaufort, North Carolina, type, USNM 118723. Drawn by Ann S. Green.

Distinctive Characters. See *Relationship.*

Description. Proportional dimensions in per cent of standard length, and counts, based on specimens listed in the *Study Material*, 91–240 mm SL.

Body: depth 36–43.
Caudal peduncle: depth 9.5–12.
Head: length 29–32.5.
Snout: length 6.8–8.0.
Eye: diameter 6.1–7.5.
Interorbital: width 6.2–7.4.
Maxillary: length 13.5–15.
Mandible: length 17–18.5.
Anal fin: length of base 19–21.
Pelvic fin: length 8.5–11.
Pectoral fin: length 18.5–21.5.
Scales: oblique series along middle of side (too irregular to count accurately) *ca.* 60–70.
Modified scales: in a series in front of dorsal fin, 39–45.
Ventral scutes: 30–32.
Fin rays: dorsal 18–20; anal 22 or 23; pectoral 16 or 17.
Vertebrae: 45–47 (9 specimens).

BODY deep, rather strongly compressed, its greatest thickness notably less than half of the depth, its greatest depth at vertical from a point somewhat in advance of origin of dorsal and about midway between tip of pectoral and base of pelvic, 2.3–2.75 in SL; ventral outline notably more strongly convex than the dorsal outline, more than half of the greatest depth being below a straight line drawn through lower margin of eye to middle of base of caudal. CAUDAL PEDUNCLE rather deep, 2.6–3.4 in head, and 3.5–4.0 in greatest depth of body.

SCALES closely adherent, the exposed part three or more times deeper than long, the scales themselves less than two times deeper than long (Fig. 85 D); scales with prominent serrae ending in blunt points, not long or hair-like and not extending across exposed part of next scale; the scales greatly reduced in size on back and at base of caudal, in rather irregular series (difficult to count accurately); about 5–8 rows of scales exposed between tip of pectoral and base of pelvic. A row of enlarged modified scales on each side of median line of back in front of dorsal fin, the scales variable in number, 39–45 in each series. VENTRAL SCUTES not strong, 18 or 19 in front of pelvics, 12–14, most frequently 13, behind them.

HEAD 3.2–3.4 in SL, its depth 3.25–3.6. SNOUT compressed, blunt, with a prominent median notch, its length 3.7–5.0 in head. EYE 4.2–5.2. INTERORBITAL 4.2–4.9. CHEEK much deeper than long. MAXILLARY broadly rounded, reaching from under middle of eye to posterior margin of pupil, 2.1–2.3 in head. MANDIBLE included in upper jaw, its upper margin (within mouth) nearly straight, its length to joint 1.7–1.9 in head. Upper section of OPERCLE with very feeble radiating striae. GILL RAKERS very numerous, those on upper limb extending downward and over those on lower limb, the longest ones fully as long as snout, 121–149 in adults. TEETH absent.

DORSAL fin rather high anteriorly, the margin rather deeply concave, the longest rays equal to length of snout and eye to posterior margin of pupil, the last ray considerably longer than preceding ones, the origin about equidistant between margin of snout and base of caudal; a very low sheath on base of fin, composed of a single row of scales. CAUDAL deeply forked, the middle rays about as long as eye, the lobes long, the lower one slightly the longer, exceeding the length of head, 2.7–3.1 in SL. ANAL notably lower than dorsal, little elevated anteriorly, its margin nearly straight, its origin under or a little behind tip of last ray of dorsal, its base 4.75–5.25 in SL; a very narrow sheath at base. PELVIC fin with an oblique margin, its length 2.8–3.4 in head, its outermost ray nearly twice the length of the innermost one, the fin inserted under or slightly behind vertical from origin of dorsal. PECTORAL fin long, scarcely falcate, its length 4.65–5.4 in SL and 1.45–1.75 in head, its longest ray fully four times longer than the shortest one, the fin failing to reach base of pelvic by a distance somewhat greater than half of diameter of eye. AXILLARY APPENDAGE of pectoral variable, reaching to or well beyond midlength of fin, 2.6–4.0 in head.

Color. Back, in fresh specimens, bluish green, lighter than in *tyrannus* (evident also in preserved specimens). Sides silvery. A large black spot at shoulder, not followed by smaller dark spots. Fins golden yellow; the margin of caudal paler than rest of fin. Peritoneum black.

Size. The largest example seen, taken at Beaufort, North Carolina, was 330 mm (13.2 in.) TL. This is about equal to the usual length of fish that compose the fall and winter runs of *tyrannus* in the same vicinity.

Reproduction and Development. Nothing is known about reproduction in this species, notwithstanding the fact that the eggs and young were sought diligently at Beaufort, North Carolina, for about six years. The several adults taken there during spring and summer and examined in the laboratory showed no signs of development.

The smallest specimen at hand, 120 mm TL, differs from large ones in having a deeper body and less strongly serrated scales. The last mentioned difference is quite in keeping with other species of *Brevoortia*, for the serrations (pectinations) apparently increase in length with age in all species. It has been pointed out that young adults of *patronus* are quite as deep as large ones, which is contrary to the rule in *tyrannus*. The very deep-bodied young adults of *smithi* suggest that the young of this species too may acquire a deep body at an early age.

Migrations and Habits. Yellowfin Shad were taken at Beaufort, where their occurrence was observed several years in succession. They seem to be present there only during spring and summer and only in the local estuaries. If they occur off Beaufort Inlet, where large *tyrannus* are taken, they escaped our nets. Although the fish probably leave brackish water to spawn, the adults, contrary to those of *tyrannus*, do frequent brackish water during a portion of the year.

According to fishermen at Beaufort, these Menhaden do not school. This was confirmed by our investigations, for we took at most 10–12 a day in a pound net operated for several years in the estuary of Newport River, and rarely were more than two taken in a single haul with a large collecting seine. In contrast, hundreds of *tyrannus*, if taken at all, generally were present when the pound net was fished.

Yellowfin Shad are much more active fish than *tyrannus*. When they are caught in a seine they dash here and there and strike the net again and again in an effort to escape, whereas *tyrannus* generally strike the net once and then allow themselves to be hauled in without making a further effort to flee. The two species, when once their habits are known, may be identified by their behavior when surrounded by a seine.

Food. These fish, like *tyrannus* and other species of menhaden, have a thick-walled gizzard-like stomach and a long intestine. A fish 330 mm TL and 247 mm SL, for example, had an alimentary canal 937 mm long; that is 380 °/₀ of its SL. The stomach contents of this same specimen consisted of diatoms and spicules of a sponge.

Parasites. Only one parasitic copepod (*Lernaeenicus radians*)[40] has been found on these Menhaden. The conspicuous isopod *Olencira praegustator*, very common in the mouth of *tyrannus*, has not been seen thus far in *smithi*.

Relationship. The differences between *Brevoortia smithi* and *B. gunteri* are given

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[40] Identification by Paul L. Illg, at the U. S. National Museum.

on p. 379. *B. smithi* differs from *B. tyrannus* in having much smaller scales, in less regular series; notably shorter serrations or pectinations on the scales of specimens of equal size (Figs. 85 B and 85 D); more feeble radiating striations on the upper part of the opercle; and a longer and more pointed pelvic fin. Furthermore, *B. smithi* has a rather more strongly compressed and deeper body and a deeper caudal peduncle, a somewhat smaller head, a rather larger anal fin with a somewhat greater number of rays and a longer base, and somewhat longer caudal and pectoral fins. Also, *B. smithi* is lighter in color, has more definitely yellow fins, and has no small dark spots behind the large shoulder spot. The two species are separable by touch, as *tyrannus* is very slimy and slippery whereas *smithi* is not.

Variations. The variations among the limited number of specimens known are not pronounced. The smallest specimen, 120 mm TL, from Cumberland Sound, Georgia, is the deepest among the 18 at hand, which suggests that in this species, as in *patronus*, young adults are as deep or deeper than large ones, whereas in *tyrannus* they are more slender. However, some half-grown fish from the mouth of the St. Johns River, Florida, are no deeper than large fish from Beaufort. The great difference in the number of gill rakers (121–149) on the lower limb may be ascribed in part to age and in part to an error in counting, as it is impossible to count the close-set rakers accurately. The fresh examples observed in the field were quite uniform in color.

Commercial Importance. Yellowfin Shad are not numerous enough to be commercially important, for only a few are taken at a time. The total annual catch at Beaufort probably does not exceed several hundred pounds. Their abundance south of Beaufort remains unknown.

The fishermen, at least at Beaufort, distinguish these Menhaden from the common one and refer to them as the "Yellowfin Shad." They claim that the edible qualities are superior to those of *tyrannus*, and the few they catch are generally put on their own table. I like the flavor of both species and could detect no difference except that the flesh of *smithi* may be a little less oily.

Methods of Fishing. The fish are caught chiefly in drag nets at Beaufort, the only place where they seem to be recognized as a distinct species.

Range. Known from Beaufort, North Carolina, to the "Indian River" (probably Indian River City), Florida, while specimens intermediate between *gunteri* and *smithi*, from Boca Ciega and from off Englewood on the west coast,[41] are nearer to *smithi* than to *gunteri*.

Synonyms and References:

Brevoortia aureus Hildebrand (not of Agassiz), Rep. U. S. Comm. Fish. (1918), Append. 6, 1919: 7, fig., pl. 1, fig. 2, scale (orig. descr. of *B. smithi* Hildebrand 1941; habits, food, cf. *B. tyrannus*; Beaufort, North Carolina).

Brevoortia smithi Hildebrand, Copeia, 1941: 224 (*B. aureus* Hildebrand recognized as a distinct species without a name; type local. Beaufort, N. C.; type USNM 118723); Hildebrand, Smithson. misc. Coll., *107* (18), 1948: 28, fig. 6 (synon., descr., relation., range).

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[41] Made available for examination through the kindness of Dr. William Gosline.

Brevoortia gunteri Hildebrand 1948

Finescale Menhaden

Figures 84, 85, 93

Study Material. A total of 55 specimens, 70–310 mm TL, 53–230 mm SL, from bays in the vicinity of Corpus Christi, Rockport, and Galveston, Texas, including several small ones from the mouth of the Rio Grande and from Brazos Santiago, part of Goode's type material of *patronus*, which included two species (*44*: 39); and from Grand Isle, Louisiana (one specimen); all in the USNM collections.

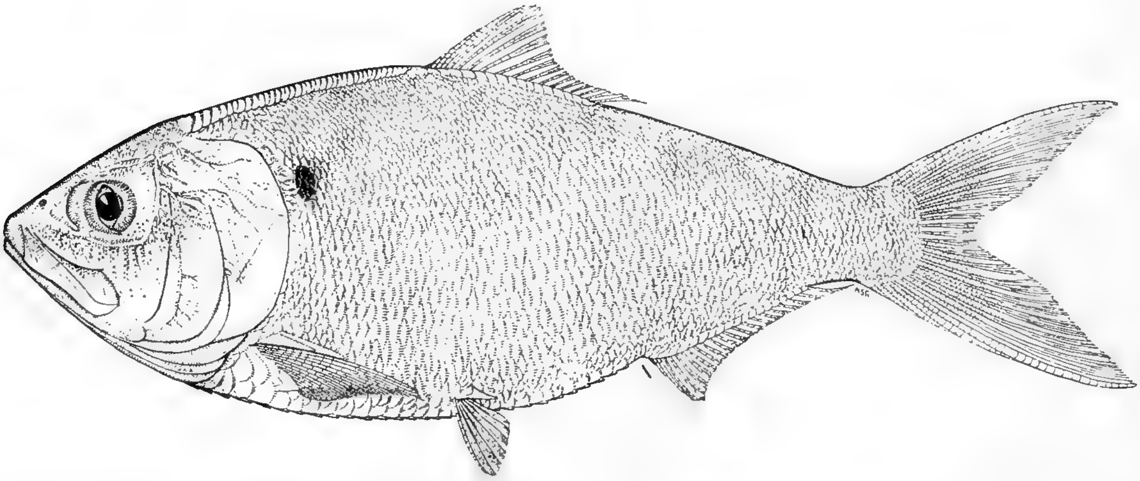

FIGURE 93. *Brevoortia gunteri*, 270 mm TL, 205 mm SL, Rockport, Texas, type, USNM 129798. Drawn by Ann S. Green.

Distinctive Characters. See *Relationship.*

Description. Proportional dimensions in per cent of standard length, and counts, based on the study specimens, 53–230 mm SL.

Body: depth 37–45, most frequently 38–41.
Caudal peduncle: depth, 9.5–12.5, most frequently 10–11.
Head: length 31–35.5, most frequently 32–34.
Snout: length 7.0–10.
Eye: diameter 6.6–9.5.
Interorbital: width 7.0–8.0.
Maxillary: length 14.5–17.5, most frequently 15.5–16.5.
Mandible: length 17.5–20.5, most frequently 18.5–19.
Anal fin: length of base 19–23, most frequently 20.5–22.5.
Pelvic fin: length 9.3–11.
Pectoral fin: length 19–23.5, most frequently 20–22.

Scales: oblique series along middle of side (too irregular to count accurately) about 60–75.

Modified scales: in a series in front of dorsal 35–45, most frequently 38–42.
Ventral scutes: 27–30, usually 28 or 29.
Fin rays: dorsal 17–20, most frequently 18 or 19; anal 20–25, most frequently 22–24; pectoral 15 or 16, rarely 14.
Vertebrae: 43 or 44, rarely 42 (22 specimens).

Body deep, strongly compressed, its greatest thickness only about a third of its depth, its greatest depth, at a vertical slightly in advance of origin of dorsal or the tip of pectoral, 2.2–2.7 in SL; ventral outline notably more convex than the dorsal one, much more than half of greatest depth below a straight line extending through lower margin of eye to middle of base of caudal. Caudal peduncle rather deep, 2.7–3.5 in head, and 3.6–4.0 in greatest depth of body.

Scales closely adherent, the exposed part 3–4 times deeper than long, the depth of scale itself about twice its length (Fig. 85 c); adults with prominent serrae ending in somewhat blunted points, not long or hair-like and not extending quite across the exposed part of the next scale; the scales much reduced in size on back and on base of caudal, in rather irregular series (difficult to count accurately); about 2–4 vertical rows of scales exposed between tip of pectoral and base of pelvic. A row of enlarged modified scales on each side of median line of back in front of dorsal fin, rather variable in number, 35–45 in each series. Ventral scutes weaker in large examples than in small ones, 17 or 18, usually 17, in front of pelvic fins, and 10–13, usually 11 or 12, behind them.

Head 2.7–3.2 in SL, its depth 2.75–3.4. Snout compressed, with a sharp median notch, its length 3.4–4.4 in head. Eye 3.6–4.8, most frequently 4.2–4.7. Interorbital 4.1–4.7. Cheek deeper than long. Maxillary broadly rounded, reaching to, or a little beyond, vertical from posterior margin of pupil, 1.9–2.2, usually 2.0–2.1, in head. Mandible included in upper jaw, its upper margin (within mouth) nearly straight, its length to joint 1.55–1.95 in head. Upper section of Opercle with very feeble radiating striae, or none. Gill rakers very numerous, those on upper limb extending downward and across those on upper part of lower limb, the longest ones somewhat exceeding length of snout; increasing in number with age and growth: 97 on lower limb of first arch in a specimen 70 mm TL, 113–120 in specimens 100–115 mm, and 135–150 in specimens 200–300 mm. Teeth absent in all specimens at hand.

Dorsal fin rather high anteriorly, its margin rather deeply concave, its longest rays about as long as snout and half of eye, the last ray considerably longer than the ones immediately before it, its origin generally about equidistant between the margin of snout and base of caudal; a very narrow sheath on its base, composed of a single row of scales. Caudal deeply forked, the middle rays about as long as eye, the lobes long, the lower one the longer, exceeding length of head, 2.55–3.1, usually 2.8–2.9, in SL. Anal fin much lower than dorsal, its margin somewhat concave, its longest rays about 0.33 as long as those of dorsal, its origin under, or a little in advance of, tip of last dorsal ray, its base 4.45–5.25 in SL; a narrow sheath of scales at base. PELVIC fin with a nearly straight oblique margin, its length 2.9–3.4 in head, its outermost ray somewhat less than twice the length of the innermost ray (Fig. 84 c), the fin inserted a little behind vertical from origin of dorsal. PECTORAL fin long, slightly falcate, its length 4.25–5.25 in SL, and 1.4–1.9 in head, its longest ray fully four times longer than the shortest one, the fin failing to reach the base of pelvic by a distance usually a little less than diameter of pupil. AXILLARY APPENDAGE of pectoral variable in length, apparently increasing in length with age, usually about half of length of fin in large examples and only about a third in small ones, 2.5–4.6 in head.

Color. Preserved specimens dark gray above a line extending through upper margin of eye to slightly above middle of base of caudal, changing rather abruptly to the silvery color of the side. A large black shoulder spot in adults, only faintly visible on those 110–125 mm long, absent in smaller ones, this spot not followed by smaller dark spots in any specimen at hand. Dorsal and caudal fins somewhat dusky, the margin of the caudal pale; other fins plain translucent. Gunter, when comparing fresh examples of this Menhaden with *patronus*, remarked: "The second species [*gunteri*] . . . was more silvery and had less green color" (*51*: 27). Peritoneum black.

Size. The specimens examined run larger in size than those of *patronus*; quite a few exceed a length of 230 mm (9.2 in.), and the largest has a length of 310 mm (12.4 in.). An example 313 mm (12.5 in.) long has been reported (*51*).

Development and Growth. The eggs of this species remain unknown, and very little has been learned about the development, for no specimens less than 50 mm SL are included in the collections examined. However, there is no reason to believe that *gunteri* and *patronus* differ essentially in their development. Judging from the smaller specimens at hand, the indications are that the young of this species, at an early age, reach a depth of body that is equally as great as that in large adults, as in the case of *patronus*. The increase in the number of gill rakers with age and growth is shown in the *Description*.

In somewhat more than four months, in 1942, from the time of their capture on February 25 until July, 0-class postlarvae 21–30 mm long (identified by Gunter as this species) grew to lengths of 25–45 mm (*51*). Gunter also spoke of a group 88–113 mm long that predominated in Aransas and Copano bays in November and December. Although he did not definitely assign these fish to the 0-class, he did conclude that "The curves indicate that this menhaden attained a length of 88 to 113 mm at the age of one year." This is about the same size as that indicated for *patronus* at a year of age.

Spawning. Gunter has reported that a 12.5-mm male taken in Aransas Bay on February 25, 1942, was exuding milt and that a ripe female 15.0 cm long was taken in Copano Bay on March 29, 1942 (*51*: 28). From Gunter's observations it appears that this species, like *patronus*, spawns during the winter, and possibly into early spring.

Migrations and Habitat. Nearly all that is known about the migrations and habitats of *B. gunteri* has been given by Gunter (*51*), the only student who seems to have recognized this species as distinct from *patronus*. He found *gunteri* to be much more common in Aransas and Copano bays than *patronus*, and he expressed the opinion that it probably is "completely euryhaline," though he did add that his data strongly suggest a midwinter exodus from Copano Bay but not from Aransas Bay. The fact that all specimens of *gunteri* in the U. S. National Museum collection were collected in inshore waters and that most of the *patronus* samples were taken offshore support Gunter's contention. However, there are some small to half-grown specimens of *patronus* in the collections that were taken inshore, where the water must have been decidedly brackish.

The habitats of *gunteri* and *patronus* in the Gulf therefore seem to parallel those of their close relatives in the Atlantic. However, *gunteri* has been reported as schooling by Gunter, and if correct, then *gunteri* apparently differs in that respect from *smithi*, which does not school while inhabiting the estuaries of Beaufort, North Carolina (p. 374).

Food. B. gunteri also is a plankton feeder, and "it may be seen in schools twisting and turning through the water, with mouth agape . . ." (*51*).

Relationship. This species differs from *patronus*, its relative in the Gulf, in having much smaller and more crowded scales, which are placed in less regular series and which in adults have notably shorter serrations (pectinations). It differs further in having much more feebly developed radiating striae, or none, on the upper part of the opercle and in the absence of dark spots behind the black shoulder spot. Gunter also said that it is not slimy when fresh, like *patronus*.

Its nearest relative is *smithi* of the Atlantic. Both of these species have deep, well-compressed bodies that are almost void of slime, small crowded scales, no dark spots on the anterior part of the body behind the black shoulder spot, and several other similar characters. But they differ in that the head is rather longer and deeper in *gunteri*, the body is more strongly compressed, the maxillary and mandible are somewhat longer, as is the pectoral fin, the ventral scutes are nearly always fewer, the scales are proportionately deeper, and the vertebrae, so far as known, are definitely fewer. But the presence on the coast of western Florida of Finescale Menhaden somewhat intermediate between *gunteri* and *smithi* emphasizes the desirability of a more detailed comparison of them than has been made as yet.

Variation. The specimens at hand vary considerably in depth, as shown in the *Description*; the smaller specimens in general are deeper than the larger ones. The variation in the number of anal rays is also rather great. The wide range shown for the number of oblique series of scales along the middle of the side may be ascribed in large part to the difficulty of counting them accurately. The great difference noted in the number of gill rakers on the lower limb of the first arch results largely from their increase in number with age. The color is quite uniform among the larger examples, but the smaller ones are lighter in color, and those less than about 115 mm TL lack the black shoulder spot.

Commercial Importance. No Menhaden plants are operated at present on the coast of Texas where this species seems to be common, and it is not known whether it is included among the menhaden processed in Mississippi. Neither is it known to what extent *gunteri* may have contributed to the reported Texas catches of 47,190,800 pounds of "menhaden" for 1950, 30,121,200 pounds for 1951, 52,983,600 pounds for 1952, and 589,300,000 pounds for 1953. Because of the extreme thinness of the fish, it probably would not yield much oil.

Range. Grand Isle, Louisiana, to the mouth of the Rio Grande, Texas.

Synonyms and References:

Brevoortia patronus Goode (in part *B. gunteri* Hildebrand), Proc. U. S. nat. Mus., *1*, 1879: 39 (diagn., tables based in part on *B. gunteri*).

Brevoortia sp. Gunter, Publ. Inst. mar. Sci. Texas, *1* (1), 1945: 27 (second species from Gulf, but not named; relation with other *Brevoortia* spp.; habitat, food, habits, spawn.).

Brevoortia gunteri Hildebrand, Smithson. misc. Coll., *107* (18), 1948: 31, fig. 7 (orig. descr.; type local. Aransas Bay, Texas; type USNM 129798).

Genus *Opisthonema* 1861

Opisthonema Gill, Proc. Acad. nat. Sci. Philad., 1861: 37; genotype by original designation, *O. thrissa* Gill equals *O. oglinum* (LeSueur).[42]

Characters. Body elongate, well compressed, its greatest depth exceeding length of head. Bony scutes with sharp points, about 32–36 on sharp edge of chest and abdomen. Cheek notably longer than deep. Vertical part of Clavicular margin (underneath opercle) with two small projections or lobes. Mouth of moderate size. Maxillary failing to reach middle of eye. Upper jaw without definite median notch. Lower jaw projecting beyond the upper. Teeth missing. Dorsal with about 17–21 rays, the last ray greatly produced, often reaching nearly to base of caudal. Anal with about 20–25 rays, the last one not greatly enlarged. Pelvic fin with 8 rays, inserted under base of dorsal fin, generally well behind origin of dorsal. Pectoral without an axillary process, lying in a slight depression. Vertebrae about 46–48.

Remarks. The chief distinguishing characters are the large dorsal fin, with nearly or equally as many rays as the anal and with the last ray greatly produced, frequently so that it reaches nearly or quite to the base of caudal; the projecting lower jaw with its abruptly ascending upper margin within the mouth; the long shallow cheek; the small pelvic, with 8 rays, inserted behind the origin of the dorsal; and the absence of a process (scale) in the axil of the pectoral.

Range. The genus is known on the Atlantic coast of America from Cape Cod, Massachusetts, to southern Brazil, and from the West Indies. On the Pacific coast it is known to range from the Gulf of California to Peru.

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[42] It is probable but not certain that Gill intended this generic name for the fish now known as *O. oglinum*. *Clupea thrissa* Linnaeus (*84*: 318) has been applied to both a Chinese and an American species, which many older authors considered identical; at the time Gill wrote (1861), they were generally so considered. In fact it was not until 1917 that they were properly separated. Regan (*106*: 308) cleared up the confusion, and Herre and Myers (*56*: 234) have diagnosed still more carefully the Chinese *Clupanodon thrissa*.—G. S. M.

Opisthonema oglinum (LeSueur) 1817

Atlantic Thread Herring, Hairyback, Shad Herring, Bristle Herring,
Sargo, Sargo de Gato, Sardinha Large, Sardinha Sargo

Figure 94

Study Material. A total of 65 or more specimens, 65–250 mm TL, 50–182 mm SL, from Massachusetts, Rhode Island, New Jersey, Virginia, North Carolina, Georgia, Florida (both coasts), and Texas; Atlantic coast of Panama; Colombia; at Recife, Barro Santos, and São Francisco, Brazil; Cuba; Puerto Rico; Jamaica; Haiti; Barbados; and Trinidad. Also several lots of juveniles from Beaufort, North Carolina; Key West, Florida; Mustang Island, Texas; Colón and Portobello, Panama.

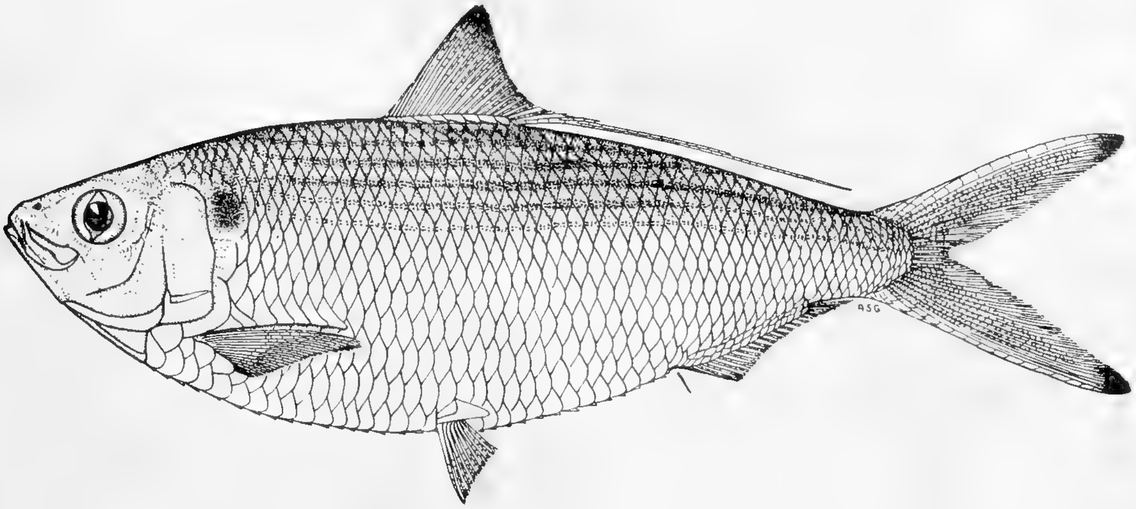

FIGURE 94. *Opisthonema oglinum,* 220 mm TL, 167 mm SL, Beaufort, North Carolina, USNM 51873. Drawn by Ann S. Green.

Distinctive Characters. See *Relationship.*

Description. Proportional dimensions in per cent of standard length, based on study specimens, 150–182 mm SL.

Body: depth 30–40.
Caudal peduncle: depth 8.5–11.
Head: length 22–28.
Snout: length 5.3–7.3.
Eye: diameter 6.0–8.5.
Interorbital: width 5.0–6.7.
Maxillary: length 8.8–12.
Anal fin: length of base 16.7–21.5.
Pelvic fin: length 8.5–11.5.
Pectoral fin: length 17–21.

Scales: 43–50.
Ventral scutes: 32–36.
Fin rays: dorsal 17–21, most frequently 19 or 20; anal 21–25, most frequently 22–24; pectoral 15–17.
Vertebrae: 45–48 (15 specimens).

BODY elongate, rather strongly compressed, its greatest thickness often only a third of the depth, its depth variable, generally greatest at origin of dorsal, 2.5–3.33 in SL; ventral outline strongly convex, the dorsal outline typically only gently convex, making the body when viewed from the side rather definitely boat-shaped. CAUDAL PEDUNCLE depth 2.3–2.8 in head.

SCALES only moderately adherent, thin, notably deeper than long, with somewhat irregular membranous edges; 3 or 4 vertical rows of scales exposed between tip of pectoral and base of pelvic. VENTRAL SCUTES moderately developed, 18 or 19, occasionally 17, in front of pelvic fins, and 14–16, occasionally 13 or 17, behind them.

HEAD small, 3.5–4.5. SNOUT blunt, without a definite median notch, 3.4–4.5. EYE moderately large, slightly longer than snout, 3.0–4.0. INTERORBITAL 3.8–5.7. CHEEK much longer than deep. MAXILLARY broadly rounded, reaching about to vertical from anterior margin of pupil, 2.15–2.75. MANDIBLE slightly projecting, its tip definitely lower than dorsal outline of head, its upper margin (within mouth) ascending abruptly, forming an obtuse angle. GILL RAKERS very numerous, close-set, those on upper limb not extending down and over those on the lower limb, the longest about 0.33 of diameter of eye; increasing in number with age and growth: about 40–50 on lower limb in specimens 40–60 mm TL and up to 100 or more in adults about 235 mm TL. TEETH not discernible.

DORSAL fin elevated anteriorly, the longest among the anterior rays generally exceeding length of snout and eye, the last ray filamentous, rather variable in length, most frequently reaching vertical from base of last ray of anal; origin of fin about half as far from posterior margin of eye as from base of caudal, the distance from margin of snout approximately 33 °/₀ of TL, or 2.3 in SL; a low sheath of scales on base of fin. CAUDAL deeply forked, its middle rays about as long as eye, its lobes long, the lower one 3.0–3.5 in SL. ANAL fin scarcely elevated anteriorly, its margin nearly straight, its last ray slightly enlarged, its origin only about a third as far behind vertical from last dorsal ray as from base of caudal, its base 1.1–1.6 in head; a low sheath of scales at base. PELVIC fin small, pointed when folded, with a nearly straight oblique margin when spread, its length 2.1–2.8 in head, its innermost ray about 66 °/₀ of length of the outermost one, the fin inserted a little in advance of vertical from middle of base of dorsal, its distance from origin of anal equal to distance from origin of anal to base of caudal. PECTORAL fin moderately long, its margin nearly straight, pointed, lying in a slight depression, its length from base of upper ray to tip of fin, 4.75–5.8 in SL, or 1.1–1.6 in head, its shortest rays only about half as long as the longest ones. AXILLARY PROCESS absent.

Color. Back bluish-green in life, the rest of body silvery. A dark shoulder spot usually present. Rows of scales on back with more or less definite dark lines. Fins chiefly translucent, the dorsal and caudal lobes generally with dark tips.

Size. A length of 300 mm (12 in.) has been reported. The size generally is much smaller, however, the usual length being only about 200–250 mm (8–10 in.).

Development and Growth. The eggs and larvae have not been described. The smallest specimens, about 22–25 mm long, rather certainly identified as this species, were taken at Key West, Florida, on August 25, 1919, but they are not in good condition, having been partly dried. Although they cannot be used for obtaining proportions, it is evident from these and others that the proportionate depth of the body in examples under 25 mm is much less than in those 100 mm and more. In fact, those up to 75 mm long generally are notably more slender than adults, though there is much individual variation at all sizes.

The chief distinctive marks in the smallest young at hand are the projecting lower jaw; the long shallow cheek; the shallow concavity in the margin of the opercle in front of the pectoral fin; the positions of the fins, which correspond to those of the adult; and the number of dorsal and anal rays, which already can be counted with a fair degree of accuracy. The last ray of the dorsal becomes prolonged much earlier in some individuals than in others; for example, it already is somewhat produced in a specimen 30 mm TL from Mustang Island, Texas, but in others up to 37 mm long from Beaufort there is no sign of prolongation. Ventral scutes can be accurately counted when the fish attain a length of about 30 mm, and even earlier in some examples. The gill rakers, as shown in the *Description*, increase in number with age and growth.

The color of the young is rather variable. The smallest ones have a silvery lateral band (dark in some lots of specimens, presumably due to preservative used) that increases in width with age and merges with the generally silvery color of the side in some specimens only 35–40 mm long; but it remains visible in others up to a length of 50 mm or so. In some young, as in some adults, the shoulder spot is absent whereas it is quite evident in others at a length of 35 mm. Occasionally there are smaller dark spots within the lateral band behind the shoulder spots; these may or may not disappear when the lateral band merges with the silvery color of the side. The black peritoneum is often visible through the body wall in the young.

Little is known about the rate of growth. A few measurements made at Beaufort indicate that the fish attain a length of about 35–60 mm at the age of one year and 90–120 mm by the end of their second summer. Sexual maturity, at least in some individuals, is reached at a length of only 150 mm.

Spawning. At Beaufort, North Carolina, spawning takes place during May and June, as determined from the gonads of adult fish.

Migrations and Habitat. These Thread Herring often school, but solitary examples were frequently taken at Beaufort, North Carolina, and on the Atlantic coast of Panama. They hold more closely to salt water than menhaden and some other Clupeidae and are not known to migrate inshore to spawn. They are essentially tropical and subtropical fish, and although they stray northward to Cape Cod, they generally are not numerous north of North Carolina. In North Carolina, where they usually are abundant during the summer, they are taken from May through September.

Food. These fish, like most of their relatives, feed largely on small organisms, which they strain from the water with the numerous close-set gill rakers. Copepods constituted the chief food of specimens from Chesapeake Bay (59: 101). However, small fish, crabs, and shrimp were also found in the stomachs of fish from Port-au-Prince, Haiti (*10*: 42).

The stomach does not have a thick wall, as in the menhaden (p. 355) and the gizzard shad (p. 443). Neither is the intestine especially long, being only about 1.33 °/₀ of TL of adult fish. Possibly to compensate for the relatively short alimentary canal, the stomach is provided with about 100 pyloric coeca.

Enemies. No doubt they are preyed upon by many predatory fishes, such as the bluefish, Spanish mackerel, weakfish, and many others. Pelicans also feed on them, especially when the fish school at the surface.

Relationship and Variation. This species is the only one of the genus recognized from the Atlantic. However, it has a near relative on the Pacific coast of tropical America, from which typical specimens of *oglinum*[43] differ in having a deeper body with a more strongly convex ventral outline, longer fins, and no small dark spots behind the shoulder spot.

In addition to these differences, there are the variations with age. The body becomes deeper as growth proceeds, especially up to a length of 100 mm or so, and the gill rakers apparently increase in number as long as the fish grow. Insufficient specimens have been studied critically to determine geographical variations. It would seem probable from the limited data based on specimens of about equal size that those from South America and the West Indies generally are rather deeper than those from the Atlantic coast of the United States and have on an average one more ventral scute.

Commercial Importance. The flesh has been reported as being dry, bony, and of inferior flavor. At Beaufort they are seldom used as food, and during a residence there for ten summers I saw none in the market. However, they appear rather regularly in the markets in Colón, Panama, and in the West Indies. At Beaufort and perhaps elsewhere on the shores of the southern states, they are sometimes taken with purse seines by the crews of menhaden boats and delivered to the menhaden reduction plants. However, the amount of oil yielded is very small. Such catches do not reach the statistical reports, presumably because they are not separated from menhaden.

Range. Middle Atlantic States, sometimes straying northward to Cape Cod; southward to southern Brazil (São Francisco); common throughout the West Indies.

Synonyms and References:

Megalops oglina LeSueur, J. Acad. nat. Sci. Philad., *1*, 1817: 359 (orig. descr.; type local. Newport, Rhode Island).

Megalops notata LeSueur, J. Acad. nat. Sci. Philad., *1*, 1817: 361 (orig. descr.; type local. Guadeloupe, West Indies; said to have longer dorsal than *oglina*, also a shorter produced dorsal ray and different color, etc.).

Chatoessus signifer DeKay, N. Y. Fauna, Pt. 4, Fishes, 1842: 264, pl. 41, fig. 132 (orig. descr.; type local. New York; type in State Coll.; cf. *C. thrissa* Bloch and *M. oglina* LeSueur).

Meletta thrissa Cuvier and Valenciennes (not *Clupea thrissa* Linnaeus 1758), Hist. Nat. Poiss., *20*, 1847: 380 (orig. descr.; type locals. New York, Santo Domingo, Guadeloupe, and Martinique).

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[43] It is entirely possible that a more critical study than time now permits would reveal the existence of more than one species on the Atlantic coast of the Americas. Specimens from Bermuda, and some from the Atlantic coast of Panama, were not used in preparing the *Description* because it was suspected that they may prove to be separate and distinct.

Alausa striata Cuvier and Valenciennes, Hist. Nat. Poiss., *20*, 1847: 429 (orig. descr.; type local. Guadeloupe).

Chatoessus eumorphus Gosse, Naturalist's Sojourn in Jamaica, 1851: 290 (orig. descr.; type local. Jamaica).

Opisthonema thrissa Poey (not *Clupea thrissa* Linnaeus 1758), Repert. Fisico-Nat. Cuba, 1868: 419 (refs., diagn., etc.); Enumerat. Pisc. Cubens., 1875: 148 (refs., distr.); Uhler and Lugger *in* Rep. Comm. Fish. Md., ed. 1, 1876: 158; ed. 2, 1876: 134 (descr., synon., Maryland); Metzelaar, Rapp. Vissch. Curaçao, ed. by Boeke, 1, West Indian Fishes, 1919: 12 (when caught, import. as foodfish, local name, range, Curaçao and St. Eustatius).

Clupea thrissa Günther (not of Linnaeus), Cat. Fish. Brit. Mus., *7*, 1868: 482 (synon., descr., range).

Opisthonema oglinum Henshall, Bull. U. S. Fish Comm. (1889), *9*, 1891: 373 (common, w. coast of Florida; Big Gasparilla and Egmont Key); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 101 (descr., size, range); Jordan and Rutter, Proc. Acad. nat. Sci. Philad., 1897: 94 (refs., Kingston, Jamaica); Evermann and Bean, Rep. U. S. Comm. Fish. (1896), 1898: 241 (in nest of pelican, counts, Indian R., Florida); Smith, Bull. U. S. Fish Comm. (1897), 17, 1898: 91 (Woods Hole, Massachusetts); Evermann and Kendall, Rep. U. S. Comm. Fish. (1899), 1900: 56 (Florida); Evermann and Marsh, Bull. U. S. Fish Comm. (1900), *20* (1), 1902: 86 (descr., range, synon., Puerto Rico); Schreiner and Miranda-Ribeiro, Arch. Mus. nac., Rio de J., *12*, 1903: 92 (Brazilian recs., notes); Bean, T. H., Bull. N. Y. St. Mus., 60, Zool. 9, 1903: 209 (synon., descr., range, local occur.); Barbour, Bull. Mus. comp. Zool. Harv., *46*, 1905: 112 (distr., Bermuda); Fowler, Rep. N. J. St. Mus. (1905), 1906: 102 (descr., refs., New Jersey); Rep. N. J. St. Mus. (1906), 1907: 266, fig.; Smith, N. C. geol. econ. Surv., *2*, 1907: 129 (refs., diagn., size, food value, range, Beaufort, North Carolina); Kendall, Occ. Pap. Boston Soc. nat. Hist., 1908: 40 (refs., New England); Sumner, Osburn, and Cole, Bull. U. S. Bur. Fish. (1911), *31* (2), 1913: 742 (Woods Hole, Massachusetts); Starks, Stanf. Univ. Publ., Univ. Ser., 1913: 8 (var. in depth, Natal, Brazil); Regan, Ann. Mag. nat. Hist., (8) *19*, 1917: 385 (synon., descr., range); Meek and Hildebrand, Field Mus. Publ., Zool., *15* (1), 1923: 187 (synon., descr., range, Atlantic, Panama); Nichols and Breder, Zoologica, N. Y., *9* (1), 1926: 41, fig. (New York and s. New England); Hildebrand and Schroeder, Bull. U. S. Bur. Fish. (1927), *43* (1), 1928: 101 (refs., descr., food, range, Chesapeake Bay); Beebe and Tee-Van, Zoologica, N. Y., *10* (1), 1928: 42, fig. (refs., descr., size, range, food, Port-au-Prince, Haiti); Jordan, Manual Vert. Anim. NE U. S., ed. 13, 1929: 41 (diagn., range); Truitt, Bean, and Fowler, Bull. Md. Conserv. Dep., 3, 1929: 51 (descr., Maryland); Breder, Field Bk. Mar. Fish. Atl. Cst., 1929: 68, fig. (distr., food, size); Nichols, N. Y. Acad. Sci., *10* (2), 1929: 203, fig. (distr., esp. West Indies and Puerto Rico, diagn.); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 44 (range, synon.); von Ihering, Rev. Indust. Anim., 1 (3), 1930: 230 (counts, discus., Brazil); Howell-Rivero, Handbk. Jamaica, 1936: 1, in reprint (small specimens, color, size); Hollister, Zoologica, N. Y., *21* (23), 1936: 284, fig. 49 (caudal skel., Bermuda); Bigelow and Schroeder, Bull. U. S. Bur. Fish., *48*, 1936: 327 (Monomoy Pt., Cape Cod, Massachusetts); von Ihering, Dict. Anim. Brazil, 1940: 716 (note, common names); Fowler, Arqu. Zool. estad. São Paulo, *3* (6), 1941: 134 (refs., Brazil); Bertin, Bull. Soc. Zool. Fr., *66*, 1941: 24 (*Alausa striata* C. and V. design. a synon.); Oliveira, Serv. Agr. Dep. nac. Producao Animal, Caca e Pesca, Rio de J., 1942: 24 (descr.); Gunter, Publ. Inst. mar. Sci. Texas, *1* (1), 1945: 25 (Texas).

Genus *Harengula* Cuvier and Valenciennes 1847[44]

Sardines

By

Luis René Rivas

Harengula Cuvier and Valenciennes, Hist. Nat. Poiss., *20*, 1847: 277; type species, *H. latulus* Cuvier and Valenciennes (not *Clupea latulus* Cuvier 1829) equals *Clupea clupeola* Cuvier 1829.

Characters. VENTRAL SCUTES 25–32, usually 26–31. SCALES 38–44, usually 39–43. Vertical anterior edge of shoulder girdle (CLAVICULAR MARGIN) with a bilobed dermal fold. UPPER JAW without distinct median notch. GILL RAKERS on epibranchial of first arch not folding downwards over those on the ceratobranchial; 26–40, usually 27–39, on lower limb of first arch. Last ray of DORSAL fin not produced into a long filament. FIN RAYS: dorsal 17–20, usually 17 or 18; anal 15–19, 17–19 in western Atlantic species, usually 16–18; pelvic 7–9, usually 8; pectoral 13–17, usually 15 or 16. VERTEBRAE 40–44.

Size. The maximum size is about 170 mm.

Range. Western North Atlantic in coastal waters of Bermuda, and from Florida southward to Brazil. Pacific coast from the Gulf of California southward to Peru.

Habits. Sardines are plankton feeders, and occur close to the coast, especially in estuaries, where they usually congregate in compact schools near the surface. Certain species ascend streams for short distances, but not beyond brackish water.

Abundance and Relation to Man. Sardines are most abundant in bays and estuaries where they may be captured with beach seines and cast nets. They are used for bait and food throughout the West Indies and are utilized in the canning industries of Cuba and Venezuela.

Key to Species

1a. Inner edge of palatines with a row of pointed teeth anteriorly; gill rakers 26–32, usually 27–31, on lower limb of first arch; ventral scutes 25–29, usually 27 or 28; scales not adherent, easily falling off from either fresh or preserved specimens; snout 2.5–3.4, usually 2.6–3.3, in distance between origins of pelvic and anal fins; humeral spot absent. Average length 80–140 mm.

humeralis Cuvier 1829, p. 387.

1b. Inner edge of palatines without a row of pointed teeth anteriorly; gill rakers

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[44] Contribution No. 44 from the Ichthyological Laboratory and Museum, Department of Zoology, University of Miami.

28–40, usually 30–39, on lower limb of first arch; ventral scutes 28–32, usually 29–31; scales adherent, not falling off from either fresh or preserved specimens; snout 3.4–4.3, usually 3.5–4.2, in distance between origins of pelvic and anal fins; humeral spot present, sometimes faint. Average length 40–90 mm.

2a. Scales in 42–44, usually 43, transverse rows, and 12 or 13, usually 12, longitudinal rows; predorsal scales 15–19, usually 16–18.
thrissina Jordan and Gilbert 1882.
Pacific coast of México from the Gulf of California to Acapulco.

2b. Scales in 38–42, usually 39–41, transverse rows, and 11 longitudinal rows; predorsal scales 11–14, usually 12 or 13.

3a. Anal with 15–17, usually 16, rays, its base usually slightly shorter than pelvic fin; tip of dorsal fin blackish. *peruana* Fowler and Bean 1923.
Pacific coast from Panama to Peru.

3b. Anal with 17–19, usually 18, rays, its base usually slightly longer than pelvic fin; tip of dorsal fin not blackish.

4a. Gill rakers 28–34, usually 30–32, on lower limb of first arch.
clupeola Cuvier 1829, p. 390.

4b. Gill rakers 30–40, usually 32–39, on lower limb of first arch.
pensacolae Goode and Bean 1879, p. 393.

Harengula humeralis (Cuvier) 1829

Red-ear Sardine, Sardina, Sardina de Ley, Sardine, Loosescale Sardine, Pilchard, Red-ear Pilchard, Sprat, Whitebill, Pincer

Figure 95

Study Material. Numerous specimens, 44–172 mm SL, from Florida, Bermuda, West Indies, and the Caribbean coast of Central America, USNM, MCZ, and UMIM.

Distinctive Characters. The presence of pointed anterior palatine teeth, the reduced number of gill rakers (26–32) and ventral scutes (25–29), and the nonadherent loose scales distinguish this species from all the others of this genus.

Description. Proportional dimensions in per cent of standard length, and counts, based on 577 specimens, 44–172 mm SL.

Body: greatest depth 26.0–30.7; greatest width 13.5–16.0.
Caudal peduncle: least depth 9.5–11.2.
Head: length 27.1–32.8; depth at occiput 22.4–25.9.
Snout: length 7.7–9.2.
Eye: diameter 8.7–11.3.
Interorbital: width 5.5–6.6.
Maxillary: length 12.4–15.3.
Dorsal fin: anterior height 18.5–23.2; length 22.2–26.0; length of base 16.6–19.0.

Anal fin: anterior height 5.6–9.9; length 18.8–21.3; length of base 14.8–16.9.

Pelvic fin: length 11.0–14.4.

Pectoral fin: length 18.2–22.1.

Distance from tip of snout to origin of: dorsal fin 43.8–46.3; anal fin 76.2–78.4; pelvic fin 51.6–55.5; pectoral fin 26.2–30.5.

Scales: transverse rows 38–42; predorsal 9–11.

Ventral scutes: 25–29, usually 27 or 28.

Gill rakers: 26–32, usually 27–31, on lower limb of first arch.

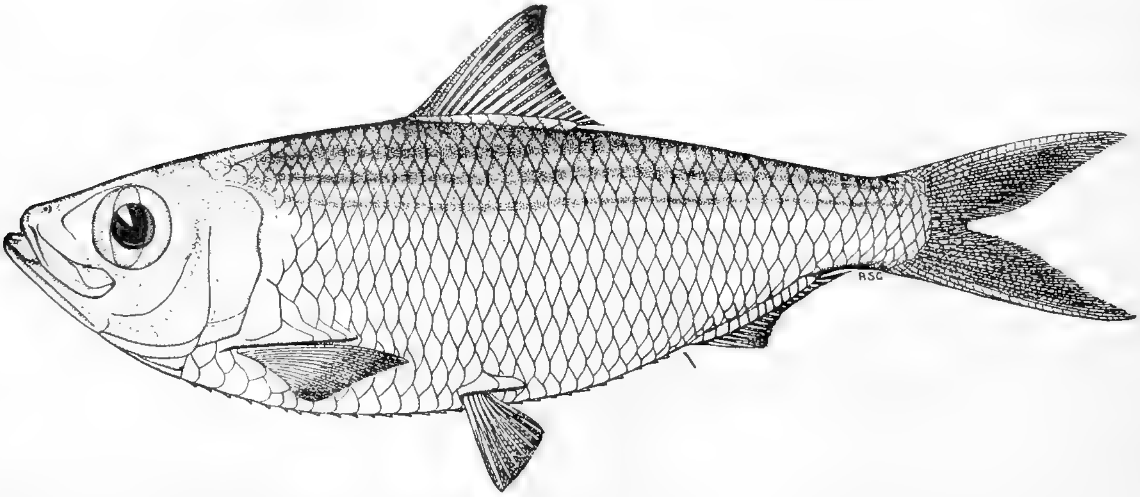

FIGURE 95. *Harengula humeralis*, gravid female, 210 mm TL, 158 mm SL, Tortugas, Florida, USNM 116873. Drawn by Ann S. Green.

PREDORSAL CONTOUR evenly and moderately convex, the POSTDORSAL CONTOUR more or less straight from origin of dorsal fin to caudal fin; VENTRAL CONTOUR much more convex than the dorsal, the body axis much closer to dorsal than to pelvic fins. DORSAL fin originating nearer to tip of snout than to caudal base. PELVIC fin inserted about midway between insertion of pectoral and origin of anal. PECTORAL fin inserted about midway between tip of snout and insertion of pelvic, or (usually) nearer pelvic.

Color. General coloration silvery, especially on lower half of head and body; the opercular plates with iridescent or pearlish, metallic reflections. Back brownish gray. Sides of body with longitudinal streaks. Humeral spot absent. Tip of snout and mandible dusky. Upper sector of iris dusky. Tip of dorsal fin dusky; pectoral, pelvic, and anal fins colorless; tip of caudal lobes dusky, the pigmentation extending along their inner margins.

Size. This is the largest species of the genus. The largest examined measures 172 mm SL.

Range. Florida Keys, Bahamas, West Indies, and Caribbean coast of Central and South America, from Yucatán to Venezuela; also Bermuda.

Synonyms and References:

Clupea humeralis (not *Harengula humeralis* Cuvier and Valenciennes 1847) Cuvier, Règne Anim., ed. 2, *2*, 1829: 318, ftn. (name only, applied to Duhamel's fig. 4 of "Sardine des Antilles," 1776); Jordan, Proc. U. S. nat. Mus., *9*, 1887: 561 (synon. in part, West Indies).

Harengula maculosa Cuvier and Valenciennes, Hist. Nat. Poiss., *20*, 1847: 292 (orig. descr., life colors, Martinique); Regan, Ann. Mag. nat. Hist., (8) *19*, 1917: 387 (synon., descr., range, Bermuda; Florida; West Indies); Jordan, Copeia, 1918: 46 (validity); Fowler, Proc. Acad. nat. Sci. Philad., *82*, 1930: 269 (Grenada); Proc. biol. Soc. Wash., *43*, 1930: 145 (size, Bermuda); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, App. 10, 1930: 43 (part. synon., West Indies); Storey, Stanf. Ichthyol. Bull., *1* (1), 1938: 41 (nomencl.); Longley and Hildebrand, Publ. Carneg. Instn. Wash., 535, 1941: 8, 9 (char. in key, synon., remarks, life colors, char., range, Tortugas, Florida).

Alosa apicalis Müller and Troschel *in* Schomburgk's Hist. Barbados, Fishes, 1848: 675 (orig. descr., Barbados); Hill, Handbook of Jamaica, 1881: 125 (comments, Jamaica); Storey, Stanf. Ichthyol. Bull., *1* (1), 1938: 41 (nomencl., orig. descr. quoted).

Harengula sardina Poey, Memorias, Cuba, *2* (49), 1860: 310 (orig. descr., Cuba); *2* (50), 1861: 384 (Cienfuegos, Cuba); Repert. Fisico.-Nat. Cuba, *2*, 1866: 16; 1868: 418 (spec. poison., char., compar., Cuba); An. Soc. esp. Hist. Nat., *5*, 1876: 147 (ref., compar.); Jordan and Bollman, Proc. U. S. nat. Mus., *11*, 1889: 550 (Green Turtle Cay, Bahamas); Jordan, Proc. U. S. nat. Mus., *12*, 1890: 645 (comments); Bean, Bull. U. S. Fish Comm., *8*, 1890: 206 (length, Cozumel, Yucatán); Jordan and Thompson, Bull. U. S. Bur. Fish., *24*, 1905: 233 (Tortugas, Florida); Fowler, Proc. Acad. nat. Sci. Philad., *58*, 1906: 83, fig. 2 (Hailer's Rock, Florida); Fowler, Proc. U. S. nat. Mus., *78*, 1926: 250 (scales, color, Boca Grande, Florida); Nichols, N. Y. Acad. Sci., *10* (2), 1929: 202 (part. synon., type local., distr., diagn., Puerto Rico); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, App. 10, 1930: 43 (synon. in part, range); Longley, Carneg. Instn. Yearbk., 31, 1932: 299 (synon., Tortugas, Florida); Beebe and Tee-Van, Field Bk. Shore Fish. Bermuda, 1933: 35, fig. (field char., part. diagn., part. distr., Bermuda); Storey, Stanf. Ichthyol. Bull., *1* (1), 1938: 41 (nomencl.); Howell-Rivero, Bull. Mus. comp. Zool. Harv., *82* (3), 1938: 171 (part. synon., type material, holotype design., Cuba); Butsch, J. Barbados Mus. Hist. Soc., 7 (1), 1939: 18 (Barbados).

Harengula jaguana Poey, Repert. Fisico-Nat. Cuba, *1*, 1865: 189 (comments, orig. descr., Bahia de Jagua, Cienfuegos, Cuba); *2*, 1868: 418 (char., compar., Cuba); An. Soc. esp. Hist. Nat., *5*, 1876: 147 (refs., type local., char., Bahia de Jagua, Cuba); Jordan, Proc. U. S. nat. Mus., *9*, 1886: 33 (compar.); Storey, Stanf. Ichthyol. Bull., *1* (1), 1938: 41 (nomencl.).

Clupea macrophthalma (not of Ranzani, 1842), Günther, Cat. Fish. Brit. Mus., *7*, 1868: 421 (synon. in part, descr., range, West Indies).

Clupea apicalis Günther, Cat. Fish. Brit. Mus., 7, 1868: 441 (descr., Barbados); Jordan, Proc. U. S. nat. Mus., *9*, 1887: 561 (ref., West Indies); Cockerell, Inst. Jamaica Bull., 1, 1892: 15 (descr., Jamaica).

Harengula macrophthalma (not *Clupea macrophthalma* Ranzani 1842), Goode, Bull. U. S. nat. Mus., 5, 1876: 10, 13, 69 (use as bait, synon. exclud., range in part, abund., length, Bermuda and West Indies); Prov. Cat. Fish. Bermuda, 1877: 6 (Bermuda); Barbour, Bull. Mus. comp. Zool. Harv., *46* (7), 1905: 112 (distr. exclud., fin rays, scales, capture, abund., Bermuda).

Harengula callolepis Goode *in* Goode and Bean, Proc. U. S. nat. Mus., *2*, 1879: 152 (orig. descr., compar., Bermuda); Storey, Stanf. Ichthyol. Bull., *1* (1), 1938: 4, 41 (nomencl.); Rivas, Proc. U. S. nat. Mus., *100* (3263), 1950: 279, 285, 286, fig. 38 (char. in key, synon., comments, compar., Bermuda).

Clupea sardina Jordan, Proc. U. S. nat. Mus., *7*, 1884: 106 (abund., habitat, compar., descr., Key West); Jordan and Swain, Proc. U. S. nat. Mus., *7*, 1884: 230 (relation., scales); Jordan, Proc. U. S. nat. Mus., *9*, 1886: 33 (comments, Havana, Cuba); Rep. U. S. Comm. Fish., App. 2, E (24), 1887: 36, ftn. (descr., range, compar., synon. in part); Proc. U. S. nat. Mus., *9*, 1887: 561 (West Indies).

Clupea callolepis Jordan, Proc. U. S. nat. Mus., *9*, 1887: 561 (Bermuda).

Clupea sp. Lee, Rep. U. S. Comm. Fish. (1886), 1889: 672 (Nassau, Bahamas).

Harengula clupeola (not *Clupea clupeola* Cuvier 1829), Jordan, Proc. U. S. nat. Mus., *12*, 1890: 646, 647 (char. in key; Key West; and Havana, Cuba, synon. in part, St. Lucia, West Indies).

Sardinella apicalis Jordan and Evermann, Bull. U. S. nat. Mus., *47* (1), 1896: 428, 429 (char. in key, descr., part. synon., Barbados); Rep. U. S. Comm. Fish. (1895), 1896: 282 (range).

Sardinella sardina Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 428, 430 (char. in key, descr., range, synon.); Rep. U. S. Comm. Fish. (1895), 1896: 282 (range); B. A. Bean, Bahama Islands, Fishes, ed. Shattuck, 1905: 297 (range, abund., Nassau, Bahamas); Barbour and Cole, Bull. Mus. comp. Zool. Harv., *50* (5), 1906: 156 (Progreso, Yucatán); Fowler, Proc. Acad. nat. Sci. Philad., *63*, 1911: 206 (Hailer's Rock, Florida); Rosen, Acta Univ. Lund., N. S. *7* (2), 1911: 48 (Nassau and Green Turtle Cay, Bahamas); Nichols, Bull. Amer. Mus. nat. Hist., *31* (18), 1912: 182 (market, Havana, Cuba); Bull. Amer. Mus. nat. Hist., *34* (7), 1915: 141 (San Juan Harbor, Puerto Rico); Bull. Amer. Mus. nat. Hist., *44* (3), 1921: 22 (Turks I., Bahamas); Metzelaar, Trop. Atlant. Vissch., 1, 1919: 11, fig. 3 (part. synon., size, habitat, Fuikbay, Curaçao, Aruba); Meek and Hildebrand, Field Mus. Publ., Zool., *15* (1), 1923: 183 (synon. in part, descr., range, Atlantic Panama); Beebe and Tee-Van, Zoologica, N. Y., *10* (1), 1928: 40, fig. (ref., char., size, weight, color, range, distr., abund., capture, food, young, Port-au-Prince Bay, Haiti); Breder, Field Bk. Mar. Fish. Atl. Cst., 1929, 1948: 68 (range, feed. habits, size, Florida); Parr, Bull. Bingham oceanogr. Coll., *3* (4), 1930: 2 (Bahama locals.).

Sardinella humeralis (not *Harengula humeralis* Cuvier and Valenciennes 1847), Evermann and Goldsborough, Bull. U. S. Fish Comm. (1901), 1902: 149 (descr., comments, Puerto Morelos, Yucatán); T. H. Bean, Field Mus. Publ., Zool., 7 (2), 1906: 34 (Bermuda).

Sardinella macrophthalma (not *Clupea macrophthalma* Ranzani 1842), Evermann and Marsh, Bull. U. S. Fish Comm., 1, 1902: 85 (descr., comments, range, synon. in part, Puerto Rico locals.); Breder, Bull. Bingham oceanogr. Coll., *1* (1), 1927: 12 (Royal I., Bahamas; Point Francis, Isle of Pines; Glover Reef, Brit. Honduras).

Sardinella macrophthalmus (not *Clupea macrophthalma* Ranzani 1842), T. H. Bean, Field Mus. Publ., Zool, 7 (2), 1906: 34 (Bermuda).

Sardinella maculosa von Ihering, Rev. Industr. Anim. São Paulo, 3, 1930: 228 (ref., diagn., comments, Brazil).

Harengula sp. Hollister, Zoologica, N. Y., *21* (4), 1936: 282–284 (caudal skel., Bermuda).

Harengula macropthalma (not *Clupea macrophthalma* Ranzani 1842) Fowler, Proc. Acad. nat. Sci. Philad., *89*, 1937: 309 (Haiti).

Harengula humeralis Storey, Stanf. Ichthyol. Bull., *1* (1), 1938: 13, 15, 21, 23, 24, 28, 39, 50 (char., relation., range, key, synon., descr., diagn.; St. Lucia; Glover Reef; Jamaica; Cuba; Florida Keys; Bahamas; nomencl., orig. descr. quoted); Fowler, Fish Culturist, *21* (9), 1942: 66 (use, size, compar., Cojimar, Cuba); Fish Culturist, 22 (2), 1942: 9 (size, length vent. fin, Bonacca I., Honduras); Monogr. Acad. nat. Sci. Philad., 6, 1944: 70, 93, fig. 27, 434, 456 (synon., ref., descr., compar., Serranilla Bank; w. Caribbean); Rivas, Proc. U. S. nat. Mus., *100* (3263), 1950: 279, 282 (char. in key, synon., comment, compar., range).

Harengula clupeola (Cuvier) 1829

False Pilchard, Sardina Escamuda, Sprat, Petit Cailleu

Figure 96

Study Material. Numerous specimens, 43–149 mm SL, from Florida, the West Indies and the Caribbean coast of Central and South America, USNM, BOC, and UMIM.

Distinctive Characters. The absence of pointed anterior palatine teeth, the small number of gill rakers (28–35), higher ventral scute count (29–32), adherent scales, and slender body distinguish this species from all the other western Atlantic forms.

Description. Proportional dimensions in per cent of standard length, and counts, based on 252 specimens, 43–149 mm SL.

Body: greatest depth 29.5–32.0; greatest width 13.7–15.1.
Caudal peduncle: least depth 10.5–11.2.
Head: length 29.0–32.4; depth at occiput 25.9–27.8.
Snout: length 8.0–9.2.

Eye: diameter 9.1–11.5.
Interorbital: width 5.9–6.5.
Maxillary: length 13.6–15.2.
Dorsal fin: anterior height 18.8–20.8; length 21.2–25.2; length of base 16.3–17.1.
Anal fin: anterior height 5.9–8.2; length 17.5–21.1; length of base 14.2–19.7.
Pelvic fin: length 13.0–15.8.
Pectoral fin: length 21.5–22.9.
Distance from tip of snout to origin of: dorsal fin 44.3–47.5; anal fin 77.4–80.4; pelvic fin 52.8–56.2; pectoral fin 28.1–30.8.

Scales: transverse rows 40–43; predorsal 11–14.
Ventral scutes: 29–32, usually 30 or 31.
Gill rakers: 28–35, usually 30–32, on lower limb of first arch.

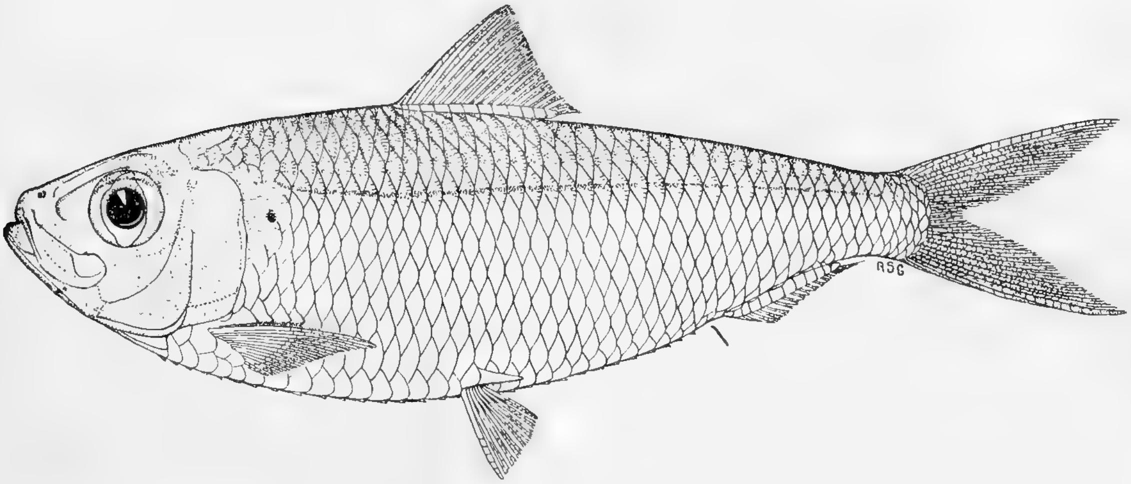

Figure 96. *Harengula clupeola*, gravid female, 180 mm TL, 138 mm SL, Tortugas, Florida, USNM 116872. Drawn by Ann S. Green.

Predorsal contour evenly and moderately convex, the Postdorsal contour more or less straight from origin of dorsal to caudal fin; Ventral contour much more convex than dorsal contour, the body axis closer to dorsal than to pelvic fins. Dorsal fin originating nearer to tip of snout than to caudal base. Pelvic fin inserted nearer to insertion of pectoral than to origin of anal. Pectoral fin inserted closer to insertion of pelvic than tip of snout.

Color. General coloration silvery, especially on the lower half of the head and body; the opercular plates with iridescent or pearlish, metallic reflections. Back dark brownish or bluish gray. Body with dark, longitudinal streaks more conspicuous on back. Humeral spot faint. Tip of snout and mandible dusky. Upper sector of iris dusky. Fins colorless except caudal, which is somewhat pigmented at tip of lobes and along inner margin.

Size. This is the smallest species of the western North Atlantic, seldom reaching a length of more than 100 mm.

Range and Subspecies. H. clupeola is the most widely distributed species and has almost the same range as *Harengula humeralis.* It is known from the Florida Keys, Bahamas, West Indies, and Caribbean coast of Central and South America, from Yucatán to Brazil. The species does not show variation throughout its range whereby it can be broken up into geographical subspecies.

Synonyms and References:

Clupea clupeola Cuvier, Règne Anim., ed. 2, *2*, 1829: 318, ftn. (name only, applied to Duhamel's fig. 2 of "Petit cailleu," 1776); Règne Anim., Disciples ed., 1843: 274, ftn. (on "Petit cailleu" of Duhamel, 1776); Jordan, Proc. U. S. nat. Mus., *7*, 1884: 107 (compar., char.); Rep. U. S. Comm. Fish. (1885), App. 2, E (24), 1887: 33 (compar., Havana, Cuba); Proc. U. S. nat. Mus., *9*, 1887: 561 (part. synon., West Indies); Storey, Stanf. Ichthyol. Bull., *1* (1), 1938: 42 (comments).

Clupea macrophthalma Ranzani, Novi Comm. Acad. Inst. Bonon., *5*, 1842: 320, pl. 23, figs. 1–4 (orig. descr., Brazil); Cope, Trans. Amer. philos. Soc., *14* (3), 1871: 483 (New Providence, Bahamas); Jordan, Proc. U.S. nat. Mus., *9*, 1887: 561 (synon. and ref. exclud., West Indies); Cockerell, Inst. Jamaica Bull., 1, 1892: 15 (teeth, color, Jamaica); Storey, Stanf. Ichthyol. Bull., *1* (1), 1938: 44, fig. 15 (char., compar., holotype).

Harengula latulus (not *Clupea latulus* Cuvier 1829), Cuvier and Valenciennes, Hist. Nat. Poiss., *20*, 1847: 280, pl. 595 (orig. descr., Caen; Dieppe); Storey, Stanf. Ichthyol. Bull., *1* (1), 1938: 3, 36, fig. 15 (comments, nomencl., type local. doubtful, on cotype, cf. *H. clupeola*).

Harengula clupeola Cuvier and Valenciennes, Hist. Nat. Poiss., *20*, 1847: 289 (descr., Martinique); Gosse, Naturalist's Sojourn in Jamaica, 1851: 210, 289 (used as bait, enemies, behav., Jamaica); Guichenot *in* Sagra, Hist. fisica. polit. nat. Cuba, *4* (2), 1853: 230 (diagn., comments, Cuba); Poey, Memorias, Cuba, *2* (49), 1860: 310 (cf. *H. sardina*); Memorias, Cuba, *2* (50), 1861: 384, 395 (compar., doubtful in Cuba); Repert. Fisico-Nat. Cuba, *1*, 1866: 378 (ref., range, Cuba); An. Soc. esp. Hist. Nat., *5*, 1876: 147 (ref., comment, range, Cuba); Hill, Handbook of Jamaica, 1881: 126 (Jamaica); Jordan and Bollman, Proc. U. S. nat. Mus., *11*, 1889: 550 (Green Turtle Cay, Bahamas); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, App. 10, 1930:43 (range, ref., West Indies); Storey, Stanf. Ichthyol. Bull., *1* (1), 1938: 3, 13, 15, 23, 24, 29, 42, 49, 50, 51, figs. 1–3, 7–9, 11, 14, 16, 17 (relation., range, char., synon., descr., diagn., Panama; Glover Reef; St. Lucia; Puerto Rico; Jamaica; Cuba; Garden Key, Bahamas; nomencl. on *H. clupeola* C. and V. 1847 and on Poey's No. 377 sp. dubia, 1861); Fowler, Fish Culturist, *19* (4), 1939: 28 (Bimini, Bahamas); Arqu. Zool. estad. São Paulo, *3* (6), 1941: 133 (Brazil); Fish Culturist, *22* (2), 1942: 9 (vent. fin; Sheen Cay, Honduras); Monagr. Acad. nat. Sci. Philad., 6, 1944: 124, 434, 456, fig. 28 (synon., ref., descr., Old Providence I., Bahamas; w. Caribbean; Honduras); Rivas, Proc. U. S. nat. Mus., *100* (3263), 1950: 280, 289–292, pl. 3, figs. 5, 6 (char. in key, synon., comments, compar., size, range).

? *Alosa bishopi* Müller and Troschel *in* Schomburgk's Hist. Barbados..., 1848: 675 (orig. descr.; compar., size, use as food, Barbados); Hill, Handbook of Jamaica, 1881: 125 (comments, Jamaica); Storey, Stanf. Ichthyol. Bull., *1* (1), 1938: 49 (nomencl., orig. descr. quoted).

Harengula species dubia Poey, Memorias, Cuba, *2* (50), 1861: 384; Repert. Fisico-Nat. Cuba, *2*, 1868: 418 (descr., cf. *H. clupeola*, Cuba); Storey, Stanf. Ichthyol. Bull., *1* (1), 1938: 49 (comments).

Clupea humeralis (not *Harengula humeralis* Cuvier and Valenciennes 1847), Günther, Cat. Fish. Brit. Mus., *7*, 1868: 422 (synon., ref., descr., range, all in part).

Harengula pensacolae (not of Goode and Bean 1879), T. H. Bean, U. S. Fish Comm., *8*, 1890: 206 (Cozumel, Yucatán).

Harengula macrophthalma Jordan, Proc. U. S. nat. Mus., *12*, 1890: 645, 646 (char. in key, synon. and ref. in part, Port Castries, St. Lucia); Jordan and Thompson, Bull. U. S. Bur. Fish., *24*, 1905: 233 (Garden Key, Tortugas, Florida); Fowler, Proc. Acad. nat. Sci. Philad., *67*, 1915: 257 (St. Vincent, Lesser Antilles); Regan, Ann. Mag. nat. Hist., (8) *19*, 1917: 388 (synon. in part, descr., range, Florida; West Indies; Bahia; Fernando Noronha exclud.); Jordan, Copeia, 56, 1918: 46 (Atlantic spp.); Fowler, Proc. Acad. nat. Sci. Philad., *71* (2), 1919: 133 (St. Martin, Lesser Antilles); *80*, 1928: 462 (Puerto Rico); Nichols, New York Acad. Sci., *10* (2), 1929: 202 (synon. and ref. in part, distr., diagn., remarks, habits, fig., Puerto Rico); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, App. 10, 1930: 43

(range, synon. in part); Fowler, Proc. Acad. nat. Sci. Philad., *82*, 1930: 269 (Grenada); 89, 1937: 309 (Haiti); Storey, Stanf. Ichthyol. Bull., *1* (1), 1938: 43 (nomencl., type local., orig. descr. quoted); Butsch, J. Barbados Mus. Hist. Soc., 7 (1), 1939: 18 (Barbados); Longley and Hildebrand, Publ. Carneg. Instn. Wash., 535, 1941: 8–10 (char. in key, compar., synon. in part, var. in depth accord. to sex, fin rays, vent. scutes, gill rakers, nomencl., range, Tortugas, Florida).

Clupea bishopi Cockerell, Inst. Jamaica Bull., 1, 1892: 15 (color, Jamaica).

Sardinella clupeola Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 428, 429 (char. in key, descr. in part, nomencl., ref.); Rep. U. S. Comm. Fish. (1895), 1896: 282 (range); B. A. Bean *in* Shattuck, Bahama Islands, Fishes, 1905: 297 (Green Turtle Cay, Bahamas); Metzelaar, Trop. Atlant. Vissch., 1919: 11, fig. 10 (synon., size, Haiti, drawing erroneously ident. as *Sardinella anchovia* C. and V. 1847).

Sardinella bishopi Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 428, 430 (char. in key, descr., relation.); Rep. U. S. Comm. Fish. (1895), 1896: 282 (range).

Sardinella macrophthalmus Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 428, 430 (char. in key, descr., compar., range, synon. in part); Rep. U S. Comm. Fish. (1895), 1896: 282 (range); Jordan and Rutter, Proc. Acad. nat. Sci. Philad., *49*, 1898: 94 (ref., body depth, Kingston, Jamaica); Fowler, Proc. Acad. nat. Sci. Philad., *51*, 1900: 118 (Port Antonio, Jamaica; St. Martin and Santa Cruz, Lesser Antilles); Nichols, Bull. Amer. Mus. nat. Hist., *31* (18), 1912: 182 (capture, Havana Harbor, Cuba); Metzelaar, Trop. Atlant. Vissch., 1, 1919: 12, fig. 4 (synon., size, habitat, commerc. import., Curaçao; St. Eustatius); Breder, Bull. Bingham oceanogr. Coll., *1* (1), 1927: 12 (Glover Reef); Beebe and Tee-Van, Zoologica, N. Y., *10*, 1928: 41 (ref., field char., size, weight, range, distr., abund., capture, Port-au-Prince Bay, Haiti); Breder, Field Bk. Mar. Fish. Atl. Cst., 1929: 68 (range, size); Zoologica, N. Y., *18* (3), 1934: 59 (Andros I., Bahamas); Parr, Bull. Bingham oceanogr. Coll., *3* (4), 1930: 3 (comments, Crooked Is., Bahamas only); von Ihering, Rev. Industr. Anim. São Paulo, 3, 1930: 229 (ref., diagn., Brazil).

Harengula pensacolae Goode and Bean 1879

Scaled Sardine, Sardine, Pilchard, Alewife, Fatback Minnow, Shiner, Sprat, Sardina Escamuda, Sardina, Sardinha

Figure 97

Study Material. Numerous specimens, 39–149 mm SL, from Florida, the Gulf of Mexico, Bahamas, West Indies, Caribbean coast of Central and South America, and Brazil, USNM and UMIM.

Distinctive Characters. The absence of palatine teeth, the high number of gill rakers (30–40), the number of ventral scutes, the adherent scales, and the deeper body distinguish this species from all other western Atlantic forms.

Description. Proportional dimensions in per cent of standard length, and counts, based on 1,394 specimens, 39–149 mm SL.

Body: greatest depth 29.5–34.7; greatest width 14.0–15.6.
Caudal peduncle: least depth 10.6–11.4.
Head: length 28.0–31.5; depth at occiput 26.5–28.8
Snout: length 6.9–8.5.
Eye: diameter 9.0–12.0.
Interorbital: width 6.0–7.6.
Maxillary: length 12.7–14.3.
Dorsal fin: anterior height 18.1–20.3; length 23.6–25.3; length of base 16.4–19.0.
Anal fin: anterior height 6.3–7.1; length 18.9–21.9; length of base 14.3–16.0.
Pelvic fin: length 12.9–13.8.

Pectoral fin: length 21.8–24.1.

Distance from tip of snout to origin of: dorsal fin 42.7–45.8; anal fin 78.6–81.7; pelvic fin 53.6–55.6; pectoral fin 27.1–30.3.

Scales: transverse rows 39–43, usually 40–42; predorsal 11–14, usually 12 or 13.

Ventral scutes: 30–32; usually 31 in *p. majorina*; 28–31, usually 29 or 30, in other subspecies.

Gill rakers: 30–40; *p. majorina* with 30–37, usually 33–35; *p. caribbaea* with 31–37, usually 32–35; *p. pensacolae*, *p. cubana*, *p. floridana*, and *p. pinensis* with 34–40, usually 35–39.

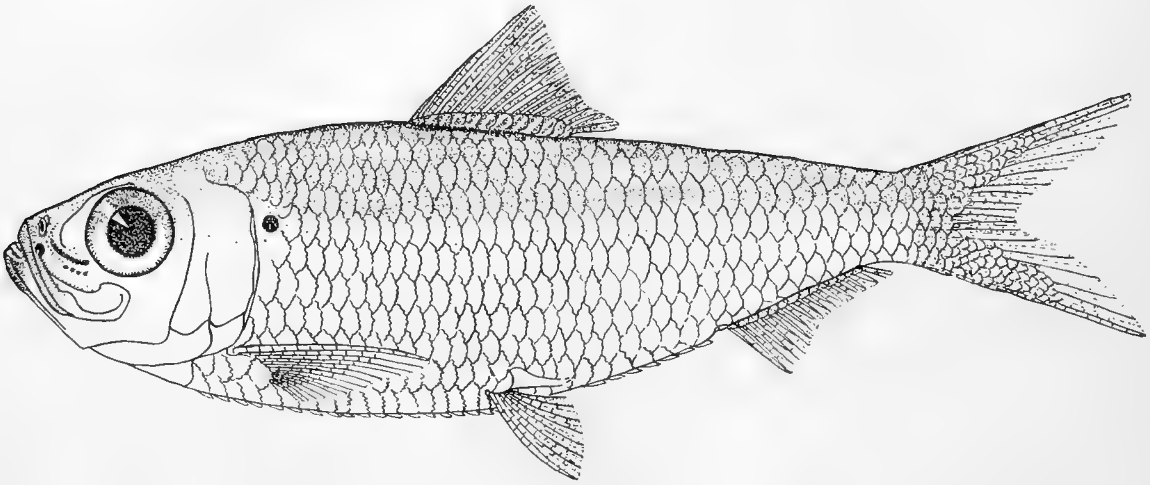

FIGURE 97. *Harengula pensacolae*, 104 mm SL, Province of Pinar del Rio, Cuba, type of *H. p. cubana*, USNM 132472. Drawn by Janet Ebeling, after Rivas (*108*).

PREDORSAL CONTOUR evenly and moderately convex, the POSTDORSAL CONTOUR more or less straight or very slightly convex from origin of dorsal to caudal fin; VENTRAL CONTOUR much more convex than dorsal contour, the body axis closer to dorsal than to pelvic fins. DORSAL fin originating nearer to tip of snout than to caudal base. PELVIC fin inserted about midway between insertion of pectoral and origin of anal, or nearer insertion of pectoral. PECTORAL fin inserted nearer to insertion of pelvic than to tip of snout.

Color. General coloration silvery, especially on the lower parts of the head and body; the opercular plates with iridescent or pearlish, metallic reflections. Back dark brownish or bluish gray. Body with dark, longitudinal streaks, more conspicuous on back. Humeral spot variable; conspicuous to faint. Tip of snout and mandible dusky. Upper sector of iris dusky. Fins colorless except caudal, which is somewhat pigmented at tip of lobes and along inner margin.

Size. The largest specimen examined measures 149 mm SL.

Range. Widely and generally distributed from Cape Canaveral, Florida, southward to Brazil, including the Gulf of Mexico, as discussed under *Variation*.

Variation. H. pensacolae has been subdived into five subspecies, namely *floridana*, *caribbaea*, *cubana*, *pinensis*, and *majorina*, the alternative characters of which were published in 1950 (*109*: key, 279): *floridana* Rivas 1950, a large-eyed form from the Florida Keys; *caribbaea* Rivas 1950, based on specimens with fewer gill rakers and a more slender body, from the Caribbean, and Central and South America—Nicaragua to Colombia, Jamaica, Hispaniola, and Puerto Rico; *cubana* Rivas 1950 and *pinensis* Rivas 1950, for those from northwestern Cuba and Isle of Pines, respectively; and *majorina* Storey 1938, for those from the Lesser Antilles, St. Lucia southward, and along the coast of South America from Venezuela to and including Brazil. These slightly different forms broadly intergrade with one another. As geographical separation of them would obviously be purely arbitrary, they are all united here under the specific name *pensacolae*.

Synonyms and References:

Harengula humeralis (not *Clupea humeralis* Cuvier 1829), Cuvier and Valenciennes, Hist. Nat. Poiss., *20*, 1847: 293 (descr., comments, local. in part; Guadeloupe, Rio de Janeiro to the West Indies; Brazil; Bahia; Surinam); Castelnau, Anim. Rares Amer. Sud, *2*, 1855: 56 (ref. in part, comments, Bahia, Brazil); Jordan, Proc. U. S. nat. Mus., *13*, 1891: 314 (Bahia, Brazil); Jordan and Thompson, Bull. U. S. Bur. Fish., *24*, 1905: 233 (abund., use as bait, Tortugas, Florida); Fowler, Proc. Acad. nat. Sci. Philad., *58*, 1906: 83, fig. 3 (color, Marquesas Keys and Hailer's Rock, Florida); *67*, 1915: 247 (Clearwater and Palm Beach, Florida).

Clupea humeralis (not of Cuvier 1829), Günther, Cat. Fish. Brit. Mus., *7*, 1868: 422 (synon., refs., descr., range, all in part); Cope, in part, Trans. Amer. philos. Soc., *14* (3), 1871: 483 (ref., St. Croix); Jordan, Proc. U. S. nat. Mus., *9*, 1887: 561 (synon. exclud., West Indies).

Harengula pensacolae Goode and Bean, Proc. U. S. nat. Mus., *2*, 1879: 152 (orig. descr., compar., Pensacola, Florida); Proc. U. S. nat. Mus., *2*, 1880: 343 (char., Clearwater Harbor, Florida); Jordan and Gilbert. Bull. U.S. nat. Mus., 16, 1882: 268 (descr.); Lönnberg, Ofvers Svensk. Vet. Akad. Forh., *51* (3), 1894: 114 (abund., use, St. Petersburg, Florida); Regan, Ann. Mag. nat. Hist., (8) *19*, 1917: 387, 388 (char. in key, synon., ref., descr.; Florida; Trinidad); Fowler, Proc. Acad. nat. Sci. Philad., *71* (2), 1919: 129, 133, 144, 151 (Rio de Janeiro, Brazil; St. Martin, West Indies; St. Croix; habitat, behav., capture, Useppa I., Florida); *78*, 1926: 250 (size, color., Boca Grande, Florida); *80*, 1928: 456, 462 (Haiti; Puerto Rico); Proc. biol. Soc. Wash., *46*, 1933: 58 (size, Calcasieu Lake, Louisiana); Proc. Acad. nat. Sci. Philad., *92*, 1940: 2 (size, Boca Grande, Florida); Monogr. Acad. nat. Sci. Philad., 7, 1945: 104, 266 (synon., ref., size, use; Elizabeth City, N. Carolina; Florida locals.); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, App. 10, 1930: 44 (range, Florida); Longley, Carneg. Instn. Yearbk., 31, 1932: 299 (nomencl.); Hubbs, Publ. Carneg. Instn. Wash., 457, 1936: 174 (char., nomencl., compar., Champoton, Campeche, Yucatán); Storey, Stanf. Ichthyol. Bull., *1* (1), 1938: 3, 7, 13, 15, 18, 21, 23, 25, 33, 50, figs. 1, 2, 4–11, 13 (relation., range, char., cf. *H. majorina*, descr., diagn., Florida and Texas locals.; Yucatán, México); Hildebrand *in* Longley and Hildebrand, Publ. Carneg. Instn. Wash., 535, 1941: 11 (synon. of *H. macrophthalma*; gill rakers).

Clupea pensacolae Jordan, Proc. U. S. nat. Mus., *7*, 1884: 107 (abund., compar., color, Key West, Florida); Jordan and Swain, Proc. U. S. nat. Mus., *7*, 1884: 230 (color, relation., Cedar Keys, Florida); Jordan, Rep. U. S. Comm. Fish. (1885), App. 2, E (24), 1887: 36 (N. America); Henshall, Bull. U. S. Fish Comm., *9*, 1891: 385 (abund., range, Florida Keys; w. Florida).

Harengula arcuata (not *Clupea arcuata* Jenyns 1842), Jordan, Proc. U. S. nat. Mus., *12*, 1890: 645, 646 (char. in key, synon. in part; St. Lucia; Florida locals.); Henshall, Bull. U. S. Fish Comm., *9*, 1891: 373 (synon. in part, abund., Florida locals.); Evermann and Kendall, Bull. U. S. Fish Comm., *12*, 1894: 105 (compar., Texas locals.).

Sardinella humeralis (not *Clupea humeralis* Cuvier 1829), Jordan and Evermann, Bull. U. S. nat. Mus., *47* (1), 1896: 428, 431 (char. in key, descr., range, synon. and ref. in part, types of *H. pensacolae* design.); Rep. U. S. Comm. Fish. (1895), 1896: 283 (range, ref.); Fowler, Proc. Acad. nat. Sci. Philad., *51*, 1900:

118 (Port Antonio, Jamaica); Evermann and Marsh, Bull. U. S. Fish Comm. (1901), 1, 1902: 85 (char. in key, descr., synon., Puerto Rico locals.); Cockerell, Proc. biol. Soc. Wash., *23*, 1910: 63 (scales, Tampa, Florida); Fowler, Proc. Acad. nat. Sci. Philad., *63*, 1911: 206 (Florida); Copeia, 24, 1915: 50 (Santo Domingo); Proc. Acad. nat. Sci. Philad., *69*, 1917: 128 (Colón, Panama); Metzelaar, Trop. Atlant. Vissch., 1, 1919: 11 (synon., size, doubt. poison., habitat, Curaçao; St. Eustatius).

Sardinella macrophthalmus (not *Clupea macrophthalma* Ranzani 1842), Meek and Hildebrand, Field Mus. Publ., Zool., *15* (1), 1923: 182, pl. 9a (char. in key, synon. in part, descr., comments, range, Toro Point, Colón, Porto Bello, Panama).

Harengula sardina (not of Poey 1860), Fowler, Proc. Acad. nat. Sci. Philad., *89*, 1937: 309 (Port-au-Prince, Haiti).

Harengula majorina Storey, Stanf. Ichthyol. Bull., *1* (1), 1938: 7, 18, 21, 23, 25, 32, 42, 44, 50, 51, figs. 1, 8, 9, 17 (char., relation., compar., range, synon., diagn., comments, nomencl., West Indies; St. Lucia; Santos [São Paulo] Brazil); Fowler, Proc. Amer. philos. Soc., *82* (5), 1940: 745 (ill., Rio de Janeiro, Brazil); Hildebrand *in* Longley and Hildebrand, Publ. Carneg. Instn. Wash., 535, 1941: 11 (comments); Fowler, Arqu. Zool. estad. São Paulo, *3* (6), 1941: 133 (ref., Brazil); Monogr. Acad. nat. Sci. Philad., 6, 1944: 144, 547, fig. 29 (synon., ref., descr., cf. *H. pensacolae*, St. Andrews I., local., ref., w. Caribbean).

Harengula macrophthalma (not *Clupea macrophthalma* Ranzani 1842), Gunter, Publ. Inst. Mar. Sci. Texas, *1* (1), 1945: 25, 128 (abund., capture, salinity, temp., size, Texas locals.).

Harengula pensacolae majorina Rivas, Proc. U. S. nat. Mus., *100* (3263), 1950: 292–294, pl. 4, fig. 1 (synon., comments, compar., size, range).

Harengula pensacolae caribbaea Rivas, Proc. U. S. nat. Mus., *100* (3263), 1950: 294–296, pl. 4, fig. 3 (synon., orig. diagn., comments, compar., size, range).

Harengula pensacolae pensacolae Rivas, Proc. U. S. nat. Mus., *100* (3263), 1950: 281, 296–298, pl. 3, figs. 7, 8 (char. in key, synon., comments, compar., size, range).

Harengula pensacolae cubana Rivas, Proc. U. S. nat. Mus., *100* (3263), 1950: 281, 298–301, fig. 40, pl. 5, fig. 1–3 (char. in key, orig. descr., compar., size, range, w. Cuba).

Harengula pensacolae floridana Rivas, Proc. U. S. nat. Mus., *100* (3263), 1950: 281, 301, 302, pl. 4, fig. 2 (char. in key, orig. diagn., compar., Florida).

Harengula pensacolae pinensis Rivas, Proc. U. S. nat. Mus., *100* (3263), 1950: 281, 302, fig. 41, pl. 5, figs. 4–6 (char. in key, orig. diagn., compar., Isle of Pines, Cuba).

Genus *Sardinella* Cuvier and Valenciennes 1847

Spanish Sardines

By

Samuel F. Hildebrand

(continued)

Sardinella Cuvier and Valenciennes, Hist. Nat. Poiss., *20*, 1847: 261; genotype *S. aurita* Cuvier and Valenciennes, first designated by Gill, Proc. Acad. nat. Sci. Philad., 1861; 35.

Generic Synonym:

Sardinia Poey, Memorias, *2*, 1860: 311; genotype by monotypy, *Sardinia pseudo-hispanica* equals *S. anchovia* Cuvier and Valenciennes.

Characters. BODY quite slender, compressed, its greatest depth equal to or less than length of head. BONY SCUTES rather weak, 32–34 along moderately sharp edge of chest and abdomen. SCALES thin, moderately adherent, with one to several vertical grooves. Vertical part of anterior CLAVICULAR MARGIN (cleithrum) with two membranous projections or lobes, a definite concavity between them (Fig. 100). OPERCLE without radiating grooves. MOUTH moderately small. MAXILLARY generally extending a little beyond anterior margin of eye. UPPER JAW without a median notch. LOWER JAW projecting slightly beyond the upper. TEETH absent in upper jaw; several in anterior part of lower jaw; minute teeth also on palatines, pterygoids, and tongue but absent on vomer. GILL RAKERS numerous, close-set, increasing in number with age, difficult to count (ftn. 47), about 70–130 on lower limb of first arch in adults; rakers on upper limb not overlapping those on lower limb, decreasing gradually in length toward anterior part of lower limb. DORSAL with 17–19 rays, the last one not produced. ANAL with 16–20 rays, the last two notably enlarged, finlet-like. PELVIC fin inserted under base of dorsal, almost constantly with 9 rays. PECTORAL fin without a free axillary process, the fin lying in a slight depression.[45] VERTEBRAE about 45–47.

Remarks. Confusion in regard to the relationship of *Sardinella* Cuvier and Valenciennes, *Sardina* Antipa,[46] and *Sardinia* Poey has existed and even now has not been cleared up completely. This relationship has been discussed by Regan (*106*: 377), Jordan (*70*: 46), Hubbs (*61*: 261–265), and Longley (*87*: 5), and apparently the conclusion may be reached that *Sardinella* differs from *Sardina* in the absence of radiating grooves (or ridges) on the opercle and in the presence of two membranous lobes on the vertical edge of the clavicular margin (cleithrum). Further, it appears that *Sardinia*

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[45] The generic description is based wholly on American specimens, as adequate material from the other side of the Atlantic is not available.

[46] *Sardina* Antipa 1905 appears to be a synonym of *Arengus* Cornide 1788 (see *23*: 43).—G. S. M.

Poey is a synonym of *Sardinella* and that *Clupanodon* has no American representative. As the last ray of the dorsal in *Clupanodon* is prolonged, its relationship is with *Opisthonema*, *Dorosoma*, and *Signalosa* (here a synonym of *Dorosoma*) rather than with *Sardinella*. In his discussion, Hubbs (*61*: 261–265) set up a new genus, *Sardinops*, for the sardines of the Pacific and South Africa. This genus differs from *Sardinella* principally in the absence of the fleshy lobes on the cleithrum, in the presence of oblique ridges on the opercle, and in the overlapping gill rakers, those on the upper arch extending downward over those on the lower limb.

Species. The species of this genus remain somewhat obscure. Among the three recognized as coming within the scope of this work, *pinnula* is definitely distinct according to the specimens at hand; however, specimens from Cuba and Jamaica, not in good condition, seem to be more or less intermediate between *anchovia* from the Atlantic coast of the United States and *brasiliensis* from Port-of-Spain, Trinidad, and southward. Such specimens also are included among collections from Rio de Janeiro, Brazil. More material and further study will be required to determine the exact relationship.

The number of gill rakers on the first arch seems to be the best diagnostic character, but the rakers are so numerous, fine, and close-set that they are exceedingly difficult to count accurately.[47] Consequently, the use of this character requires much time and patience. Its ready use is limited further by the increase in number with age and growth, making it necessary to compare the number present in specimens of nearly equal size.

Other characters having limited diagnostic value are depth of body, size of head, eye, and mouth, development of the palatine and pterygoid teeth, the position of dorsal and pelvic fins, and length of pectoral fin. The color, so far as can be determined from the preserved specimens at hand, is rather uniform among the species recognized. The species are carnivorous, occur in schools, and are marine in habitat.

Range. Cape Cod, Massachusetts, to southern Brazil, but not yet known from México to Colombia. They occur also off Bermuda, Cuba, Jamaica, Trinidad, in the eastern Atlantic, and in the Indo-Pacific (*106*: 377).

Key to Species of the Western Atlantic

1a. Distance from margin of snout to origin of dorsal about equal to 33 % of TL, 41–43.5 % of SL; eye equal to, or usually shorter than, snout, its diameter 5.3–7.3 % of SL; snout 6.0–7.6; gill rakers about 70–100 on lower limb of first arch (fewer in young); pectoral fin failing to reach base of pelvic by a distance nearly or quite equal to length of snout and eye.

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[47] It was found necessary to remove the gill rakers from the arch to make an accurate count. The arch was severed from the body near the base of the rakers, the membrane was freed from the bony arch at one end, the loosened end was grasped with forceps, and a gentle pull then freed the membrane with the rakers intact. In a watch glass under low power of a binocular, the rakers could be separated by ones, twos, or threes, an accurate count thus being obtained. The counts made previously either with the arch in its natural position or after removal from the body ran much too high, the error being greatest among those with the highest number of rakers.

2a. Greatest thickness of body exceeding half its depth; head length greater than depth of body, 24–26 %, and its depth 18–22 % of SL, the depth at vertical from crossgroove at occiput 15.5–17.5 % of SL; pectoral failing to reach base of pelvic by a distance somewhat shorter than snout and eye, leaving 6 or 7 rows of scales exposed between its tip and base of pelvic, its length 16–18.5 % of SL. *pinnula* T. H. Bean 1912, below.

2b. Greatest thickness of body generally less than half its depth; head length about equal to greatest depth of body, 22.3–27.2, and its depth 21–26.9 % of SL, the depth at vertical from crossgroove at occiput 17.6–19.7 % of SL; pectoral failing to reach base of pelvic by a distance generally equal to length of snout and eye, leaving 6–8 rows of scales exposed between its tip and base of pelvic, its length 15–17.6 % of SL.
anchovia (Cuvier and Valenciennes) 1847, p. 401.

1b. Distance from margin of snout to origin of dorsal notably greater than 33 % of TL, 44–47.5 % of SL; eye equal to or longer than snout (rarely slightly shorter), its diameter 6.9–7.9 % of SL; snout 7.3–8.15; gill rakers about 110–130 on lower limb in specimens 70 mm and upward (fewer in young); pectoral fin failing to reach base of pelvic by a distance about equal to diameter of eye.
brasiliensis (Steindachner) 1879, p. 407.

Sardinella pinnula T. H. Bean 1912

Bermuda Anchovy

Figure 98

Study Material. A total of 41 specimens with caudal fins broken, 74–135 mm SL, including five specimens of type material, 93–135 mm TL, 74–114 mm SL; no holotype designated; all specimens from Bermuda.

Distinctive Characters. This species is very close to the species herein recognized as *anchovia*, from which it differs in the more elongated and more robust body and especially in the lower head.

Description. Proportional dimensions in per cent of standard length, and counts, based on 24 study specimens within the length ranges given above.

Body: depth 18–22.
Caudal peduncle: depth 6.4–8.2.
Head: length 24–26; depth 15.5–17.5.
Snout: length 7.0–7.6.
Eye: diameter 5.9–7.0.
Interorbital: width 4.2–5.2.
Maxillary: length 9.2–10.5.
Anal fin: length of base 13–16.
Pelvic fin: length 9.2–10.7.
Pectoral fin: length 16–18.5.
Distance from snout to origin of: dorsal 41–42.5.

Scales: *ca.* 43–47, often lost from preserved specimens.

Ventral scutes: 32–34.

Fin rays: dorsal 17–19; anal 15–18; pectoral 16 or 17.

Vertebrae: 46–47 (3 specimens).

Body with greatest thickness exceeding half of depth, its greatest depth 4.5–5.5 in SL; ventral outline notably more strongly convex than dorsal outline. Caudal peduncle slender, its depth 3.0–3.75 in head.

Scales lost in most specimens, apparently not different from those of *S. anchovia*; 6 or 7 rows of scales exposed between tip of pectoral and base of pelvic. Ventral scutes not strong, 18 or 19 in advance of pelvics and 14 or 15 behind them.

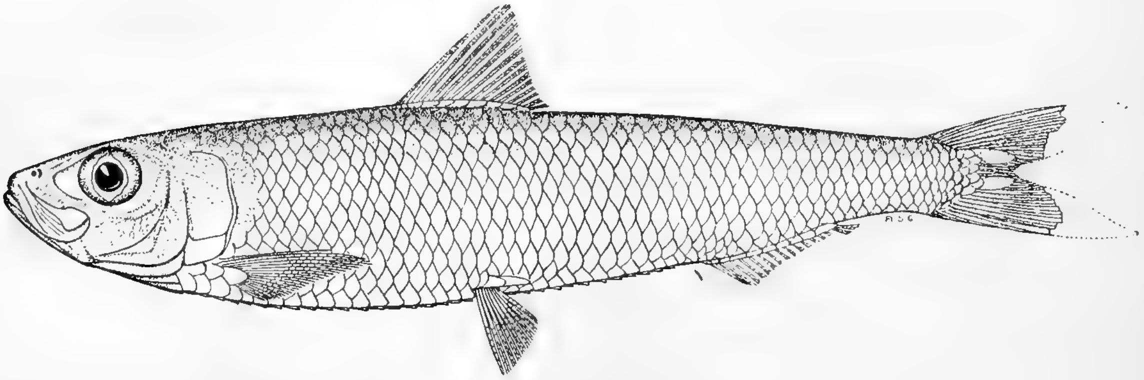

Figure 98. *Sardinella pinnula*, about 124 mm TL (caudal damaged), 100 mm SL, Bermuda, USNM 21252. Drawn by Ann S. Green.

Head small, slender, 3.85–4.15 in SL, its depth at vertical from crossgroove at occiput 5.0–6.1 in SL. Snout moderately long, 3.2–3.4 in head. Eye small, its diameter definitely shorter than snout, 3.55–4.15 in head. Interorbital 4.7–5.9. Cheek longer than deep. Maxillary rather broadly rounded posteriorly, scarcely reaching vertical from anterior margin of pupil, 2.3–2.6 in head. Mandible projecting moderately, its margin within mouth rising rather gradually, without a definite angle. Gill rakers long, slender, close-set, difficult to count, those at angle about as long as eye, the serrations on inner edge of rakers minute; the rakers increasing in number with age: about 75 on lower limb of first arch in specimens about 85 mm long, about 90 in those about 100 mm SL (gill rakers removed for counting). Teeth as in *S. anchovia.*

Dorsal fin rather high anteriorly, its margin definitely concave, its longest ray generally reaching to or beyond tip of last ray if deflexed, its origin rather nearer to margin of snout than to vertical from base of last anal ray, its distance from margin of snout 2.3–2.4 in SL; the base with a very narrow sheath of scales. Caudal forked; broken in all specimens at hand. Anal fin much lower than dorsal, with a slight lobe anteriorly, its last two enlarged rays nearly as long as the longest ones in anterior lobe of fin, its origin about equidistant between insertion of pelvic and base of caudal, its base 1.55–1.9 in head. Pelvic fin reaching a little more than a third of the way to origin of anal, inserted about equidistant between base of pectoral and origin of anal, 2.4–2.75 in head; the axillary process reaching about to beginning of distal third of fin. PECTORAL fin rather short, not falcate, its length 5.4–6.25 in SL, 1.35–1.55 in head, failing to reach base of pelvic by a distance generally equal to snout and about half of eye.

Color. Specimens at hand badly faded; apparently not different from *S. anchovia.* Described as "steel blue above, silvery below, iridescent. Head, in spirits with golden tints; no opercular spot" (*9*: 122).

Size. This, the Anchovy of Bermuda, reaches a length of 6 or 7 inches (*11*: 35). The average length of those observed by Goode was about 5 inches (*42*: 69).

Habits. Like the others of the genus, this little sardine schools, usually in the offshore waters, and tends to come inshore in large schools "about sunrise or sunset" (*4*: 112).

Commercial Importance. This little Sardine was sold "in quantities along the quay" in March 1872, presumably for human consumption (*42*: 69). Barbour said that in 1903 it was seined regularly for bait in Hamilton Harbor and Flatts Inlet (*4*: 112). Although it was reported as "uncommon close in shore but very abundant in mid-water in greater depths" (*11*: 35), it was not stated that it is either eaten by man or used as bait. A small fish occurring in the abundance indicated must be of considerable value as forage for larger predatory foodfishes.

Range. Known only from Bermuda.

Synonyms and References:

Sardinella anchovia Goode (not of Cuvier and Valenciennes), Bull. U. S. nat. Mus., 5, 1876: 69 (Bermuda, average size); Barbour, Bull. Mus. comp. Zool. Harv., *46* (7), 1905: 112 (distr.; in part not *pinnula*; Hamilton Harbor, Bermuda); Beebe and Tee-Van (in part not of C. and V.), Field Bk. Shore Fish. Bermuda, 1933: 35 (field char., diagn., distr.); Beebe and Tee-Van (not of C. and V.), Zoologica, N. Y., *13* (7), 1933: 135 (*S. pinnula* synon. with *S. anchovia*); Hollister (not of C. and V.), Zoologica, N. Y., *21* (4), 1936: 186 (caudal skel.).

Sardinella pinnula T. H. Bean, Proc. biol. Soc. Wash., *25*, 1912: 122 (orig. descr.; type local. Bermuda; types USNM 74086; local name).

Sardinella anchovia (Cuvier and Valenciennes) 1847

Spanish Sardine, Sardina de España, False Sardine, Sardina, Bang

Figures 99, 100

Study Material. Many specimens, from Woods Hole, Massachusetts; Blue Point Cove, Long Island, New York; Beaufort, North Carolina; and Tortugas, Florida. Several additional specimens from Cuba, Jamaica, and Rio de Janeiro, Brazil, apparently belong to this species also.

Distinctive Characters: See *Relationship* and *Variation.*

Description. Proportional dimensions in per cent of standard length, based on 32 specimens, 90–155 mm TL, 70–127 mm SL.

Body: depth 21–26.9.
Caudal peduncle: depth 7.7–10.
Head: length 22.3–27.2; depth 17.6–19.7.
Snout: length 6.0–7.5.
Eye: diameter 5.3–7.3.
Interorbital: width 4.2–5.3.
Maxillary: length 8.75–11.
Anal fin: length of base 13.7–16.
Pelvic fin: length 8.5–11.
Pectoral fin: length 15–17.6.
Distance from snout to origin of: dorsal fin 40–43.5.

Scales: about 41–46, often lost from preserved specimens.
Ventral scutes: 32–34.
Fin rays: dorsal 17–19, occasionally 20; anal 16–18; pectoral 15 or 16.
Vertebrae: 45–47 (7 specimens).

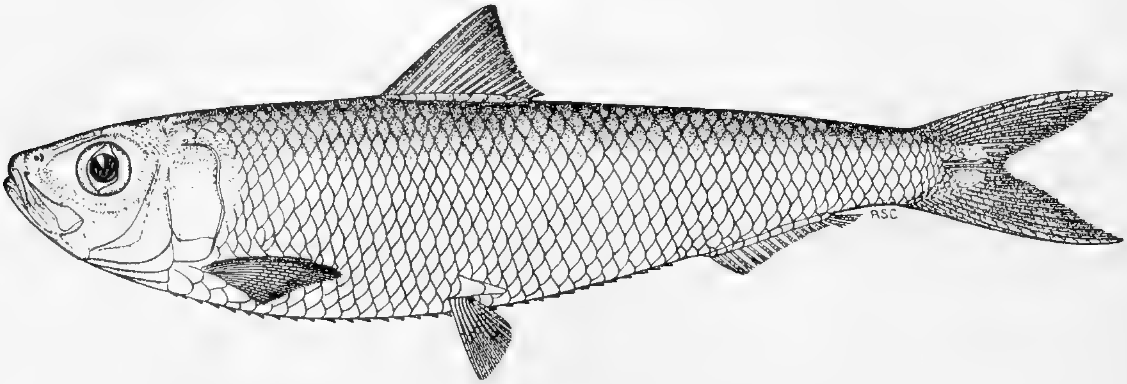

FIGURE 99. *Sardinella anchovia*, about 120 mm TL, 95 mm SL, Woods Hole, Massachusetts, USNM 90233. Drawn by Ann S. Green.

BODY rather strongly compressed, its greatest thickness generally less than half of its depth, its greatest depth 3.7–4.75 in SL; ventral outline notably more strongly convex than dorsal outline. CAUDAL PEDUNCLE slender, moderately compressed, its depth 2.5–3.6 in head.

SCALES moderately adherent, those from middle of side below anterior rays of dorsal scarcely deeper than long, with 3 or 4 more or less complete vertical grooves, the margin of these scales scarcely indented but scales on back in front of dorsal fin definitely indented; 6–8 rows of scales exposed between tip of pectoral and base of pelvic fin. The pair of modified scales at nape small, shorter than eye. VENTRAL SCUTES small, 18 or 19 in front of pelvic fins and 14 or 15 behind them.

HEAD 3.65–4.35 in SL, its depth at vertical from crossgroove at occiput 4.95–5.1. SNOUT 3.0–3.9 in head, its margin without a median notch. EYE shorter than snout, 3.4–4.5 in head. INTERORBITAL bone (over middle of eye) 4.3–6.0. CHEEK longer than deep. MAXILLARY rounded posteriorly, reaching to or a little beyond vertical from anterior margin of pupil, 2.3–2.7 in head. MANDIBLE projecting only slightly, its margin without mouth rising rather gradually without a definite angle. GILL RAKERS long, slender, close-set, those at angle about as long as eye, the serrations on inner edge minute, the rakers increasing in number with age, difficult to count; about 55–60 on lower limb of first arch in specimens 37–44 mm, about 70–75 in examples 70–80 mm, and 85–100 in specimens 105–125 mm SL (gill rakers removed from arch for counting). TEETH absent on upper jaw; some fine points on margin of maxillary; lower jaw with a few small teeth anteriorly on each side of a median interruption; a few minute teeth on palatines, pterygoids, and tongue.

DORSAL fin only moderately elevated anteriorly, its margin somewhat concave, its longest ray usually failing to reach the tip of last one if deflexed, its origin about equidistant between margin of snout and vertical from middle of base of anal, its distance from the margin of snout 2.3–3.5 in SL; its base with a very narrow sheath composed of a single row of elongated scales, the posterior ones with a free lower margin. CAUDAL fin rather deeply forked, the lower lobe slightly the longer, without scales except for a few modified ones on its base. ANAL fin much lower than dorsal, its last two rays notably enlarged and scarcely shorter than the longest ones in anterior lobe of fin, its origin about equidistant between the insertion of pelvic fin and base of caudal, its base 1.45–1.8 in head; a sheath of scales at base somewhat broader than that of dorsal. PELVIC fin with margin scarcely convex when spread, reaching a little more than halfway to origin of anal, its shortest ray about 75 % of the length of longest ray, the fin inserted about equidistant between base of pectoral and origin of anal, 2.1–3.0 in head; the axillary process reaching to or beyond midlength of fin. PECTORAL fin scarcely falcate, failing to reach base of pelvic fin by a distance nearly equal to, or quite equal to, length of snout and eye, its length from base of upper ray to tip of fin 5.7–6.6 in SL, 1.35–1.6 in head.

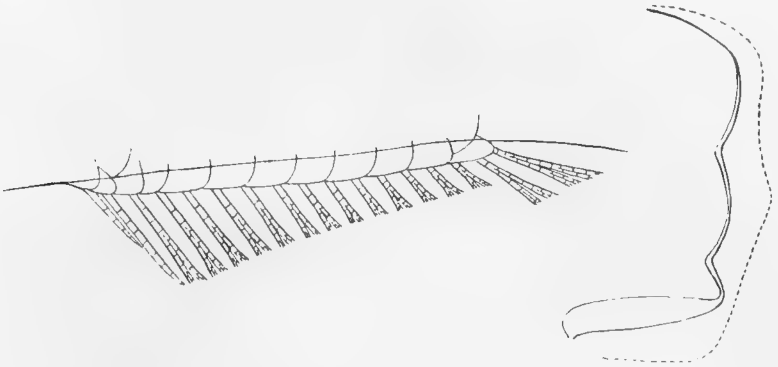

FIGURE 100. *Sardinella anchovia.* LEFT, anal fin showing last two large rays; RIGHT, left-hand rim of pectoral girdle (cleithrum), showing two lobes underneath free edge of gill cover; both from specimen in Fig. 99. Drawn by Ann S. Green.

Color. Bluish black above, changing rather abruptly to bright silvery at level of upper margin of eye. Head and especially snout with many dusky punctulations; dorsal and caudal rays with numerous dark dots, these especially crowded on distal parts of longest rays of dorsal, giving the lobe a blackish appearance when folded; the other fins plain, translucent, except for dark dots on 2 or 3 of the uppermost rays of the pectoral.

Live fish have been described as very dark blue above and silvery on the side and below (*87*: 7).

Size. The largest specimen at hand, with damaged caudal fin, is about 163 mm (6.5 in.) TL and 130 mm SL. However, a length of eight inches has been reported, though the usual length, judging from the examples at hand, probably is about four or five inches.

Development and Growth. The smallest specimens at hand are 26 mm SL (32 mm TL), taken at Tortugas, Florida, and 31–44 mm SL, from Beaufort, North Carolina, taken on June 30, 1913. These young, as is usual among Clupeidae, are notably more slender than their adults; the depth in the smallest ones (26–31 mm SL) is contained 5.1–6.2 times in SL; at about 60 mm SL the fish have attained near adult proportions.

As already noted (p. 402), the gill rakers increase with age and growth: about 50–60 on the lower limb of specimens 37–44 mm, 70–75 at 70–80 mm, and 85–100 at 105–125 mm SL. The smallest reported for Tortugas, up to 32 mm length, had only "22 or 23 gill rakers" (*87*: 8), and the smallest now at hand, 26 mm SL, has about 36 gill rakers on the lower limb. These data, then, indicate that the greatest proportional increase in the number of rakers takes place in the young under about 70 mm SL.

Spawning. Although Longley did not give the collection dates for the young 26-mm fish referred to above and for young "up to 32 mm in length" reported for Tortugas (*87*: 8), it is known that he worked at Tortugas only from about the last half of June to the early part of September. As such small young probably had not strayed far from the place where they were hatched, it may be assumed that at least some spawning takes place there during the summer.

Habits. These fish, like most of the herrings, run more or less in schools. In the fall of the year at Woods Hole, Massachusetts, the fish occur irregularly and in varying degrees of abundance (*120*: 91). Since these warm-water fish are not permanent residents there and since only adults seem to have been taken, it is surmised that they may migrate northward in the Gulf Stream. The fish in the vicinity of Tortugas, at least, seem to be most common some distance offshore where the water is 10–20 fms. deep, although they do come inshore (*87*: 7). Similar habits have been reported for the Bermuda sardine (*11*: 35).

Food. Numerous copepods were found in the alimentary canal of specimens taken at Woods Hole (*85*: 438). The numerous close-set gill rakers provide an effective straining apparatus for extracting minute organisms from the water. Therefore, an almost exclusively planktonic diet is assumed.

Enemies. Examples of this species were reported among the refuse on the tern rookery, Bird Key, Tortugas, Florida (*87*: 8). Other water birds and many predatory fish no doubt also feed on this sardine.

Parasites. The trematode, *Distomum appendiculatum*, was reported for the intestinal tract of specimens from Woods Hole, Massachusetts (*85*: 438), and the parasitic copepod, *Bomolochus eminens* Wilson, was found on the gills of specimens taken at Tortugas (*134*: 370).

Relationship. Longley discovered that the type material of *S. anchovia*, from Rio de Janeiro, Brazil, in Paris, consists of two species that are separable by the number of gill rakers on the lower limb of the first arch (*87*: 7); he reported that one example, 116 mm SL, has 105 rakers, while the other four, 114–148 mm SL, have 160–178. Although Longley's counts are probably not entirely accurate, the difference may be accepted as valid. Since the specimen with the smallest number of rakers was mentioned first in the original description, Longley accepted it as the type of *S. anchovia*; this specimen was taken by M. Delalande, the other four by M. d'Orbigny and M. Gay; Longley assigned the other four specimens to *brasiliensis* (p. 409) because they had many more rakers and a more strongly compressed body than the abovementioned type of *anchovia*, specimens of approximately equal length having been considered.

The number of gill rakers given for this "type" by Longley (105) corresponds approximately to the number counted in the specimens herein described (85–100), and since Longley gave no other character that disagrees with these specimens, *anchovia* has been accepted as available for this species, but with considerable doubt. This doubt results from an apparent absence among many Brazilian specimens of fish that have as low a gill raker count as the northern specimens of *anchovia* herein described. Indeed, there are slender specimens from Brazil with fewer rakers than in *brasiliensis*, as herein understood, but the raker counts and the relative pectoral fin length are somewhat intermediate between those for *anchovia* of the eastern United States coast and the *braziliensis* from Trinidad and elsewhere. Therefore, they may be at least subspecifically distinct from eastern United States specimens described here. If they should prove to be specifically distinct, then the South American species would stand as *anchovia* while Poey's name, *pseudo-hispanica*, may be available for the northern species. However, this cannot be definitely determined from the material at hand. In fact, specimens from Cuba, presumably identified as *pseudoharengus* by Poey, seem to belong to *brasiliensis* rather than to *anchovia*.

In the northern part of the range, *S. anchovia*, most frequently listed in the past as *Clupanodon pseudohispanicus*, has frequently been confused with *Clupea harengus* (the common Atlantic herring). This has led to some confusion, as pointed out by Longley (*87*: 6) and others. The two species, indeed, resemble each other superficially in having approximately an equally elongated body, but *anchovia* is easily distinguishable from *C. harengus* by the more anterior position of its dorsal fin, absence of vomerine teeth, fewer ventral scutes, fewer vertebrae, a smaller eye, and the enlargement of the last two anal rays. These differences are all shown in detail in the descriptions.

S. anchovia of the American coast probably was incorrectly synonomized with *S. aurita* of Europe and elsewhere by Regan in his revision of the genus (*106*: 378). This tentative conclusion was reached by Longley after he had examined the type material of both species in Paris (see above). From Longley's data it appears that *aurita* grows larger than any American representative of the genus and that it is somewhat intermediate between *anchovia* and *brasiliensis* (as herein understood) in the number of gill rakers. Based upon two specimens of *aurita* from the Bay of Naples, Italy, the body is more slender than that of *anchovia* (comparing specimens of equal size), the pectoral fin is somewhat shorter, and the ventral scutes are slightly more numerous, 35 and 37. However, the exact relationship must remain undetermined until more adequate material becomes available for comparison.

S. anchovia and the species herein designated *brasiliensis* are represented by close relatives in Cuba and Jamaica even though other specimens, such as those from Woods Hole, Massachusetts, and from Port-of-Spain, Trinidad, differ rather prominently. However, the material from Cuba and Jamaica is too meager and too indifferently preserved to determine the exact relationship (see *Relationship*, pp. 405, 409).

Variation. The increase in body depth and the number of gill rakers have already been noted (pp. 398, 399); examples of equal size also vary to a considerable degree in these respects. There is variation also in the position of the dorsal and pelvic fins, relative size of eye, shape of dorsal, and length of pectoral (see *Description*, p. 401).

Commercial Importance. These fish are not common enough regularly north of the Florida Keys to be of commercial importance, but at Tortugas, Florida, particularly offshore in 10–20 fms., they are common (*87*: 7, 8). Longley reported that terns fed upon them. Undoubtedly they are also preyed upon by predacious foodfishes. They were observed in the market in Havana, Cuba, in February and March 1912, by Nichols, who said: "Abundant in the Havana market" (*98*: 180).

Range. Woods Hole, Massachusetts, to the Florida Keys, and probably southward to southern Brazil. The specimens from the Gulf of Mexico coast seem to be *brasiliensis.* Apparently they do not occur regularly north of Florida. In the vicinity of Woods Hole, where they appear only during autumn (*124*: 741), they were abundant in the fall of 1892 at least. It has been said that they are generally common in the West Indies region.

Synonyms and References:

Sardinella anchovia Cuvier and Valenciennes, Hist. Nat. Poiss., *20*, 1847: 269 (orig. descr.; type local. Rio de Janeiro, Brazil); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 429 (descr., range); Meek and Hildebrand, Field Mus. Publ., Zool., *15* (1), 1923: 183 (synon., descr., range); Breder, Field Bk. Mar. Fish. Atl. Cst., 1929: 67, fig. (abund., food, size); Nichols, N. Y. Acad. Sci., *10* (2), 1929: 201 (distr., diagn., remarks, habits); Longley and Hildebrand, Publ. Carneg. Instn. Wash., 535, 1941: 7 (synon., relation. with *Clupea harengus*, *S. brasiliensis*, and *S. aurita*, descr., Tortugas, Florida, range).

Clupea anchovia Günther, Cat. Fish. Brit. Mus., *7*, 1868: 421 (diagn., range).

Clupea pseudohispanicus Kendall and Smith (in part, *Clupea harengus*), Bull. U. S. Fish Comm. (1894), *14*, 1895: 17 (distr., descr., probably two or more species; cf. specimens from diff. locals.).

Clupanadon pseudohispanicus Jordan and Evermann (in part *Clupea harengus*), Bull. U. S. nat. Mus., 47 (1), 1896: 423 (descr., after Kendall and Smith; relation. to European species); Smith, Bull. U. S. Fish Comm. (1897), *17*, 1898: 91 (Woods Hole, Massachusetts; usually found with young *Clupea harengus*); Linton, Bull. U. S. Fish Comm. (1899), *19*, 1901: 438 (food, parasites, Woods Hole, Mass.); Evermann and Marsh, Bull. U. S. Fish Comm. (1900), *20* (1), 1902: 84 (descr., distr., Puerto Rican names, size, synon.); Wilson, Proc. U. S. nat. Mus., *39*, 1911: 370 (parasitic copepod, *Bomolophus eminens*, on gills); Nichols, Bull. Amer. Mus. nat. Hist., *31* (18), 1912: 180 (abund. Havana, Cuba, market); Sumner, Osburn, and Cole, Bull. U. S. Bur. Fish. (1911), *31* (2), 1913: 741 (refs., Woods Hole, Mass., food, parasites); Meek and Hildebrand, Field Mus. Publ., Zool., *15* (1), 1923: 180 (synon., descr., distr.); Beebe and Tee-Van (in part *S. brasiliensis*), Zoologica, N. Y., *10* (1), 1928: 39 (refs., field char., discus.).

Sardinella aurita Regan (in part *S. brasiliensis*), Ann. Mag. nat. Hist., (8) *19*, 1917: 378 (synon., in part not this species; descr. in part, range); Jordan (in part not of C. and V.), Manual Vert. Anim. NE U. S., ed. 13, 1929: 41 (diagn., range); Jordan, Evermann, and Clark (in part not of C. and V.), Rep. U. S. Comm. Fish. (1928), 2, 1930: 43 (range, synon.).

Sardinia anchovia Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 43 (range, synon.).

Sardinia pseudo-hispanica Howell, Bull. Mus. comp. Zool. Harv., *82* (2), 1938: 171 (*S. pseudo-hispanica* Poey to synon. of *S. anchovia* C. and V.; cotypes).

Doubtful References:

Sardinia pseudo-hispanica Poey, Memorias, Cuba, 2, 1860: 311 (orig. descr.; type local. Cuba; cotypes Nos. 17768 and 17771; local name).

Clupea pseudohispanica Günther, Cat. Fish Brit. Mus., 7, 1868: 442 (descr. after Poey).

Sardinella brasiliensis (Steindachner) 1879

Sardinia, Sardinia de España, Spanish Sardine, Sardinha Verdadeira

Figure 101

Study Material. Numerous specimens, 82–129 mm TL, 64–98 mm SL, from Port-of-Spain, Trinidad. Also specimens for comparison, from Island of Marguerita, Venezuela; Cuba; Jamaica; Palmetto Key, and Pensacola, Florida; and many from Rio de Janeiro, Brazil, not used in preparing the description, since they are extralimital and may prove to be at least subspecifically distinct; all in the USNM collections.

Distinctive Characters. See *Relationship.*

Description. Proportional dimensions in per cent of standard length, and counts, based principally on study specimens, 64–98 mm SL.

Body: depth 22.4–26.9.
Caudal peduncle: depth 7.5–9.5.
Head: length 25.3–28.7; depth 18.7–22.
Snout: length 7.3–8.15.
Eye: diameter 6.9–7.9.
Interorbital: width 4.9–5.7.
Maxillary: length 10.7–11.7.
Anal fin: length of base 15.1–16.5.
Pelvic fin: length 9.9–11.2.
Pectoral fin: length 17.3–19.5.
Distance from snout to origin of: dorsal 44–47.5.
Scales: 42–47.
Ventral scutes: 32–34.
Fin rays: dorsal 17 or 18; anal 18–20; pectoral 15 or 16.
Vertebrae: 46 (4 specimens).

Body slender, strongly compressed, its greatest thickness about half of its depth, its greatest depth generally at dorsal origin, 3.7–4.45 in SL; ventral outline much more strongly convex than dorsal outline. Caudal peduncle strongly compressed, its depth 2.9–3.75 in head.

Scales only moderately adherent; those on middle of side below base of dorsal scarcely deeper than long, with 3 or 4 partly incomplete vertical grooves, the margin membranous and scarcely indented, but those on back in front of dorsal fin with definitely indented margin, and no vertical grooves; 4 or 5 rows of scales exposed between tip of pectoral and base of pelvic. The pair of modified scales at nape shorter than eye. Ventral scutes not prominent, 18 or 19 in front of pelvic fins and 14 or 15 behind them.

Head with length rather exceeding greatest depth of body, 3.5–3.95 in SL, its depth at vertical from slight crossgroove at occiput 4.55–5.35 in SL. Snout rounded, its margin without a median notch, 3.4–3.8 in head. Eye with diameter equal to, or a little longer than, snout (rarely slightly shorter), 3.4–3.8 in head. Interorbital (over middle of eye) 4.8–5.8. Cheek longer than deep. Maxillary broadly rounded posteriorly, reaching nearly or quite to vertical from anterior margin of pupil, 2.3–2.5 in head. Mandible projecting slightly, its margin within mouth rising rather gradually without forming a definite angle. Gill rakers long, very slender, extremely close-set, very difficult to count, the longest about as long as eye, the serrations on inner edge extremely minute; the rakers increasing in number with age and growth: 82 and 83 in specimens 64 and 68 mm SL, 116 in an 89-mm specimen, and 130 and 132 in specimens 91 and 93 mm SL (gill rakers removed for counting). Teeth absent in upper jaw; some fine points present on margin of maxillary; lower jaw with a row of 5–7 very small teeth anteriorly on each side of a median interruption; very small granular teeth present on palatines, pterygoids, and tongue.

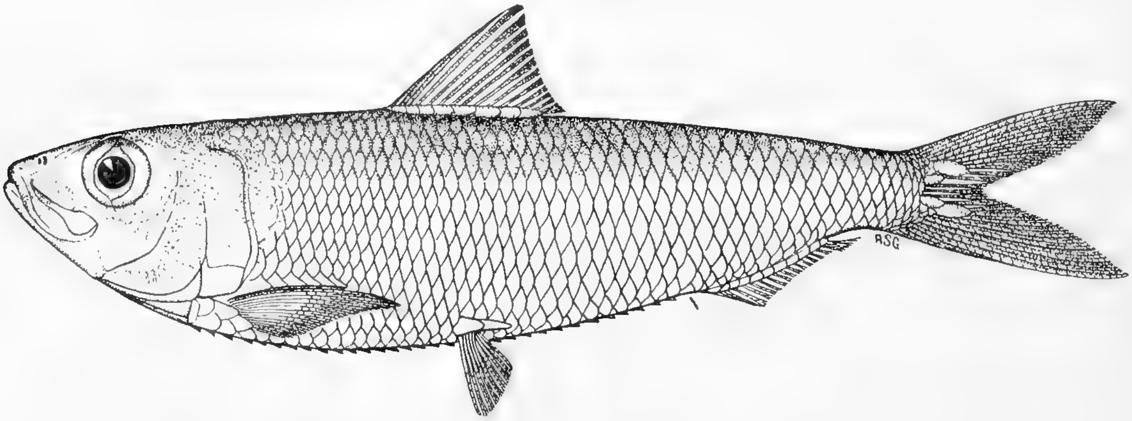

Figure 101. *Sardinella brasiliensis*, 122 mm TL, 94 mm SL, Port-of-Spain, Trinidad, USNM 124317. Drawn by Ann S. Green.

Dorsal fin moderately elevated anteriorly, its margin definitely concave, its longest rays usually failing to reach the tip of last ray if deflexed, its origin a little nearer to margin of snout than to vertical from last ray of anal, its distance from margin of snout 2.15–2.25 in SL; the base of fin with a very narrow sheath composed of a single row of elongated scales, the posterior ones having a free lower margin. Caudal fin rather deeply forked, the lower lobe slightly the longer; no small scales, but a few large modified ones on base of fin (Fig. 101). ANAL much lower than dorsal, its last two rays considerably enlarged and scarcely shorter than the longest ones in anterior lobe of fin, its origin generally a little nearer to base of caudal than to base of pelvic, its base 1.7–1.85 in head; a moderately broad sheath of scales at base. PELVIC fin with margin slightly convex when spread, reaching notably less than halfway to origin of anal, its shortest ray about 75 % of the length of the longest one, the fin inserted equidistant between base of pectoral and origin of anal, or a little nearer to the former, 2.5–2.8 in head; the axillary process reaching to or beyond midlength of fin. PECTORAL fin slightly falcate, generally failing to reach base of pelvic fin by a distance nearly equal to diameter of eye, its length from base to tip of longest ray 5.1–5.8 in SL, 1.4–1.55 in head.

Color. Bluish black above, changing abruptly to bright silvery at level of upper margin of eye. Region of shoulder, upper surface of head, snout, and mandible with dusky punctulations. Dorsal and caudal more or less dusky, the lobe of the dorsal dusky when folded, the dusky appearance being caused by dark dots on the rays (missing on inter-radial membranes); the other fins plain, translucent, except for dark dots on one or two uppermost rays of pectoral. Peritoneum black.

Size. The largest example included in the collections examined is 180 mm (7.2 in.) TL, 145 mm SL. However, examples 230 mm (9.2 in.) long have been reported (*25*: 189).

Development. No young definitely identified as this species are included in the collections examined, the smallest being 82 mm TL, 64 mm SL. Nevertheless, it is evident that the remarks on the development of young *S. anchovia* (p. 404) also apply to this species, as the smallest examples are the slenderest and have the fewest gill rakers on the lower limb.

Food. The food of this species has not been listed. However, the very numerous close-set gill rakers and the stomach with heavy walls and numerous pyloric coeca suggest a diet consisting of plankton.

Relationship. This species has been here designated as *brasiliensis* principally because of Longley's discovery that the type material of *anchovia*, in Paris, consisted of two species (*87*: 7), as stated in the account of *anchovia* (p. 405). Accordingly, Longley assigned the specimens with the more numerous gill rakers to *brasiliensis*, which may be correct, but positive proof is lacking, as the original description of *brasiliensis* gives neither the number of rakers nor any other diagnostic character as herein understood. The specimens (or species) with the greater number of rakers were compared with one identified as "*Clupea brasiliensis* Steindachner," also from Rio de Janeiro, Brazil; they were found to be identical with it.

S. brasiliensis is close to *anchovia* according to a limited number of rather indifferently preserved specimens, from Cuba and Jamaica. However, specimens from Port-of-Spain, Trinidad, and from Venezuela are quite distinct from those of our Atlantic coast, the most outstanding difference being the greater number of gill rakers in *brasiliensis*; other differences include the position of the dorsal and pelvic fins, the size of the eye, and the length of maxillary and pectoral fin.

The numerous specimens from Rio de Janeiro, Brazil, examined and measured in part, differ somewhat from those taken at Port-of-Spain, Trinidad, which serve chiefly as the basis for this description. In fact, the former are less distantly removed from specimens of *anchovia* from the eastern United States than from those of Trinidad, as the eye runs a little smaller (5.75–7.25 % of SL), the maxillary is rather shorter (9.5–11 % of SL), the pectoral is a little shorter (16–18 % of SL), and the gill rakers are somewhat less numerous (108–117 in specimens 97–109 mm SL). Therefore, a subspecific difference is suggested. Indeed, it seems highly probable that further study will show some intergradation among all species recognized in these pages.

S. brasiliensis, like *S. anchovia*, apparently was incorrectly synonomized with *S. aurita* of Europe and elsewhere by Regan (p. 405). According to data based on specimens from Messina, Sicily, its type locality, *aurita* grows larger than *brasiliensis* and has fewer gill rakers in examples of equal size. These species may therefore be regarded as valid unless further evidence shows this opinion to be incorrect.

Commercial Importance. This sardine is of at least some commercial importance at Port-of-Spain, Trinidad, where Waldo L. Schmitt of the U. S. National Museum obtained from the market (April 18, 1939) the fine series of specimens used in preparing the foregoing description. It is abundant and occurs also in large numbers in the market at Rio de Janeiro, Brazil, but southward in the state of São Paulo it is less numerous (*25*: 188).[48]

Range. The west coast of Florida, the West Indies, and Venezuela to southern Brazil. Not reported for México to Colombia.

Synonyms and References:

Clupea brasiliensis Steindachner, S. B. Akad. Wiss. Wien, *80*, 1879; Ichthyol. Beitr., 8: 64 (orig. descr.;[49] type local. Rio de Janeiro, Brazil).

Sardinella aurita Regan (in part), Ann. Mag. nat. Hist., (8) *19*, 1917: 378 (synon., in part *anchovia*; descr. in part; range); Campos, Arqu. Zool. estad. São Paulo (1941), *3* (7), 1942: 188, fig. 2 (synon., descr., abund. in market, range, specimens coll. in Brazil); Oliveira (not of Cuvier and Valenciennes), Min. Agr. Dep. Nac. Pro. Anim., Div. Caça e Pesca, 1942: 22 (ref., range).

Clupanodon pseudohispanicus Beebe and Tee-Van (in part *anchovia*), Zoologica, N.Y., *10* (1), 1928: 39 (refs., field char., discus.).

Sardinella brasiliensis Longley *in* Longley and Hildebrand, Publ. Carneg. Instn. Wash., 535, 1941: 7 (cf. *anchovia* and *aurita*).

Doubtful References:

Clupanodon pseudohispanicus Evermann and Kendall, Rep. U. S. Comm. Fish. (1899), 1900: 55 (Pensacola and Snapper Banks, Florida).

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[48] The Brazilian Sardinha, or Sardinha Verdadeira (true sardine), is the most important market fish in the area between Victoria, Espirito Santo, and Santos, São Paulo. It is not taken commonly north of this area, and it is to be questioned that this fish is identical with the populations farther to the north.—G.S.M.

[49] Fowler has shown that *Clupea brasiliensis* Steindachner 1879 is a primary homonym of *Clupea brasiliensis* Schneider 1801 (equals *Albula vulpes*). Fowler uses the specific name *allecia* (of Rafinesque), but the latter applies to European fish, which Fowler, following Regan, would apparently unite with the American form. If the American form is distinct it would appear to be nameless, unless changes in the International Rules of Zoological Nomenclature, now said to be imminent, would restore the availability of Steindachner's name. Until this genus is adequately revised for the entire Atlantic and the relationships of the American and European populations are worked out, it would seem premature to disturb the nomenclature.—G. S. M.

Sardinella anchovia Schreiner and Miranda-Ribeiro, Arch. Mus. nac., Rio de J., 12, 1903: 91 (Rio de Janeiro, range, names); Metzelaar (probably not of Cuvier and Valenciennes), Rapp. Vissch. Curaçao, ed. by Boeke, 1, W. Indian Fishes, 1919: 10, fig. 2 (Dutch West Indies: fig. seems based on *brasiliensis* as herein understood).

Sardinella aurita von Ihering (not of Cuvier and Valenciennes), Rev. Industr. Anim., 1 (3), 1930: 228 (synon., fin rays, scales, ventral scutes, Brazil).

Genus *Rhinosardinia* Eigenmann 1912

Rhinosardinia Eigenmann, Mem. Carneg. Mus., *5*, 1912: 445; type species by original designation, *Rhinosardinia serrata* Eigenmann. Myers, Copeia, 1929: 1; *Heringia* preoccupied in *Diptera.*

Generic Synonym:

Heringia Fowler, Proc. Acad. nat. Sci. Philad., *63*, 1911: 207; type species by original designation, *Clupea amazonica* Steindachner; name preoccupied in Diptera.

Characters. BODY moderately elongate, strongly compressed; ventral outline more strongly convex than dorsal outline. BONY SCUTES on chest and abdomen well developed, the posterior one ending in a rather long sharp spine. SCALES adherent, each with a prominent vertical groove having more or less horizontal laterals (not verified in *bahiensis*). MOUTH strongly oblique. MANDIBLE projecting. MAXILLARY broadly rounded posteriorly, with a strong sharp backward projecting spine near its anterior end (Fig. 103); maxillary-premaxillary margin continuous, composed of a soft membranous section; entire margin toothless. TEETH absent on vomer, but present on mandible (at least in *serrata* and *bahiensis*), palatines, pterygoids, and tongue. GILL RAKERS rather numerous (about 30–40 on lower limb of first arch in *serrata*), close-set. DORSAL fin about over middle of body, with approximately 14–17 rays. ANAL fin scarcely longer than dorsal and placed well behind it, with about 15–18 rays. PELVIC well developed, with 8 rays. PECTORAL rather small, more or less equal to head in length.

Remarks. This genus differs from all others of this family in the presence of a small sharp spine on the anterior part of the maxillary, close behind the premaxillary. It differs further from related genera in the small anal fin, which is situated well behind the dorsal fin.

Range. This genus of small herrings is confined to northeastern and northern South America, from Rio de Janeiro to Venezuela, in fresh, brackish, and salt water.

Key to Species

1 a. Sides with a prominent silvery lateral band, about as wide as eye; origin of dorsal about over insertion of pelvic fin and nearly an eye's diameter nearer to tip of snout than to base of caudal; teeth present on mandible, maxillary, and premaxillary; dorsal with 17 rays; anal with 18; scales 44. *bahiensis* (Steindachner) 1879.
Coast of Brazil from Bahia (Baía) to Rio de Janeiro.

1 b. Sides without silvery band; origin of dorsal definitely behind insertion of pelvic fin and about equidistant between margin of snout and base of caudal; teeth missing on maxillary and premaxillary; dorsal with 14 or 15 rays; anal with 15–17 rays; scales 35–38.

2 a. Greatest depth of body 3.5–4.0 in SL (75- and 40-mm specimens, respectively); depth of caudal peduncle close to half of greatest depth of body; head 4.0 in SL; snout 4.0 in head; base of dorsal fin about as long as its longest rays. *amazonica* (Steindachner) 1879, below.

2 b. Greatest depth of body 3.1–3.4 (60–68-mm specimens) in SL; depth of caudal peduncle definitely less than half of greatest depth of body; head 4.25–5.1 in SL; snout 4.6–5.5 in head; base of dorsal fin notably shorter than its longest rays. *serrata* Eigenmann 1912, p. 413.

Rhinosardinia amazonica (Steindachner) 1879

Study Material. None.

Distinctive Characters. This species is closely related to *serrata*. However, *amazonica* differs from *serrata*, according to the original description, in the somewhat more slender body, slightly larger head, longer snout, the proportionately deeper caudal peduncle, in the absence of teeth on the mandible, and in the somewhat different proportion of the longest dorsal rays with respect to the head length and dorsal base.

Description. Proportional dimensions in per cent of standard length, and counts, modified after the original description by Steindachner (see Synonyms and References).

Body: depth 27.5 in 75-mm examples, about 25 in those 40 mm long.
Head: length 25.

Scales: 37.
Ventral scutes: 27.
Fin rays: dorsal 15; anal 16.

BODY strongly compressed, its ventral outline notably more strongly convex than dorsal outline, its greatest depth 3.5 in SL in large examples, 4.0 in smaller ones. CAUDAL PEDUNCLE deep in comparison with depth of body, close to half of greatest depth.

SCALES adherent; about 37 in a horizontal row between margin of opercle and base of caudal; a vertical groove dividing the free (exposed) part of scale from the covered part, 2 or 3 sharp grooves on the former. VENTRAL SCUTES on chest and abdomen, 15 in front of pelvic fins and 12 behind them.

HEAD 4.0 in SL. SNOUT 4.0 in head. EYE 3.0. MOUTH small. MAXILLARY reaching little beyond anterior margin of eye. MANDIBLE projecting little. TEETH absent on premaxillary, mandible, and vomer.

DORSAL fin with base about as long as longest rays, its origin a little behind vertical at insertion of pelvic, and equidistant between end of head (snout) and base of caudal.

Caudal about 1.5 times length of head, with slender pointed lobes covered with scales anteriorly.

Color. Body silvery; head yellowish white.

Size. The largest example reported was 75 mm long.

Development. Small specimens (40 mm) are more slender than larger ones (75 mm), according to the original description, and the ventral outline is strikingly less convex in the smaller ones. However, the proportionate depth of the caudal peduncle and the greatest depth of the body are about the same in both small and large specimens.

Range. Known only from Pará, Brazil.

Synonyms and References:

Clupea amazonica Steindachner, S. B. Akad. Wiss. Wien, *80*, 1879; Ichthyol. Beitr., *8*: 65 (orig. descr., type local. "Amazon R. at Pará"); von Ihering, Dic. Anam. Brasil, 1940: 716 (habitat).

Rhinosardinia amazonica Myers (in part not of Steindachner), Copeia, 1929: 1 (*R. serrata* thought to be a synon., following Regan, which seems to be incorrect).

Sardinella (*Rhinosardinia*) *amazonica* von Ihering, Rev. Indust. Anim., 1 (3), 1930: 229 (synon., diagn., relation.).

Negative Reference:

Heringia amazonica Regan (not of Steindachner), Ann. Mag. nat. Hist., (8) *19*, 1917: 394 (descr. based on cotypes of *R. serrata*; synon. apparently incorrect).

Rhinosardinia serrata Eigenmann 1912

Figures 102, 103

Study Material. Five cotypes, 60–68 mm TL, 46–49 mm SL, from Morawhanna, British Guiana, USNM 66284.

Distinctive Characters. See *Relationship.*

Description. Proportional dimensions in per cent of standard length, and counts, based on the five cotypes, 46–49 mm SL.

Body: depth 29.5–32.
Caudal peduncle: depth 1.55–1.95.
Head: length 19.5–23.5; depth 20.5–21.5.
Snout: length 4.1–4.55.
Eye: diameter 6.2–6.75.
Interorbital: width 4.25–4.8.
Maxillary: length 9.1–10.
Mandible: length 8.4–9.1.
Anal fin: length of base 12.7–14.3.
Pelvic fin: length 15.5–17.
Pectoral fin: length 19.2–20.5.
Distance from snout to origin of: dorsal 47–51.

Scales: 35–38.
Ventral scutes: 27–29.
Fin rays: dorsal 14 or 15; anal 15–17; pectoral 11 or 12.
Vertebrae: 29 (105: 394).

Body rather deep but not excessively compressed, its greatest thickness about a fourth of its depth, its greatest depth 3.1–3.4 in SL; dorsal outline gently convex anteriorly, the ventral outline somewhat more strongly convex. CAUDAL PEDUNCLE scarcely as long as deep, its depth definitely less than half of greatest depth of body, 1.55–1.95 in head.

SCALES closely adherent, thin, almost circular, with even margin and with a prominent, nearly complete vertical groove provided with 1–3 horizontal branches on each side; scales extending well out on caudal fin. VENTRAL SCUTES well developed, especially the posterior ones, each with a prominent spine, 16 in advance of pelvic fins and 11–13 behind them.

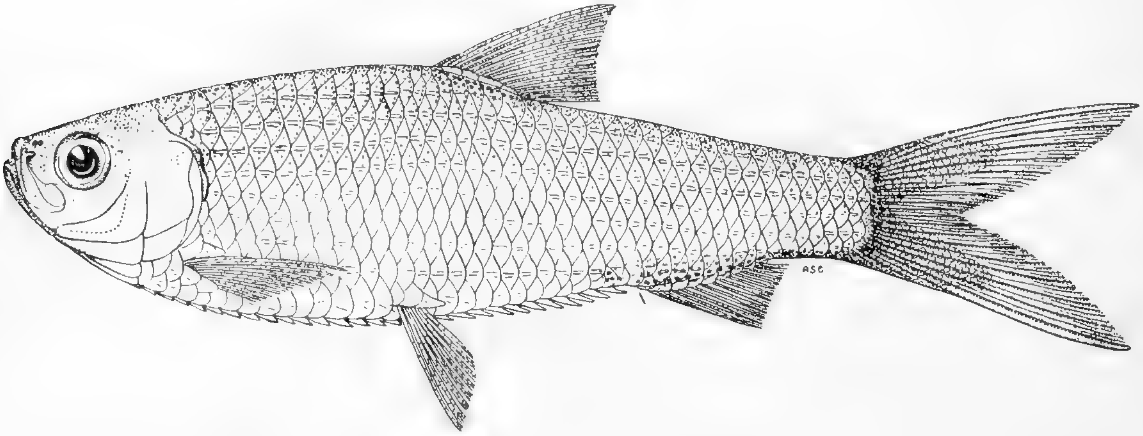

FIGURE 102. *Rhinosardinia serrata,* 63 mm TL, 47 mm SL, Morawhanna, British Guiana, cotype, USNM 66284. Drawn by Ann S. Green.

HEAD rather short and deep, its length 4.25–5.1 in SL, its depth at vertical from crossgroove at occiput 4.65–4.9. SNOUT definitely shorter than eye, 4.6–5.5 in head. EYE 3.0–3.8. INTERORBITAL moderately narrow, 4.1–5.25 in head. CHEEK longer than deep. MOUTH strongly oblique. MAXILLARY broadly rounded posteriorly, reaching nearly or quite below anterior margin of pupil, 2.1–2.5 in head. MANDIBLE projecting moderately, its margin within mouth rising strongly, forming a broadly rounded obtuse angle, 2.15–2.6 in head. GILL RAKERS slender, close-set, very difficult to count, approximately half as long as eye, about 35–40 on lower limb. TEETH all minute, present on mandible anteriorly and on palatines, pterygoids, and tongue, but absent on maxillary, premaxillary, and vomer.

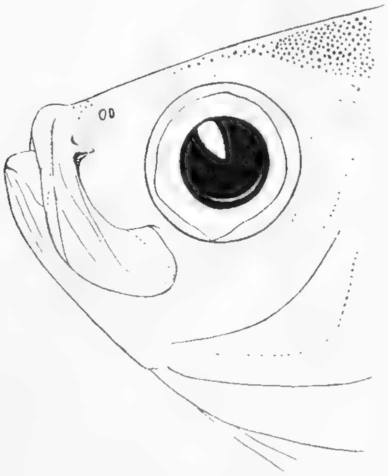

FIGURE 103. *Rhinosardinia serrata* head showng spine near end of maxillary, from specimen in Fig. 102. Drawn by Ann S. Green.

DORSAL fin well developed, rather high anteriorly, its margin concave, its longest rays exceeding the length of base, about as long as head, reaching far beyond tip of last ray if deflexed, its origin slightly nearer to margin of snout than to base of caudal, its distance from margin of snout 1.95–2.1 in SL, its base nearly as long as that of the anal; a narrow sheath of scales on anterior part of base. CAUDAL fin long, rather deeply forked, the upper lobe exceeding greatest depth of body by more than diameter of eye. ANAL fin small, its origin about half of length of head behind base of dorsal and a little nearer to base of caudal than to insertion of pelvic, its base notably shorter than head, 6.9–7.8 in SL; a narrow sheath of scales at base. PELVIC fin long, pointed, inserted about half of eye's diameter in advance of dorsal fin and about equidistant between base of pectoral and vent, 1.2–1.5 in head. PECTORAL failing to reach base of pelvic by diameter of eye, scarcely as long as head, 4.9–5.0 in SL.

Color. Brownish in alcohol, with metallic reflections. Sides of head silvery. Back, upper surface of head, snout, and mandible with dusky dots; dusky dots also on the fins, exclusive of pelvics.

Size. The largest specimens reported to date are only 85 mm (3.4 in.) TL.

Relationship. This species was synonymized with *R. amazonica* by Regan in his revision of this and related genera (*106*: 394). A careful rereading of the original description of *amazonica*, with syntypes of *serrata* in hand, reveals some differences that seem too important to dismiss. Accordingly, the species herein are recognized as distinct. For a definite determination of the relationship of the two species, a more accurate description of specimens from the type locality of *amazonica* is needed.

Range. Known from Venezuela and from Dutch and British Guiana.

Synonyms and References:

Heringia amazonica Fowler (probably not of Steindachner, but *serrata* Eigenmann), Proc. Acad. nat. Sci. Philad., *63*, 1911: 207 (14 specimens from "Surinam"; made type of a new genus, *Heringia*; preoccupied in Diptera); Regan (not of Steindachner), Ann. Mag. nat. Hist., (8) *19*, 1917: 394 (*Rhinosardinia serrata* Eigenmann apparently incorrectly synon.; descr. based on cotypes of *R. serrata*).

Rhinosardinia serrata Eigenmann, Mem. Carneg. Mus., *5*, 1912: 445, text fig. 39, pl. 62, figs. 3 and 4 (orig. descr., type local. Morawhanna and Mora Passage, British Guiana; type CM 2443).

Rhinosardinia amazonica Myers (in part not of Steindachner), Copeia, 1929: 1 (*R. serrata* thought to be synon., following Regan, which seems to be incorrect); Fowler (probably not of Steindachner, but *serrata* Eigenmann), Proc. Acad. nat. Sci. Philad., *83*, 1931: 406 (name and locals. only; Caño Guanoco and Punta Tigre at mouth of San Juan R., Venezuela).

Genus *Ilisha* Gray 1846

Ilisha Gray *in* Richardson, Ichthyol. Seas of China, Japan, Rep. Brit. Ass. Adv. Sci. (1845), 1846: 306; type species by monotypy, *Ilisha abnormalis* Gray equals *Alosa elongata* Bennett; Myers, Copeia, 1950: 63; notes on identity with *Neosteus* and *Pseudochirocentrodon*.

Generic Synonyms:

Platygaster Swainson, Nat. Hist. Fish. Amphib. Rept., *2*, 1839: 294; type species *Clupea africana* Bloch, first designated by Jordan, Genera Fishes, 1919: 203; name preoccupied in bees.

Pellona Cuvier and Valenciennes, Hist. Nat. Poiss., *20*, 1847: 300; type species *Pellona orbignyana* Cuvier and Valenciennes, first designated by Gill, Proc. Acad. nat. Sci. Philad., 1861: 37; but *P. orbignyana* equals *Pristigaster flavipinnis* Valenciennes (*in* d'Orbigny), Voyage Amer. Merid., Poiss., 5 (2), 1847: 8; Atlas, d'Orbigny, 1839: pl. 10, fig. 2.

Zunasia Jordan and Metz, Mem. Carneg. Mus., 6, 1913: 7; type species by monotypy, *Pristigaster chinensis* Basilewsky equals *Alosa elongata* Bennett.

Pseudochirocentrodon Miranda-Ribeiro, Publ. Comm. Linhas Telegr. Estrat. Matto Grosso Amazonas, 58, 1923 ("1920"): 8; type species by monotypy, *P. amazonicum* Miranda-Ribeiro.

Neosteus Norman, Ann. Mag. nat. Hist., (9) *11*, 17, 1923: type species *Pellona ditchela* Valenciennes by subsequent designation of Norman, Zool. Rec., Pisces, for 1923: 25.

Characters. BODY elongate, rather strongly compressed, its ventral outline more strongly convex than dorsal outline. BONY SCUTES strong, about 25–37 along sharp edge on chest and abdomen. SCALES small to rather large, often missing on preserved specimens, generally with several irregular vertical grooves. SNOUT with or without a definite median notch. MOUTH moderate, strongly oblique. MANDIBLE projecting strongly. MAXILLARY generally reaching under anterior half of eye, with a bone or ligament between it and premaxillary. TEETH all small, present in a single series on anterior part of mandible, on premaxillaries, maxillaries, and usually in bands on palatines, pterygoids, and tongue, but none on vomer. GILL RAKERS strong, serrate, about 12–25 on lower limb of first arch (in American species). DORSAL fin with about 15–20 rays (in American species). ANAL fin long, its origin under posterior rays of dorsal or just behind that fin, with about 36–52 rays (in American species). PELVIC fin small (occasionally absent in one species), with 6 or 7 rays (in American species).

Remarks. This genus is characterized by the elongated, compressed body with a strongly convex ventral outline, by the very long anal fin, and by the small pelvic fin, inserted in advance of the dorsal fin and consisting of only 6 or 7 rays. Furthermore, the premaxillary and maxillary are not adjoined, a soft ligament (in *Ilisha*) or a bone (in *Neosteus*) being present between them.[50]

Range. Tropical parts of the Atlantic, Indian, and Pacific oceans. Fresh waters of the Amazon Basin. One species, *I. narragansetae*, reported from Rhode Island.

Key to Species of the Western Atlantic and Tributary Rivers

1a. Ventral scutes 20–25 before and 10–14 behind pelvic fins, total number 32–37.
  2a. Gill rakers only 12 or 13 on lower limb; scales 72–75 in a lateral series; depth of body less than a third (27.5–30 %) of SL.
    altamazonica Cope 1872, p. 417.
  2b. Gill rakers 23–31 on lower limb; scales fewer than 70 in a lateral series; depth of body about equal to a third (30–37 %) of SL.
    3a. Dorsal fin with 19 or 20 rays; gill rakers on lower limb 23–26; axillary process of pectoral reaching middle of first ray.
      castelnaeana (Cuvier and Valenciennes) 1847, p. 419.

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[50] See Myers (97: 63) for discussion.

3b. Dorsal fin with 17 or 18 rays; gill rakers on lower limb 30 or 31; axillary process of pectoral not reaching middle of fin.
flavipinnis Valenciennes 1839.
Buenos Aires, Argentina.

1b. Ventral scutes 19–25 before and only 6 or 7 behind pelvic fins, total number 25–32.

4a. Depth of body less than a third (30 %) of SL; scales about 60 in a lateral series; gill rakers 19 on lower limb; anal with 47–52 rays.
amazonica (Miranda-Ribeiro) 1923, p. 421.

4b. Depth of body about equal to or greater than a third (33–40 %) of SL; scales 33–45 in a lateral series; gill rakers 22–25 on lower limb.

5a. Depth of body greater than a third (37–40 %) of SL; ventral scutes 19–21 before and 6 behind pelvic fins; pectoral with 13–15 rays; anal with 36–42 rays. *harroweri* Fowler 1917, p. 423.

5b. Depth of body about equal to a third (33 %) of SL; ventral scutes 25 before and 7 behind pelvic fins; pectoral with 16 rays; anal with 45 rays.
narragansetae Fowler 1911, p. 426.

Ilisha altamazonica (Cope) 1872

Apapa

Figure 104

Study Material. Three specimens, 280, 305, and 360 mm TL, 220, 234, and 275 mm SL, from "the Amazon River region, Pará to Manáos," Brazil, USNM 52548.

Distinctive Characters. This species is characterized by the slender body and small scales. It differs especially from related species in the very few gill rakers on the lower limb of the first arch.

Description. Proportional dimensions in per cent of standard length, and counts, based on study specimens, 220–275 mm SL.

Body: depth 27.5–30.
Caudal peduncle: depth 9.4–9.5.
Head: length 25.5–27; depth 21.5–23.5.
Snout: length 5.15–5.5
Eye: diameter 6.2–6.8.
Interorbital: width 12–13.5.
Maxillary: length 12.8–13.5.
Mandible: length 14–15.
Anal fin: length of base 29–31.
Pelvic fin: length 7.5–8.1.
Pectoral fin: length 20.5–22.7.
Distance from snout to origin of: dorsal 50–52.

Scales: 72–75.
Ventral scutes: 32 or 33.
Fin rays: dorsal 18; anal 37–40; pectoral 16 or 17.

BODY quite slender, rather strongly compressed, its greatest thickness about 2.5 times in its depth, its greatest depth 3.3–4.65 in SL; the dorsal outline gently convex, the ventral outline much more strongly convex. CAUDAL PEDUNCLE rather strong, its depth 2.7–2.8 in head.

SCALES adherent; those on middle of side below anterior rays of dorsal definitely deeper than long, without vertical grooves, closely imbricated; the exposed part rather more than two times deeper than long: the membranous margin only slightly irregular. VENTRAL SCUTES moderately developed, 22 or 23 in advance of pelvic fins and 10 or 11 behind them.

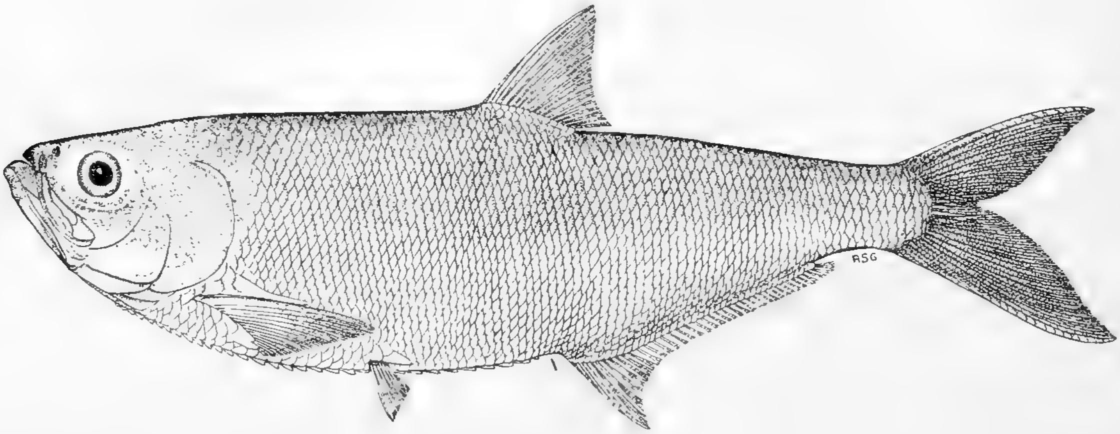

FIGURE 104. *Ilisha altamazonica,* 360 mm TL, 275 mm SL, Amazon River somewhere between Pará and Manáos, Brazil, USNM 52548. Drawn by Ann S. Green.

HEAD 3.7–3.9 in SL, its depth at vertical from slight crossgroove at occiput 4.25–4.65. SNOUT only a little shorter than eye, with a prominent median notch, 2.0–2.05 in head. EYE with much adipose tissue, 3.9–4.3. INTERORBITAL 2.0–2.15 in head. CHEEK deeper than long. MAXILLARY rather narrowly rounded posteriorly, reaching below middle of eye, 2.0–2.05 in head; a narrow bone with teeth between premaxillary and maxillary. MANDIBLE projecting strongly, its tip scarcely below dorsal outline of head, its margin within mouth rising gently, 1.8–1.85 in head. GILL RAKERS at angle of first arch about 75 % of length of eye, only 12 or 13 on lower limb. TEETH small, in a single row, on anterior part of mandible and on premaxillaries; minute teeth on margin of maxillary, and still smaller teeth on the bone between premaxillary and maxillary; bands of minute granular teeth on palatines, pterygoids, and tongue.

DORSAL fin rather high anteriorly, its longest rays reaching far beyond the tip of last ray if deflexed, its origin equidistant between margin of snout and base of caudal, or a little nearer to snout, its distance from margin of snout 1.9–2.0 in SL; a sheath composed of a single row of scales at its base. CAUDAL fin well forked, the lower lobe much the longer; small scales extending onto the fin, covering most of it. ANAL fin long, with a definite lobe anteriorly, its origin immediately behind a vertical from last dorsal ray, only a little nearer to margin of opercle than to base of caudal, its base 3.2–3.4

in SL; a sheath composed for the most part of two rows of scales at its base. Pelvic fin small, inserted fully an eye's diameter in advance of vertical from origin of dorsal and a little nearer to base of pectoral than to origin of anal, 3.15–3.45 in head; free axillary process about 66 % of the length of fin. Pectoral fin reaching well beyond base of pelvic, its length 4.4–4.9 in SL, 1.15–1.3 in head; a free axillary process present along about 66 % of length of fin.

Color. Old preserved specimens grayish brown above, silvery below, with indefinite alternating light and dark streaks along the rows of scales. A slight shoulder spot present. Interorbital, upper surface of snout, and tip of mandible dark brown. Dorsal, caudal, and pectoral fins largely dusky, the lower lobe of caudal with a dark area on its middle rays, this area narrow anteriorly but spreading posteriorly.

Range. Originally described from the Ambyiacu River, a tributary emptying into the Amazon near Pebas, Peru; also reported from Iquitos, Peru, and the Tocantins River, Brazil. The three specimens now at hand are from the lower Amazon.

Synonyms and References:

Pellona altamazonica Cope, Proc. Acad. nat. Sci. Philad., 1872: 265 (orig. descr.; type local. Ambyiacu R., trib. of upper Amazon).

Ilisha altamazonica Eigenmann, Rep. Princeton Exped. Patagonia, 1896–1899, *3* (4), 1910: 452 (ref., range); Eigenmann and Allen, Fishes West. S. Amer., 1942: 333 (refs., range); Myers, Copeia, 1950: 64 (synon.).

Neosteus altamazonica Norman, Ann. Mag. nat. Hist., (9) *11*, 1923: 19 (ref., descr.).

Ilisha (*Neosteus*) *altamazonica* von Ihering, Rev. Indust. Anim., 1 (3), 1930: 230 (fin rays; note "Amazonas, rio Tocantins").

Ilisha desuratus Nakashima, Bol. Mus. Hist. Nat., "Javier Prado," 5 (16), 1941: 77, fig. (orig. descr.; type local., environs of Iquitos, Peruvian Amazon).

Negative Reference:

Ilisha altamazonica de Menezes (not of Cope). Publ. Serv. Piscic., Dep. Nac., Ceará, Brazil, 113, 1946: 1 (notes on common name; local. of coll., ident., etc. Later publication [113A, 1947: 1] refers this to synon. of *I. castelnaeana*).

Ilisha castelnaeana (Cuvier and Valenciennes) 1847

Cagona, Apapa, Sardinha Grande, Pirapema, Gros Hareng

Study Material. None.

Distinctive Characters. See *Relationship.*

Description. Proportional dimensions in per cent of standard length, and counts, after Norman (99: 19), "three specimens 280–390 mm in length," presumably TL.

Body: depth 33.3–37.
Head: length 26.5–27.5.
Anal fin: length of base 28–29.
Scales: 63–66.
Ventral scutes: 34–37.
Fin rays: dorsal 19 or 20; anal 40 or 41.

Body with greatest depth 3.25–3.33 in SL; the ventral outline more strongly convex than dorsal outline. Scales relatively small. Ventral scutes 21–23 in advance of pelvics and 13 or 14 behind them. Snout a little shorter than eye. Eye 3.8–4.0 in head. Maxillary extending to or a little behind middle of eye. Mandible projecting strongly. Gill rakers 23–26 on lower limb of first arch. Dorsal origin nearer to margin of snout than to base of caudal. Anal with origin behind dorsal base, its base 3.5–3.6 in SL. Pelvic longer than eye, inserted much nearer to base of pectoral than to origin of anal. Pectoral with axillary process reaching to or beyond middle of first ray of fin.

Color. According to the original account, greenish above, silvery ventrally. Lower lobe of caudal with a large dark spot; other fins yellowish.

Size. See *Description.*

Relationship. This species seems to be closely related to *I. flavipinnis*, a species apparently reported only from Buenos Aires, Argentina, with which *castelnaeana* has sometimes been considered identical. According to Norman, the latest revisor of this and related genera, *flavipinnis* has more gill rakers on the lower limb of the first arch (30 or 31) and an axillary process of the pectoral fin that is shorter, not reaching the middle of the first ray (*99*: 17). These differences seem to be substantiated by two specimens (USNM 77357) about 220 and 230 mm TL (caudal damaged), 173 and 187 mm SL, from Buenos Aires. Furthermore, the dorsal and anal of *flavipinnis* seem to have fewer rays (D. 17 and 18; A. 38 and 39) and a shorter anal fin base (3.45 and 3.55 in SL). In color the specimens of *flavipinnis* differ from *castelnaeana*, as described, in the absence of a dark spot on the lower lobe of the caudal.

Range. "Coast of Surinam and Brazil; Upper Amazons" (Norman).

Synonyms and References:

Pellona castelnaeana Cuvier and Valenciennes, Hist. Nat. Poiss., *20*, 1847: 306 (orig. descr.; type local., around mouth of Amazon R.); Fowler, Arqu. Zool. estad. São Paulo, 3 (6), 1941: 134 (refs.).

Pellona flavipinnis Günther (not of Valenciennes), Cat. Fish. Brit. Mus., *7*, 1868: 454 (descr. based on specimens from Surinam, where species does not occur); Boulenger (not of Valenciennes), Ann. Mag. nat. Hist., (6) *20*, 1897: 298 (Marajó I., Brazil); Goeldi (not of Valenciennes), Bol. Mus. Paraense Hist. Nat., *2* (3), 1898: 486 (refs., names); Puyo (not of Valenciennes), Bull. Soc. Hist. nat. Toulouse, *70*, 1936: 166 (refs., descr., habits, habitat, commerc. import.).

Ilisha flavipinnis Jordan and Evermann (not of Valenciennes), Bull. U. S. nat. Mus., 47 (1), 1896: 435 (descr. after Günther, 1868); Eigenmann (in part not of Valenciennes), Rep. Princeton Exped. Patagonia, 1896–1899, *3* (4), 1910: 452 (*I. castelnaeana* incorrectly synon., range, includ. both species); Eigenmann (not of Valenciennes), Mem. Carneg. Mus., *5*, 1912: 446 (descr., Georgetown, British Guiana, where species does not occur); Starks (not of Valenciennes), Stanf. Univ. Publ., Univ. Ser., 1913: 8 (Pará, Brazil, where species apparently does not occur).

Neosteus castelnaeana Norman, Ann. Mag. nat. Hist., (9) *11*, 1923: 19 (synon., descr., range).

Ilishe (*Neosteus*) *castelnaeana* von Ihering, Rev. Industr. Anim., 1 (3), 1930: 230 (refs., fin rays; "Amazonias e Guyana; entra no rias").

Ilisha altamazonica de Menezes (not of Cope), Publ. Serv. Piscic. Dep. Nac., Ceará, Brazil, 113, 1946: 1 (notes on common name; local. of coll., ident., etc.).

Ilisha castelnaeana de Menezes, Publ. Serv. Piscic. Dep. Nac., Ceará, Brazil, 113A, 1947: 1 (*I. altamazonica* of de Menezes, 1946, to synon. of this species).

Ilisha amazonica (Miranda-Ribeiro) 1923

Apapa, Sardina, Asuna Nãhui

Figure 105

Study Material. Type of *I. apapae*, about 200 mm TL (caudal damaged), 160 mm SL; exact place of capture unknown, being registered merely as having been collected in "the Amazon River region, Pará to Manáos," Brazil; USNM 52550.

Distinctive Characters. This species differs from the other local species in having a ligament between the premaxillary and maxillary; the others have a narrow bone bearing fine teeth along the margin. Its body is slender as in *altamazonica*, but its scales are apparently somewhat larger, its dorsal rays fewer, and its anal rays more numerous. It has more gill rakers than *altamazonica* but fewer than the other species herein described. It is nearest to *furthii* of the Pacific coast of tropical America, which also has a ligament between the premaxillary and maxillary; but it differs from that species in having fewer ventral scutes (34–37 in *furthii*), and in the position of the pelvic fin—inserted notably nearer to the origin of anal than to the base of pectoral in *amazonica* but equidistant between these points in *furthii*; also they differ in several other respects.

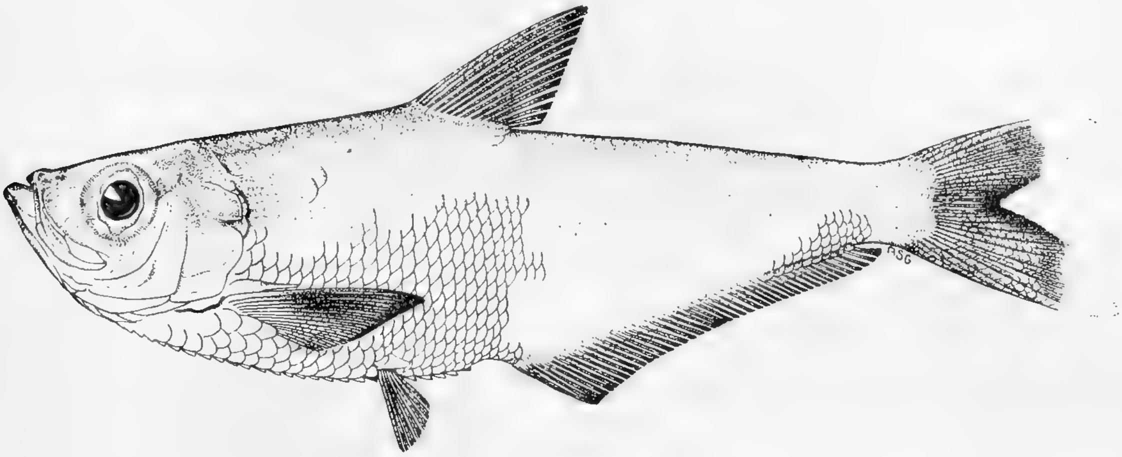

FIGURE 105. *Ilisha amazonica*, about 200 mm TL (caudal damaged), 160 mm SL, Amazon River, Brazil, type of *I. apapae*, USNM 52550. Drawn by Ann S. Green.

Description. Proportional dimensions in per cent of standard length, and counts, based on *Study Material*, specimen 160 mm SL.

Body: depth 30.5.
Caudal peduncle: depth 8.75.
Head: length 25; depth 23.5.
Snout: length 5.6.
Eye: diameter 6.8.
Interorbital: width 2.5.
Maxillary: length 13.2.
Mandible: length 14.5.

Anal fin: length of base 42.
Pelvic fin: length 10.5.
Pectoral fin: length 23.
Distance from snout to origin of: dorsal 44.
Scales: *ca.* 60, mostly missing.[51]
Fin rays: dorsal 15; anal 47;[51] pectoral 14.
Ventral scutes: 26.[51]

Body strongly compressed, its greatest thickness scarcely a third of its depth, its greatest depth 3.25 in SL; the dorsal outline anterior to dorsal nearly straight, the ventral outline strongly convex. Caudal peduncle 2.85 in head.

Scales mostly lost; the scales on middle of side below base of dorsal scarcely deeper than long, with 4 or 5 vertical striae, only the posterior one complete; not very closely imbricated; the exposed part of scale notably greater than half of its depth, the margin nearly smooth. Ventral scutes well developed, 20 in advance of pelvic fins and 6 behind them.

Head 4.0 in SL, its depth at vertical from slight crossgroove at occiput 4.2. Snout definitely shorter than eye, without a definite median notch, 4.45 in head. Eye 2.9. Interorbital 10 in head. Cheek fully as deep as long. Maxillary narrowly rounded posteriorly, reaching below anterior margin of pupil, 1.85 in head. A soft ligament between premaxillary and maxillary. Mandible projecting strongly, its tip scarcely below dorsal outline of head, its margin within mouth rising rather strongly, forming an obtuse angle, 1.75 in head. Gill rakers at angle of first arch scarcely half of length of eye, 19 on lower limb of first arch. Teeth small; a few in a single row on anterior part of mandible, a series on premaxillary and on margin of maxillary, and bands of granular teeth on palatines, pterygoids, and tongue.

Dorsal fin high anteriorly, its longest rays reaching far beyond tip of last ray if deflexed, only a little shorter than the head, its origin nearer to margin of snout than to base of caudal by a distance equal to length of snout and eye, its distance from margin of snout 2.3 in SL. Caudal forked (damaged), the lower lobe evidently the larger; small scales covering most of fin. Anal fin long, scarcely elevated anteriorly, its anterior rays not forming a definite lobe, its origin under last ray of dorsal and equidistant between posterior margin of eye and base of caudal, its base 2.4 in SL; a scaly sheath present. Pelvic fin long (for an *Ilisha*), inserted rather less than an eye's diameter in advance of vertical from origin of dorsal and nearer to origin of anal than to base of pectoral, 2.3 in head; a short broad axillary process present. Pectoral fin reaching beyond base of pelvic by a distance fully equal to diameter of pupil, 4.3 in SL, 1.05 in head; the short free axillary process only a little more than a third of the length of fin.

Color. Old preserved specimen grayish above, yellowish to silvery below. Upper surface of snout and tip of mandible dark brown; a brownish area behind eye. All fins with dusky punctulations, these few and scattered on pelvic, most numerous on dorsal, caudal, and upper half of pectoral.

Range. Known only from the Amazon.

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[51] If Myers (97: 63–64) is correct in referring *I. apapae* and *I. iquitensis* to the synonymy of this species, then the anal rays vary from 47 (types of *amazonica*) to 52 (type of *iquitensis*), the scales from 57 to about 60, and the total number of ventral scutes 25 or 26.—G. S. M.

Synonyms and References:

Pseudochirocentrodon amazonicum Miranda-Ribeiro, Publ. Comm. Linhas Telegr. Estrat. Amazonas, 58, 1923 ("1920"): 8 (orig. descr., type local. Manáos, Estado de Amazonas, Brazil).

Ilisha iquitensis Nakashima, Bol. Mus. Hist. Nat. "Javier Prado," 5 (16), 1941: 66, fig. (orig. descr.; type local. environs of Iquitos, Peruvian Amazon).

Ilisha apapae Hildebrand, Smithson. misc. Coll., *110* (9), 1948: 3, fig. 2 (orig. descr.; type local. Rio Amazonas somewhere between Pará and Manáos, Brazil; type USNM 52550).

Ilisha amazonica Myers, Copeia, 1950: 63 (synon., types of *P. amazonicum* and *I. apapae*).

Ilisha harroweri Fowler 1917

Caille (Trinidad)

Figure 106

Study Material. Twenty-two specimens, 45–155 mm TL, 34–122 mm SL, from Atlantic coast of Panama (20 specimens) and Port-of-Spain, Trinidad (2). One from Barro Santos and another from Porto Inhuana, southern Brazil, were compared and probably belong to this species.

Distinctive Characters. See *Relationship.*

Description. Proportional dimensions in per cent of standard length, and counts, based on study specimens, 34–122 mm SL.

Body: depth 36.5–40.
Caudal peduncle: depth 9.0–10.4.
Head: length 28–30; depth 28.5–31.5.
Snout: length 6.0–7.5.
Eye: diameter 9.75–11.8.
Interorbital: width 3.6–4.1.
Maxillary: length 14.3–16.
Mandible: length 15.5–17.
Anal fin: length of base 37–43.
Pelvic fin: length 7.4–9.0.
Pectoral fin: length 18–21.5.
Distance from snout to origin of: dorsal 47–51.

Scales: *ca.* 33–37, usually lost in preserved specimens.
Ventral scutes: 25–27.
Fin rays: dorsal 15 or 16 (rarely 17); anal 36–42; pectoral 13–15.
Vertebrae: 39 or 40 (5 specimens).

Body deep, strongly compressed, its greatest thickness definitely less than a third of its depth, its greatest depth 2.5–2.75 in SL; the dorsal outline only slightly convex, the ventral outline strongly convex. Caudal peduncle strongly compressed, its depth 2.8–3.2 in head.

Scales mostly lost in preserved specimens; those from middle of side below anterior rays of dorsal definitely deeper than long, with about 3–7 vertical grooves, all except the posterior one interrupted, the margin of these scales irregularly indented. Ventral scutes strong, 19–21 (usually 20) in advance of pelvic fins and 6 behind them.

Head 3.33–3.55 in SL, its depth at vertical from crossgroove at occiput 3.15–3.5. Snout shorter than eye, with a slight median notch, 4.15–5.15 in head. Eye 2.55–2.8

in head. Interorbital 6.5–8.35. Cheek fully as long as deep. Maxillary rather narrowly rounded posteriorly, generally reaching nearly below middle of eye, 1.8–2.0 in head; a narrow bone with teeth between premaxillary and maxillary. Mandible projecting strongly, its tip scarcely below dorsal outline of head, its margin within mouth rising strongly, 1.7–1.85 in head. Gill rakers at angle of first arch only about as long as pupil, apparently not increasing in number with age, 23–25 on lower limb. Teeth small, in a single series on mandible and premaxillary; a row of minute teeth on margin of maxillary; present in bands on palatines, pterygoids, and tongue.

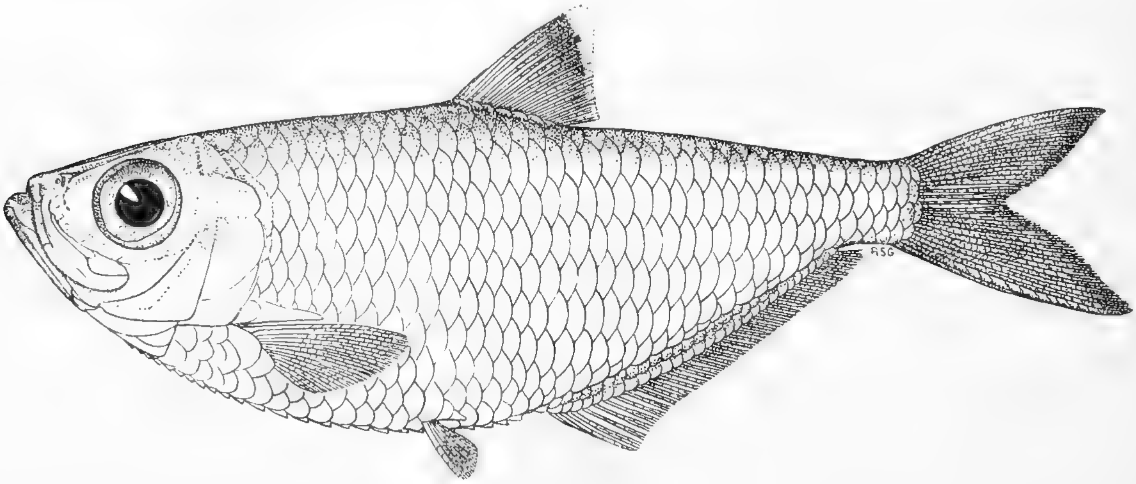

Figure 106. *Ilisha harroweri,* 160 mm TL, 123 mm SL, Colón, Panama, USNM 81749. Drawn by Ann S. Green.

Dorsal fin moderately elevated anteriorly, its longest rays reaching far beyond tip of last ray if deflexed, its origin a little nearer to margin of snout than to base of caudal, its distance from margin of snout 1.7–2.1 in SL; a sheath composed of one row of scales at base. Caudal fin forked, the lower lobe slightly the longer; small scales extending onto base of fin. Anal fin long, its anterior rays somewhat elevated but not forming a definite lobe, its margin nearly straight, its origin somewhat variable, generally under posterior rays of dorsal, usually about equidistant between posterior margin of eye and base of caudal, its base 2.3–2.7 in SL; the sheath composed of two rows of scales anteriorly and one row posteriorly. Pelvic fin small, rarely missing, reaching halfway or more to origin of anal, inserted under, or more usually somewhat in advance of, vertical from origin of dorsal, much nearer to origin of anal than to base of pectoral, 3.1–3.8 in head; no free axillary process. Pectoral fin moderately developed, not falcate, reaching base of pelvic in some but failing to reach it in others, its length 4.7–5.5 in SL, 1.3–1.65 in head; a free axillary process reaching about to midlength of longest rays.

Color. Bluish gray above. Sides silvery. Upper surface of anterior part of snout and mandible dusky. Dorsal and anal fins yellowish in life, the tip of the dorsal lobe and generally the margin of the caudal dusky; vertical fins with dusky punctulations.

Size. The largest example at hand is 155 mm (6.2 in.) TL and 122 mm SL. This specimen was among the larger ones seen in the Colón, Panama, market.

Development. Nothing concerning reproduction is known, and larval and postlarval stages have not been described. However, at hand are a few small specimens that are proportionately quite as deep as large ones. In two specimens, 34 and 50 mm SL, the depth equals 38.3 and 40 % of SL, whereas in the two largest, 115 and 122 mm SL, the depth equals 39 and 37.6 %; furthermore, the ventral profile is much more strongly convex anteriorly in the small examples. This is contrary to the usual development, as small specimens of this family ordinarily are slenderer than large ones. A development similar to that of *harroweri* has been noticed in *Brevoortia patronus.*

Relationship. It is not possible to distinguish this species from *Neosteus ternetzi* as described by Norman (*100*: 593) or by a comparison of two specimens from southern Brazil (Barro Santos, USNM 87718, Porto Inhuana, USNM 100837) with others from Colón, Panama, and Port-of-Spain, Trinidad. The following proportions and counts, which are generally in agreement with those given in the original description of *ternetzi* (from Panama and Trinidad), are based on the two specimens from Brazil, with the figures for the Barro Santos specimen first: Body depth 2.6, 2.75 in SL. Caudal peduncle depth 2.95, 3.1. Head length 3.4, 3.5; depth at vertical from cross-groove at occiput 3.15, 3.55. Snout length 5.0, 4.0 in head. Eye diameter 2.5, 2.7. Interorbital width 6.5, 6.55. Maxillary length 1.85, 1.8. Mandible length 1.85, 1.75. Anal base 2.4, 2.9. Predorsal distance 2.0, 1.95. Scales lost, about 35. Ventral scutes 18+6, 19+7. Fin rays: dorsal 16, 16; anal 36, 39; pectoral 15, 15. It seems proper to conclude, therefore, that *ternetzi* cannot be distinguished from *harroweri* specifically. It may be subspecifically distinct, but that can be determined only when more material becomes available for study.

Variation. The pelvic fins are well developed, but there is at hand a specimen 50 mm SL from Colón, Panama, in which these fins are missing. Inasmuch as no scar can be detected, it is assumed that it never possessed the fins. It seems highly probable that the specimen without pelvics, taken on the Atlantic coast of Panama and described as a new species by Borodin under the name *Pristigaster vanderbilti* (*19*: 6, pl. 1, fig. 1), also is this species. The occasional absence of pelvic fins in this species seemingly may be looked upon as a variation.

Range. Atlantic coast of Panama, Trinidad, and southern Brazil. Not reported as yet from intermediate points.

Synonyms and References:

Ilisha harroweri Fowler, Proc. Acad. nat. Sci. Philad., *69*, 1917: 128, fig. 1 (orig. descr.; type local. Colón, Panama; type ANSP 46959).

Neosteus harroweri Norman, Ann. Mag. nat. Hist., (9) *11*, 1923: 19 (descr. after Fowler).

Ilisha argentata Meek and Hildebrand, Field Mus. Publ., Zool., *15* (1), 1923: 190, pl. 9 (orig. descr.; type local. Fox Bay, Colón, Panama; type USNM 81749).

Neosteus ternetzi Norman, Ann. Mag. Nat. Hist., (9) *12*, 1923: 593 (orig. descr.; type local. Rio de Janeiro, Brazil).

Pristigaster vanderbilti Borodin, Bull. Vanderbilt oceanogr. Mus., *1* (1), 1928: 6, pl. 1, fig. 1 (orig. descr.; type local. Limon Bay, Colón, Panama; type VOM 12; apparently based on an "abnormal" specimen of *Ilisha harroweri* without pelvics).

Ilishe (*Neosteus*) *ternetzi* von Ihering, Rev. Industr. Anim., 1 (3), 1930: 230 (fin rays, notes, Rio de Janeiro, Brazil).

Ilisha narragansetae Fowler 1911

Figure 107

Study Material. None.

Distinctive Characters. This species, according to the original description, seems to be related to *harroweri*, having a similar deep body and rather large scales. It seems to differ, however, in having a greater number of ventral scutes, more numerous anal and pectoral rays, and a longer pectoral fin.

Description. Proportional dimensions in per cent of standard length, and counts, condensed from Fowler (*38*: 208), specimen about 145 mm TL (caudal damaged), reported as taken off Newport, Rhode Island.

Body: depth 33.
Head: length 25.5.

Scales: *ca.* 44.
Ventral scutes: 32.
Fin rays: dorsal 17; anal 45; pectoral 16.

BODY much compressed, its greatest depth at insertion of pelvic fin, 3.33 in SL; the dorsal outline slightly convex, the ventral outline more strongly convex anteriorly. CAUDAL PEDUNCLE compressed, its length a trifle less than its depth, 3.4 in head.

SCALES large, cycloid, each with as many as 6 vertical striae. VENTRAL SCUTES developed, 25 in advance of pelvics and 7 behind.

HEAD compressed, slightly concave above, convex below, greatly inclined, 3.5 in SL. SNOUT shorter than eye, a median notch scarcely developed, 4.3 in head. EYE 3.0. INTERORBITAL 6.25. MAXILLARY reaching somewhat beyond a vertical from anterior margin of pupil, 1.9 in head. MANDIBLE strongly projecting, its margin within mouth well elevated. GILL RAKERS half of length of eye, 22 on lower limb of first arch. TEETH small; a series on anterior part of mandible and premaxillaries, a double series on each palatine; also present on tongue.

DORSAL fin graduated downward from the first branched ray, its origin equidistant between tip of mandible and base of caudal. CAUDAL forked (damaged); small scales on base of fin. ANAL fin low, its margin straight, its anterior rays little elevated, its origin slightly behind base of dorsal, about equidistant between anterior margin of eye and base of caudal. PELVIC fin very small, inserted rather less than an eye's diameter in advance of vertical from origin of dorsal and much nearer to origin of anal than to base of pectoral. PECTORAL fin falcate, rather broad, reaching far beyond tip of pelvic fin, 1.3 in head.

Color. "Brownish on back and upper surface of head behind, sides and lower regions silvery white in alcohol; fins all pale brownish."

Range. Known only from the holotype, purported to have been taken at Newport, R.I. It is stated in the original account of this species, "it would appear undoubtedly to have been obtained at Newport as a waif of the Gulf Stream, probably from some tropical region in America." This remark dates back to 1911 and no other example like it has been reported since then. The genus, in fact, is not known from the West Indies (except Trinidad), nor from any other locality north of the Atlantic coast of Panama.

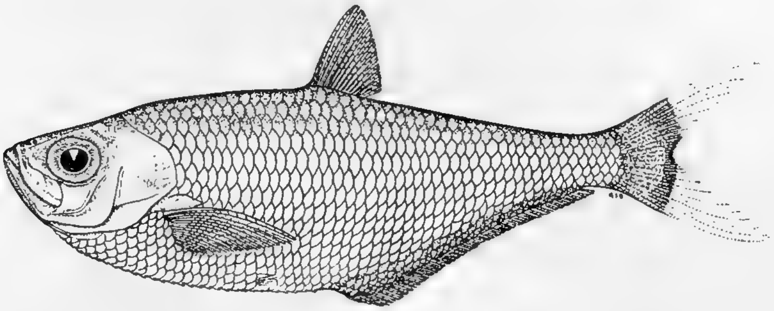

FIGURE 107. *Ilisha narragansetae,* about 165 mm TL (caudal damaged). Modified by Ann S. Green after Fowler, type, ANSP 15314.

Synonyms and References:

Ilisha narragansetae Fowler, Proc. Acad. nat. Sci. Philad., *63,* 1911: 208, fig. 1 (orig. descr.; type local. Newport, Rhode Island; type ANSP 15314; cf. *Pellona bleekeriana, Pristigaster flavipinnis,* and *Pellona castelnaeana*); Fowler, Proc. Boston Soc. nat. Hist., *35* (4), 1917: 112.

Neosteus narragansetae Norman, Ann. Mag. nat. Hist., (9) *11,* 1923: 20 (descr. after Fowler); Jordan, Manual Vert. Anim. NE U.S., ed. 13, 1929: 42 (diagn.).

Genus *Pristigaster* Cuvier 1817[52]

Pristigaster Cuvier, Règne Anim., ed. 1, *2,* 1817: 176; and *4*: pl. 10, fig. 3; type species by monotypy, figured but no specific name given; this same figure repeated in ed. 2 of Règne Anim., in which name *cayanus* is provided; generic type by monotypy, *Pristigaster* sp. Cuvier 1817 equals *P. cayanus* Cuvier 1829.

Characters. BODY strongly compressed; the dorsal outline straight to slightly convex; the chest and abdomen greatly dilated, forming a pronounced arc. SPINES on median line between occiput and origin of dorsal, 4 or 5. TEETH small; no canines. DORSAL fin small, with about 13–15 rays, its origin well in advance of origin of anal. ANAL fin long, its origin under or just behind base of last dorsal ray, with about 46–55 rays. PELVIC fin missing.

Remarks. The greatly dilated, rounded, half-moon-shaped outline of the chest

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[52] Nomenclature and synonymy for both genus and species rewritten by G. S. Myers.

and abdomen and the several short spines on the median line of the back between the occiput and origin of dorsal sufficiently characterize this genus.

Range. Known from a single species, as herein understood, which ranges from the Guianas to northern Brazil and ascends freshwater streams.

Pristigaster cayana Cuvier 1829

Sardinha d'Agua Doce, Apapa (Brazil)

Figure 108

Study Material. None.

Distinctive Characters. In bodily shape, *cayana* resembles somewhat *Ilisha harroweri*, but its chest and abdomen are even more strongly convex, forming a very pronounced arc (see Fig. 108). The shape strikingly resembles that of the freshwater characin, *Gasteropelecus*, but its pectoral fin is much shorter.[53] The several spines on the median line of the back between the occiput and the dorsal fin separate it from all American species of the family.

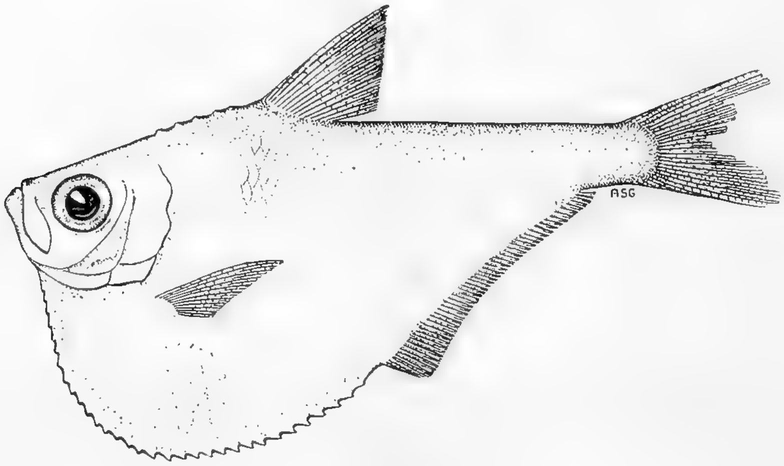

FIGURE 108. *Pristigaster cayana*, about 110 mm TL (caudal damaged). Drawn by Ann S. Green after Compos' *P. martii*.

Description. Proportional dimensions in per cent of standard length, and counts, from several published accounts, drawings, and a photograph.

Body: depth 50–56.
Head: length 25–29.

Scales: 39–42.
Ventral scutes: 30–33.

Gill rakers: on lower limb of first arch, 20–23.
Fin rays: dorsal 13–15; anal 46–55; pectoral 11.

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[53] Moreover it does not appear to possess the enormous pectoral muscles which enable the characin to buzz its wings during aerial flight.—G. S. Myers.

Body much compressed, its ventral outline strongly convex, forming a pronounced arc, its greatest depth over basal half of pectoral, 1.8–2.0 in SL. Caudal peduncle short, its depth 3.0 in head.

Ventral scutes prominent, especially the posterior ones. A median series of 5 spines between occiput and origin of dorsal.

Head 3.65–4.0 in SL. Snout shorter than eye, 3.5 in head. Eye 2.5 in head. Interorbital half of width of eye. Mouth almost vertical. Maxillary extending below anterior margin of eye, 2.5 in head. Mandible projecting, extending nearly into dorsal outline of head. Gill rakers slender, about 2.25 times in diameter of eye, 20–23 on lower limb.

Dorsal fin high anteriorly, its longest rays reaching far beyond tip of last ray if deflexed, nearly as long as head, its origin much nearer to margin of snout than to base of caudal. Caudal fin well forked, the lobes a little shorter than head. Anal long, its origin under or just behind last rays of dorsal, a little less than 0.5 of SL. Pectoral a little shorter than head.

Color. After Fowler: "Color in alcohol with back pale brown and under surfaces bright shining silvery white. Iris silvery white. Back and occiput with scattered dark to blackish dots. Dorsal and caudal yellowish buff basally, pale gray terminally. Other fins dull buff."

Size. A maximum length of only 110 mm (4.4 in.) has been reported.

Range. Coast of the Guianas to Brazil, ascending streams; reported from the Ucayali River Basin in the upper Amazon system, Peru.

Synonyms and References:

Pristigaster Cuvier, Règne Anim., ed. 1, *2*, 1817: 176 and *4*: pl. 10, fig. 3 (diagn. of genus and species combined; no specific name given; type local. "Seas of America"); Cuvier, Règne Anim., ed. 2, *3*, 1830: pl. 12, fig. 3 (no specific name on plate, but includ. in 1829 text; see under *P. cayanus* below).

Pristigaster cayanus Cuvier, Règne Anim., ed. 2, *2*, 1829: 321 (two spp. referred to; name *cayanus* provided for Amer. species figured in 1817; type local. fixed by specific name as Cayenne, French Guiana; fig. on 1830 plate of ed. 2 Règne Anim. ident. to that in ed. 1); Cuvier and Valenciennes, Hist. Nat. Poiss., *20*, 1847: 334, pl. 597 (descr., discus.); Günther, Cat. Fish. Brit. Mus., *7*, 1868: 463 (synon., descr., range); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 438 (descr. after Cuvier and Valenciennes, synon.); Starks, Stanf. Univ. Publ., 1913: 9 (Madeira R., Brazil, 400 miles above mouth); Norman, Ann. Mag. nat. Hist., (9) 11, 1923: 14 (synon., descr., range); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 45 (range, synon.); von Ihering, Rev. Indust. Anim., 1 (3), 1930: 230 (ref., diagn.); von Ihering, Dic. Anim. Brasil, 1940: 716 (habitat, notes); Eigenmann and Allen, Fish. West. S. Amer., 1942: 333 (Peruvian Amazon).

Pristigaster martii Agassiz, *in* Spix and Agassiz, Genera Species Pisc. Brazil., 1829: 55, pl. 24a (orig. descr.; type local. mouth of Amazon); Cuvier and Valenciennes, Hist. Nat. Poiss., *20*, 1847: 337 (presumed differences from *P. cayanus*; rec. for the mouth of Amazon); Castelnau, Anim. Nouv. Rares Amer. Sud, Poiss., 1855: 57 (Amazon); Fowler, Proc. Acad. nat. Sci. Philad., *91*, 1940: 221, fig. 2 (Rio Ucayali, Peruvian Amazon, synon., descr.); Campos, Arqu. Zool. estad. São Paulo (1941), *3* (7), 1942: 187, fig. 2 (synon., descr., geogr. distr.); Fowler, Arqu. Zool. estad. São Paulo, *6*, 1948: 16, fig. 6 (synon.).

Pristigaster americanus Guerin-Meneville, Iconogr. Règne Anim. Cuvier, Poiss., 1829–1844: 33, pl. 57, fig. 3 (type local. coast of S. Amer. in Atlantic).

Pristigaster phaeton Cuvier and Valenciennes, Hist. Nat. Poiss., *20*, 1847: 338 (orig. descr., type local. Amazon);

Castelnau, Anim. Nouv. Rares Amer. Sud, Poiss., 1855: 57, pl. 28, fig. 3 (based on material of Valenciennes).

Pristigaster cayana Myers, Copeia, 1956: 64 (nomencl., early synon. corrected).

Negative Reference:

Pristigaster martii Fowler, Bull. Amer. Mus. nat. Hist., 70 (1), 1936: 179, fig. 72 (synon. in part incorrect; descr. after *P. dolloi* Boulenger, which is not this species).

Genus *Odontognathus* Lacépède 1800

Odontognathus Lacépède, Hist. Nat. Poiss., 2, 1800: 220; type species by monotypy, *Odontognathus mucronatus* Lacépède.

Generic Synonym:

Gnathobolus Bloch and Schneider, Syst. Ichthyol., 1801: 556; type species by monotypy, *Odontognathus mucronatus* Lacépède.

Characters. Body strongly compressed; the dorsal outline more or less concave over head, the ventral outline rather strongly convex anteriorly. Bony scutes on sharp keel of chest and abdomen, the outer margin of the posterior scutes more or less denticulate. Mouth strongly oblique to nearly vertical, with strongly projecting lower jaw. Maxillary greatly produced in large examples; maxillary and premaxillary separated by a toothless membranous section, forming a continuous (uninterrupted) margin with maxillary and premaxillary. Teeth small to minute, present on both jaws, palatines, pterygoids, and tongue, but wanting on vomer. Gill rakers not numerous, about 19–25 on lower limb of first arch. Dorsal fin rather feebly developed, with about 10–14 rays. Anal fin long, with about 52–80 rays, beginning far in advance of dorsal fin, generally well in advance of midlength of SL. Pelvic fins wanting. Pectoral fins generally longer than head.

Remarks. The species of this genus have greatly compressed bodies, a concavity over the head, a membranous section between the maxillary and premaxillary that forms a continuous margin with the two elements it separates, a very oblique to nearly vertical mouth, and a very long anal fin. Several of the posterior ventral scutes generally are denticulate.

Range. Known from both coasts of Panama, on the Atlantic side southward to Guiana.

Key to Species

1a. Depth of body 4.65 in SL; anal fin with 79 or 80 rays (71–82 by earlier descriptions); dorsal fin over middle of anal, its origin about twice as far from posterior margin of eye as from base of caudal. *mucronatus* Lacépède 1800, p. 431.

1b. Depth of body 3.5–4.25 in SL in adults; anal fin with only 52–60 rays; dorsal fin ending over middle of anal, its origin nearly twice as far from margin of snout as from base of caudal. *compressus* Meek and Hildebrand 1923, p. 433.

Odontognathus mucronatus Lacépède 1800

Figure 109

Study Material. Two large specimens, 135 and 152 mm TL, 111 and 136 mm SL, from Port-of-Spain, Trinidad, in only fair condition, the fins being more or less damaged and the color badly faded. Both specimens have the ventral scutes missing below the pectoral fins, causing a concavity in the ventral outline; this probably is an abnormality, even though it is present in both specimens.

Distinctive Characters. See *Relationship.*

Description. Proportional dimensions in per cent of standard length, and counts, based on study specimens, 111 and 136 mm SL.

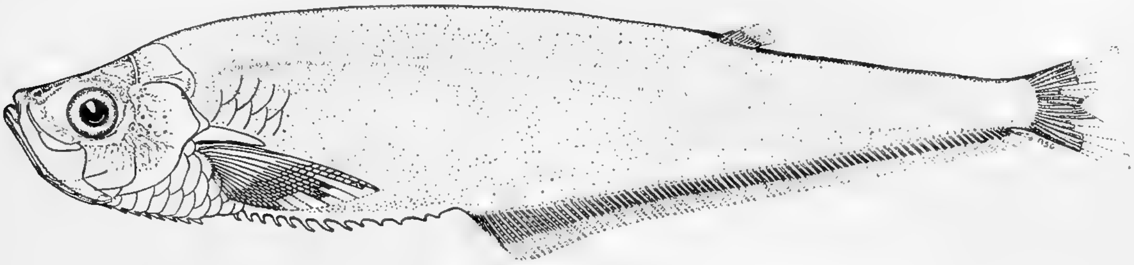

FIGURE 109. *Odontognathus mucronatus,* about 152 mm TL (caudal damaged), 136 mm SL, Gulf of Paria, Trinidad, USNM 123085. Drawn by Ann S. Green.

Body: depth 20.5–21.5.
Caudal peduncle: depth 5.1–5.4.
Head: length 17.5–19; depth 15–17.
Snout: length 4.7.
Eye: diameter 5.0–5.5.
Interorbital: width 1.5–1.9.
Maxillary: length 14–14.5.
Mandible: length 11–12.5.
Anal fin: length of base 52–56.
Pectoral fin: length 19–22.
Distance from snout to origin of: dorsal 70–71.5.
Scales: *ca.* 45–48 pockets, mostly lost in preserved specimens.
Ventral scutes: *ca.* 21 or 22 (some may be missing because of an abnormality).
Fin rays: dorsal 10–12; anal 79 or 80; pectoral 12.

BODY with greatest thickness about 0.25 of its depth, its greatest depth 4.65–4.8 in SL; the dorsal outline over head concave, the ventral outline moderately convex anteriorly and then concave (possibly abnormal). CAUDAL PEDUNCLE very short, its depth 3.4–3.5 in head.

SCALES nearly all lost, a few remaining over base of anal, these very thin, notably deeper than long, with nearly smooth margin and without vertical grooves. VENTRAL SCUTES rather prominent, all except the last 3 or 4 ending in prominent spines, the last ones with nearly smooth margin, missing for a short distance below base of pectoral (p. 432), forming a slight concavity.

HEAD small, its length 5.25–5.7 in SL, its depth at vertical from slight cross-groove at occiput 5.9–6.65. SNOUT a little shorter than eye, 3.75–4.05 in head. EYE 3.5–3.55. INTERORBITAL very narrow, 10–11.5 in head. CHEEK about as long as deep. MOUTH nearly vertical. MAXILLARY produced into a long narrow process reaching margin of opercle in larger one, 1.25–1.3 in head. MANDIBLE projecting strongly, its tip a little below dorsal outline, its margin within mouth rising strongly, forming a broadly rounded obtuse angle, 2.1–2.2 in head. GILL RAKERS fairly strong, only about half of length of eye, their inner margin rather strongly serrate, 24 or 25 on lower limb of first arch. TEETH all small to minute, in a single series on mandible, premaxillary, and maxillary; missing on membranous section between the last mentioned elements; minute teeth on palatines and pterygoids, but none on vomer; an elongated patch on tongue.

DORSAL fin small, feebly developed (damaged specimens at hand), its origin notably more than length of head behind origin of anal, about twice as far from the posterior margin of eye as from base of caudal, its distance from margin of snout 1.35–1.45 in SL. CAUDAL fin damaged, the lower lobe evidently the longer. ANAL fin very long, its origin nearer to tip of mandible than to base of caudal by about twice diameter of eye, its base 1.8–1.9 in SL. PECTORAL moderately large, a little longer than head, reaching 4th or 5th from last ventral scute, 4.55–5.25 in SL.

Color. Large preserved specimens pale; sides of head silvery. A pale lateral band (no doubt silvery in life), very narrow (a mere line), anteriorly, becoming fully half as broad as eye over posterior half of anal. Back with dusky punctulations extending forward onto head and snout and onto tip of mandible; punctulations also on fins.

Relationship. Compared to *O. compressus*, the body of *O. mucronatus* is more slender and apparently less compressed, the anal fin is longer, and the dorsal fin is more posteriorly placed. And in all these respects *mucronatus* is nearer to the Pacific *panamensis* than to *compressus*; however, it is even more slender than *panamensis*, and its gill rakers and anal rays are more numerous. If the interruption in the series of ventral scutes below the pectorals (p. 431) were normal, which seems doubtful, this would constitute another important difference that separates *mucronatus* from the other species of the genus. However, a slight concavity in the ventral outline has been noticed in a large specimen of *O. panamensis* and in a much smaller specimen of *O. tropicus* from northern Peru, recently referred to a new genus; however, in each instance the scutes are fully developed in the concavity. Other specimens of the same species have no such concavity in the ventral outline, nor do any of the numerous specimens of *O. compressus* examined. Furthermore, this question of abnormality is not answered in Norman's revision (*99*: 15), wherein he gave no information other than "Ventral scutes 8 + 12," which is in approximate agreement with the number of scutes before and after the interruption at the concavity on the specimens at hand. It may be significant, however, that in the description of *O. panamensis* in his revision, the number of ventral scutes is also written "13 + 16"; there certainly is no interruption in the series of scutes in the specimen of that species before me.

Range. Known from the coast of Guiana and from Trinidad (Port-of-Spain).

Synonyms and References:

Odontognathus mucronatus Lacépède, Hist. Nat. Poiss., *2*, 1800: 221, pl. 7, fig. 2 (orig. descr. under "L'odontognathe aiguillone," but a footnote gives the binomial *Odontognathus mucronatus*; type local., Cayenne, French Guiana); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 438 (descr., synon.); Eigenmann, Mem. Carneg. Mus., *5*, 1912: 447 (synon., diagn., Georgetown, British Guiana); Norman, Ann. Mag. nat. Hist., (9) *11*, 1923: 15 (synon., descr.); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 45 (ref. to orig. descr.).

Gnathobolus mucronatus Cuvier and Valenciennes, Hist. Nat. Poiss., *21*, 1848: 91 (descr.).

Pristigaster mucronatus Günther, Cat. Fish. Brit. Mus., *7*, 1868: 462 (synon., descr.).

Odontognathus compressus Meek and Hildebrand 1923

Figures 110, 111

Study Material. Numerous specimens, about 30–145 mm TL (caudal damaged on 30-mm fish), 23–123 mm SL, including the holotype and 25 paratypes, from the Atlantic coast of Panama, and a few lots from the Gulf of Venezuela.

Distinctive Characters. The nearest relative of *O. compressus* is *O. panamensis* of the Pacific coast of Panama, but these species differ in having 52–60 and 65–68 anal rays, respectively. Furthermore, in *compressus* the dorsal fin is notably in advance of the middle of the anal base, whereas in *panamensis* it is about over the middle of the anal fin. Its relationship with *O. mucronatus* is shown in the Key to Species (p. 430).

Description. Proportional dimensions in per cent of standard length, and counts, based on *Study Material*, specimens 23–123 mm SL.

Body: depth 23.5–28.5.
Caudal peduncle: depth 7.25–8.3.
Head: length 18–21; depth 18–22.
Snout: length 4.2–5.1.
Eye: diameter 5.25–6.25.
Interorbital: width 2.0–2.75.
Maxillary: length 12–16.
Mandible: length 9.3–10.2.
Anal fin: length of base 47–54.
Pectoral fin: length 21–25.
Distance from snout to origin of: dorsal 65–67.

Scales: lost, *ca.* 36–43 pockets.
Ventral scutes: 25–29.
Vertebrae: 46 or 47 (3 specimens).
Fin rays: dorsal 11–14, usually 11 or 12; anal 52–60; pectoral 12–14.

Body elongate, excessively compressed, its greatest thickness about 0.17 of its depth, its greatest depth 3.5–4.25 in SL; the dorsal outline of head concave in adults; the ventral outline strongly convex anteriorly. Caudal peduncle much shorter than depth, its depth 2.3–2.9 in head.

Scales mostly lost; very thin, deeper than long, with nearly smooth margin, without evident vertical striations. Ventral scutes well developed, the last 8–10 with serrate margin.

Head small, its length 4.75–5.5 in SL, its depth at vertical from slight cross-groove at occiput 4.5–5.55. Snout a little shorter than eye, 3.6–4.7 in head. Eye 2.9–

3.8. INTERORBITAL very narrow, 7.0–10 in head. CHEEK fully as long as deep. MOUTH nearly vertical. MAXILLARY broad, rounded in young, with an oblique margin in somewhat larger ones, ending under anterior half of eye, becoming produced into a narrow process in examples 65 mm SL and upward, extending to or beyond margin of opercle in large individuals, about 2.2 in head in small examples to 1.1 in large specimens.

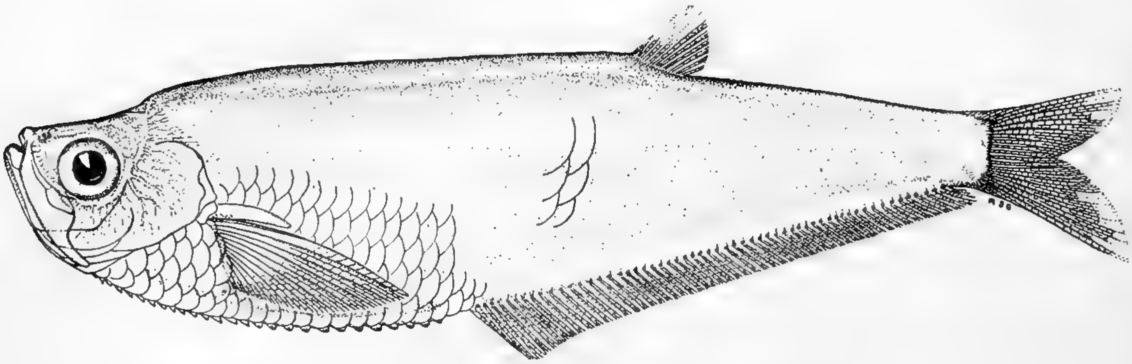

FIGURE 110. *Odontognathus compressus,* about 105 mm TL (caudal damaged), 88 mm SL, Colón, Panama, type, USNM 79533. Drawn by Ann S. Green.

MANDIBLE projecting strongly, its tip a little below dorsal outline of head, its margin within mouth rising abruptly, forming an obtusely rounded angle, 1.75–2.0 in head. GILL RAKERS rather slender, about half as long as eye, with rather well-developed serrae along inner edge, 19–23 on the lower limb. TEETH small to minute; apparently in a single series on mandible and on margin of premaxillary and maxillary but absent on membranous section between the last mentioned elements; minute teeth present on palatines, pterygoids, and on median section of tongue.

DORSAL fin small, rather feebly developed, more or less damaged in all specimens at hand, ending over middle of anal fin, its origin more than a head-length behind origin of anal, not quite twice as far from margin of snout as from base of caudal, its distance from margin of snout 1.5–1.55 in SL. CAUDAL fin rather broadly forked, the lower lobe the longer, about as long as head. ANAL fin long, its origin about an eye's diameter nearer to tip of mandible than to base of caudal, its base 1.8–2.1 in SL. PECTORAL fin a little longer than head, often reaching opposite to last ventral scute, sometimes failing to reach this point, 4.0–4.75 in SL; free axillary process about half as long as fin.

Color. Pale in alcohol. Sides of head silvery. Body with a silvery lateral band, about as broad as pupil. Back with dusky points and a median pale line in ad-

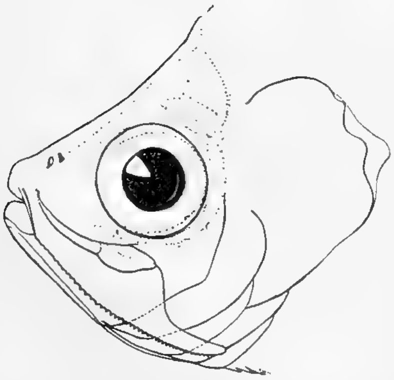

FIGURE 111. *Odontognathus compressus* head showing produced maxillary bone; same specimen as shown in Fig. 110. Drawn by Ann S. Green.

vance of dorsal; and a dark median streak behind it; margin of mandible and usually the snout behind premaxillary with a dark crossline; base of caudal with a dark crossline; base of anal with a row of dark dots; upper rays of pectoral with dusky points.

Size. This is one of the smaller of the excessively compressed herrings. The largest among the *Study Material* is 145 mm (5.7 in.) TL, 123 mm SL, which may be near the maximum.

Development. The body increases greatly in depth with age and growth, as in many other herrings. The depth in the smallest five examples at hand, 23–38 mm SL, is contained 4.1–4.7 in SL whereas this proportion in the five largest is 3.5–3.6. Furthermore, the dorsal profile anteriorly is about straight in the small specimens but concave in the large ones. The maxillary, as indicated in the *Description*, is short in small examples but becomes produced in large adults; in the smaller examples it is broadly rounded posteriorly and reaches under the anterior half of the eye; at about 50 mm SL it is no longer rounded posteriorly and has an oblique margin; as growth proceeds, the lower angle of the oblique margin becomes longer and sharper, and at 65 mm SL it is already well produced. However, it is only in large examples, upward of 100 mm SL, that the narrow process reaches to, or even slightly beyond, the margin of the opercle.

Range. Known from the Atlantic coast of Panama, from the Gulf of Venezuela, and from Trinidad.

Reference:

Odontognathus compressus Meek and Hildebrand, Field Mus. Publ., Zool., *15* (1), 1923: 194 (orig. descr., type local. Colón, Panama; cf. *O. mucronatus*; type USNM 79553).

Genus *Neoopisthopterus* Hildebrand 1948

Neoopisthopterus Hildebrand, Smithson. misc. Coll., *110* (9), 1948: 6; type species by original designation, *Odontognathus tropicus* Hildebrand.

Characters. Body slender, strongly but not excessively compressed; ventral outline anteriorly much more strongly convex than dorsal outline. Bony scutes moderately strong with entire (smooth) margin, the chest and abdomen with a sharp keel. Mouth moderately oblique, with slightly projecting lower jaw. Maxillary short (with no indication in the rather small specimens that it will become produced in adults, as in *Odontognathus*), anteriorly overlapping distal end of premaxillary. Teeth small, present on jaws, palatines, pterygoids, and tongue, but missing on vomer. Gill rakers about 17–21 on lower limb of first arch. Dorsal fin small, with about 13–16 rays. Anal fin moderately long, with about 39–48 rays, beginning a short distance in advance of origin of dorsal. Pelvic fin wanting. Vertebrae about 46 or 47.

Remarks. This genus is characterized chiefly by the structure and relative position of the bones in the upper jaw. In *Neoopisthopterus* the maxillary and premaxillary overlap, with the margin of the jaw interrupted at the point where the maxillary passes over the premaxillary. In related genera (*Odontognathus* and *Opisthopterus*) these bones are separated by a membranous toothless section, with the margin of the upper jaw continous. The genus differs further from the other genera that lack the pelvic in having fewer anal rays.

Range. Known from two species, *N. tropicus* from the Pacific coast of Panama and Peru and *cubanus* from Cuba.

Neoopisthopterus cubanus Hildebrand 1948

Figures 112, 113

Study Material. Six small specimens, 43–50 mm TL, 35–41 mm SL, apparently young adults not fully mature; collected at Havana, Cuba, and sent to the writer by Dr. Luis Howell-Rivero of the Museo Poey at Havana; USNM 143569 and 143570.

Distinctive Characters. N. cubanus is very closely related to *N. tropicus* Hildebrand (57: 94, fig. 19), known from Panama and northern Peru, from which it differs only in having somewhat fewer dorsal and anal rays (*cubanus*: D. 13 or 14, A. 39–43; *tropicus*: D. 14–16, A 43–48). Also, these fins are somewhat differently placed; in *cubanus* the dorsal originates slightly more than an eye's diameter behind the beginning of anal and about equidistant between the margin of the opercle and the base of caudal, whereas in *tropicus* it begins scarcely an eye's diameter behind the origin of anal and is about equidistant between the posterior margin of the eye and the base of caudal. The average number of gill rakers on the lower limb of the first arch apparently is lower in *cubanus* than in *tropicus* (respectively, 17–19, 18–21). This, then, is another instance of the rather common occurrence of "twin" species in the Atlantic and Pacific, generally found on the opposite coasts of the Isthmus of Panama. As the West Indian and Atlantic Panamanian faunas are largely identical, *cubanus* may be expected on the Atlantic coast of Panama and neighboring countries.

Description. Proportional dimensions in per cent of standard length, and counts, based on study specimens 35–41 mm SL.

Body: depth 17–21.
Caudal peduncle: depth 6.5–8.5.
Head: length 21.5–23.5; depth 18.5–20.5.
Snout: length 5.3–6.8.
Eye: diameter 5.5–6.8.
Interorbital: width 2.6–3.1.
Maxillary: length 13.2–14.8.
Mandible: length 12.8–13.7.
Anal fin: length of base 33–39.
Distance from snout to origin of: dorsal 60–64.

Scales: lost, *ca.* 43 pockets.
Ventral scutes: 23–28.
Fin rays: dorsal 12–14; anal 39 to 43; pectoral 13.
Vertebrae: 47 (1 specimen).

Body elongate, strongly but not excessively compressed, its greatest thickness between a third and a fourth of its depth, its greatest depth 4.75–5.75 in SL; the dorsal outline of head straight to slightly convex; the ventral outline rather strongly convex anteriorly. Caudal peduncle shorter than deep, its depth 2.6–3.4 in head.

Scales mostly lost; rather large, very thin with smooth edge, and without evident striations. Ventral scutes well developed, all with entire (smooth) margin.

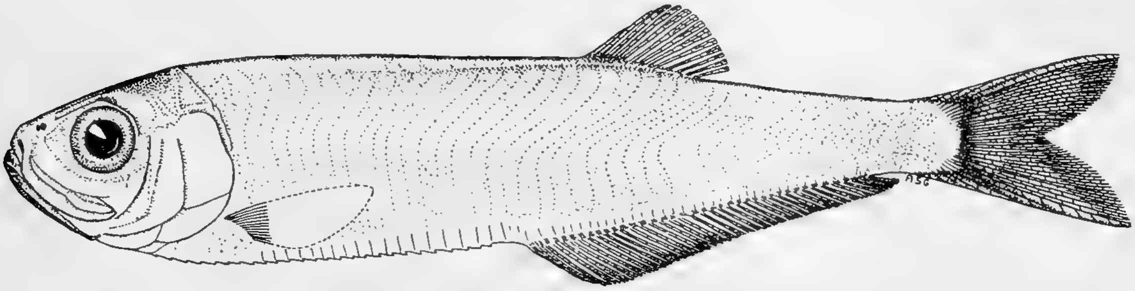

Figure 112. *Neoopisthopterus cubanus*, 50 mm TL, 41 mm SL, Havana, Cuba, type, USNM 143569. Drawn by Ann S. Green.

Head fairly short and deep, its length 4.25–4.65 in SL, its depth at vertical from slight crossgroove at occiput 4.9–5.4. Snout about as long as eye (in small specimens), 3.3–4.5 in head. Eye 3.4–4.1. Interorbital very narrow, 7.3–9.0. Cheek about as long as deep. Mouth moderately oblique. Maxillary quite narrowly rounded posteriorly, reaching to or somewhat beyond vertical from posterior margin of pupil, 1.55–1.8 in head. Mandible projecting slightly, its margin within mouth rising rather abruptly, 1.6–1.75 in head. Gill rakers slender, those at angle of first arch about as long as pupil, with very fine serrae along the inner edge. Teeth small to minute, apparently in a narrow band on anterior part of lower jaw; those on maxillary and premaxillary in a single series, interrupted at point of overlapping of maxillary and premaxillary; very small teeth on palatines and pterygoids and on median line of tongue.

Dorsal fin quite small, somewhat elevated anteriorly, its margin convex, its rays rather feeble, its origin rather more than an eye's diameter behind origin of anal and about equidistant between margin of opercle and base of caudal, its distance from margin of snout 1.55–1.65 in SL. Caudal fin rather broadly forked, the lower lobe slightly the longer, scarcely as long as head. Anal fin moderately long, its origin about equidistant between posterior margin of eye and base of caudal, its base 2.55–3.0 in SL. Pectoral fin damaged in all specimens at hand, apparently

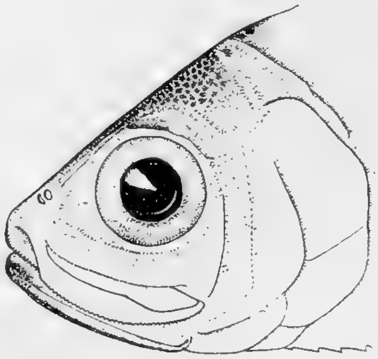

Figure 113. *Neoopisthopterus cubanus* head to show overlapping maxillary and premaxillary bones; same as shown in Fig. 112. Drawn by Ann S. Green.

rather large, inserted below margin of opercle, and about 1.5 times farther from origin of anal than from tip of mandible.

Color. Pale in alcohol. Side with a whitish band (no doubt silvery in life) about half as broad as eye. Upper surface of head brownish posteriorly, with rather large dusky dots; dusky dots on margin of snout medianly and on mandible anteriorly; median line of back also with scattered dusky dots; dusky points on base of caudal forming an oblique dark crossline and extending onto outer rays of fin; base of anal with a row of dark spots, with fine punctulations on the fin, chiefly near the margin.

Size. This species belongs to a group of herrings that attains a small size, few exceeding a length of 150 mm (6 in.). The known specimens of *cubanus* are all small (apparently immature). A specimen of the closely related Pacific *N. tropicus*, which seemingly is mature, is 66 mm SL or about 77 mm TL (3.1 in.), the caudal fin broken. It may be conjectured, therefore, that *N. cubanus* attains a length of only about 75–100 mm (3–4 in.).

Range. Known only from the type locality, Havana, Cuba.

Reference:

Neoopisthopterus cubanus Hildebrand, Smithson. misc. Coll., *110* (9), 1948: 7, figs. 3 and 4 (orig. descr.; type local. Havana, Cuba; type USNM 143569; cf. *N. tropicus* of the Pacific).

Genus *Chirocentrodon* Günther 1868

Chirocentrodon Günther, Cat. Fish. Brit. Mus., 7, 1868: 463; genotype by monotypy, *Chirocentrodon taeniatus* Günther equals *Pellona bleekeriana* Poey. Myers, Copeia, 1929: 1; *Medipellona* a synonym. Breder, Copeia, 1942: 134; relationships.

Generic Synonym:

Medipellona Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67* (11), 1926: 417; genotype by original designation, *Pellona bleekeriana* Poey.

Characters. BODY slender, strongly compressed; ventral outline anteriorly much more strongly convex than dorsal outline. BONY SCUTES rather strong, about 24–28, the chest and abdomen with a sharp keel. MOUTH oblique, with moderately projecting lower jaw. TEETH on jaws, vomer, palatines, pterygoids, and tongue; each jaw (in adults) with two or more canines anteriorly. GILL RAKERS few, about 14–18 on lower limb of first arch. DORSAL fin small, with about 14–16 rays. ANAL fin long, beginning in advance of origin of dorsal, with about 39–43 rays. PELVIC fin very small, with 6 rays. VERTEBRAE about 44 or 45.

Remarks. This genus is characterized by the elongated and strongly compressed body with a strongly convex ventral outline anteriorly, the vomerine teeth, the canines anteriorly in each jaw, and the long anal fin beginning in front of the dorsal.

Discussion. Chirocentrodon generally has been placed in the family Clupeidae, but Jordan and Seale (75: 417), who evidently considered *Chirocentrodon taeniatus* Günther distinct from *Pellona bleekeriana* Poey (which has been disproved), erected a new genus

Medipellona on *Pellona bleekeriana* and doubtfully assigned it to the family Engraulidae (anchovies). Myers referred *Medipellona* to *Chirocentrodon* (*96*: 1). There seems to be no sound reason for removing from the Clupeidae this little herring, which has much in common with *Ilisha* (and *Neosteus*), but it apparently should be considered as having subfamily rank, Chirocentrinae, as already pointed out by Breder, who also discusses the possible relationship to *Chirocentrus*, an Asiatic genus (*22*: 136).[54]

Range. Known from the West Indies and from the Atlantic coast of South America from Panama to São Paulo, Brazil.

Chirocentrodon bleekerianus (Poey) 1867

Figures 114, 115

Study Material. Twenty-two specimens, *ca.* 52–107 mm TL (caudal fins damaged), 42–84 mm SL, including the holotype and paratype of *Ilisha caribbaea* Meek and Hildebrand (equals *C. bleekerianus*), and a cotype of *Pellona bleekeriana* Poey, in poor condition (USNM 120426); from Cuba; Jamaica; Puerto Rico; off Trinidad; at Fort Sherman (Toro Point) and Porto Bello, Panama; Pt. Macolla, Gulf of Venezuela; and Ubatuba, São Paulo, Brazil.

Distinctive Characters. The canine teeth in the anterior part of each jaw (in adults) are characteristic. The presence of vomerine teeth also distinguishes *bleekerianus* from all American Clupeidae, except the common Atlantic herring, *Clupea harengus.*

Description. Proportional dimensions in per cent of standard length, and counts, based on specimens 42–84 mm SL.

Body: depth 17.5–27.
Caudal peduncle: depth 7.8–9.5.
Head: length 22–26; depth 17–22.
Snout: length 5.7–8.2.
Eye: diameter 6.0–8.5.
Interorbital: width 2.9–4.5.
Maxillary: length 15–19.
Mandible: length 13.7–16.9.
Anal fin: length of base 35–39.
Pelvic fin: length 3.4–4.9.
Pectoral fin: length 14.8–18.5.
Distance from snout to origin of: dorsal 58–62.

Scales: lost, *ca.* 43 pockets.
Ventral scutes: 24–28.
Fin rays: dorsal 14–16, usually 15; anal 39–43, rarely 44 or 45; pectoral 13–15, usually 14.
Vertebrae: 44 or 45 (2 specimens).

Body moderately slender, strongly compressed, its greatest thickness about a third of its depth, its greatest depth 3.85–5.55 in SL; the dorsal outline gently convex, the ventral contour strongly convex anteriorly. Caudal peduncle rather short, strongly compressed, its depth 2.55–3.7 in head.

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[54] Following Breder's excellent paper, there remains little doubt that *Chirocentrodon* is closely related to the two large Indo-Pacific species of *Chirocentrus* and that both genera should be placed together in a separate subfamily or family.—G. S. Myers.

Scales lost from specimens at hand; fairly large (judging from pockets). Ventral scutes strong, 15–19 (most frequently 16 or 17) before pelvic fins and 8–10 (usually 9 or 10) behind them.

Head 3.85–4.55 in SL, its depth at vertical from crossgroove at occiput 4.55–5.9. Snout generally about equal to length of eye, without a definite median notch, 3.25–4.0 in head. Eye 3.0–4.0 in head. Interorbital 6.0–8.2. Cheek triangular, rather longer than deep. Mouth moderately oblique. Maxillary rather strongly convex, narrow posteriorly, generally reaching vertical from posterior margin of eye, 1.25–1.55 in head. Mandible projecting moderately, its tip well below dorsal outline of head, its margin within mouth rising rather gradually, 1.45–1.75 in head. Gill rakers strongly serrate along inner margin, those at angle of first arch a little shorter than eye, not increasing in number with age, 14–18 (most frequently 15 or 16) on lower limb of first arch. Teeth prominent; an outer series of small teeth on mandible, with 1 or 2 canines on each side anteriorly forming an incomplete inner series; a somewhat irregular series on premaxillaries, with some of the anterior teeth (2 or 3 on each side) somewhat canine-like; a series of rather prominent slender pointed teeth, generally irregular in size, on margin of maxillary; a few pointed ones on vomer laterally; small teeth on palatines and pterygoids; and a narrow band of minute teeth on midline of tongue.

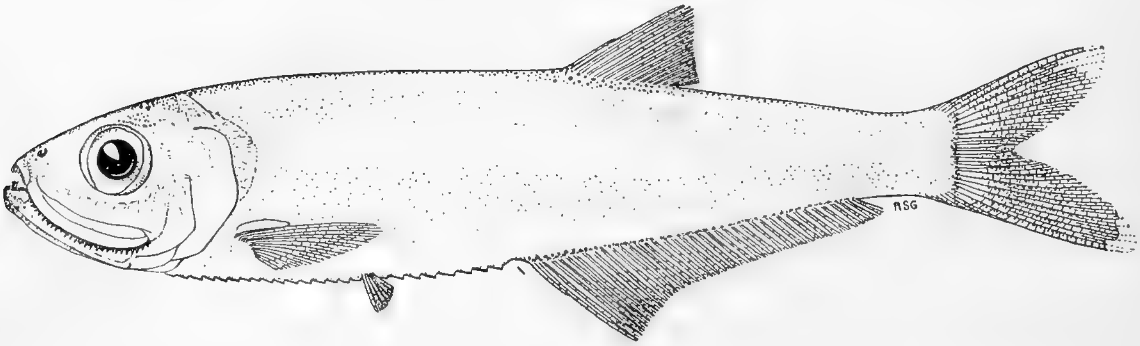

Figure 114. *Chirocentrodon bleekerianus*, about 87 mm TL (caudal damaged), 70 mm SL, Kingston, Jamaica, USNM 128274. Drawn by Ann S. Green.

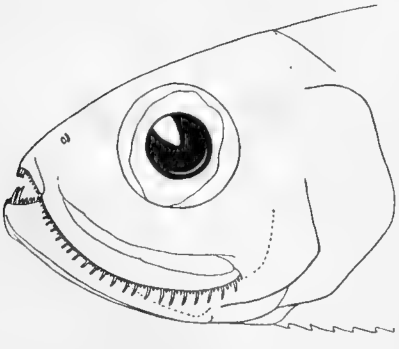

Figure 115. *Chirocentradon bleekerianus*, enlarged head showing teeth, same specimen as shown in Fig. 114. Drawn by Ann. S. Green.

Dorsal fin small, not greatly elevated anteriorly, its longest rays generally reaching nearly or quite to tip of last ray if deflexed, its origin a little nearer to base of caudal than to posterior margin of eye, its distance from margin of snout 1.6–1.7 in SL. Caudal fin broadly forked, the lower lobe the larger, nearly as long as head (Fig. 114). Anal fin long, its anterior rays somewhat elevated, its origin about an eye's diameter in advance of dorsal, its base 2.5–2.95 in SL. PELVIC fin shorter than eye, inserted a little nearer to origin of anal than to base of pectoral, 5.4–6.9 in head. PECTORAL fin reaching well beyond base of pelvic, 5.4–6.75 in SL, 1.3–1.6 in head; the free axillary process about a third of the length of the fin.

Color. In alcohol, pale with a fairly definite white lateral band (presumably silvery in life); nape and tip of snout with dusky punctulations; the more recently preserved specimens with dusky punctulations on entire median section of back, mostly arranged in two parallel series behind dorsal fin; dorsal and caudal fins with dusky punctulations; base of anal generally with a row of small dark spots.

Size. This species is among the smallest of herrings. The largest at hand, about 107 mm TL (4.3 in.; 84 mm SL), seems to be the largest example known.

Development. Specimens less than 52 mm TL, 42 mm SL, remain unknown. Nevertheless, a considerable increase in proportionate depth takes place with age and growth, as the large specimens at hand are notably deeper than the smaller ones. The greatest depth in a specimen 42 mm SL is contained 5.7 times in SL whereas in one 84 mm SL this proportion is only 3.7.

Although proportionate increase in the body depth with age and growth is so usual among Clupeidae that it is expected, a proportionate increase in the size of eye during development is so unusual as to be subject to question. However, the specimens that are now at hand, suspected at first, did in fact show this characteristic. Using again the two extremes in size, it is found that the eye in the 42-mm specimen is contained 3.55 times in the head and is only 7.1 % of SL, whereas in the 84-mm fish it is contained 3.0 times in the head and is 8.3 % of SL. From the fairly complete and graduated growth series within the range already mentioned, it is evident that the eye does increase in proportionate size with age and growth. It may be assumed, therefore, that this development, the reverse of what usually obtains in fishes, is normal in *C. bleekerianus.*

Spawning. A female about 107 mm TL, containing well-developed eggs fully 0.5 mm in diameter, was taken off Trinidad by the ALBATROSS, in 31–34 fms. As it was caught on February 3 (1884), the indication is that *C. bleekerianus* spawns during the northern winter.

Relationship. This species, as now understood, is the only one belonging to the genus *Chirocentrodon.* It has been described under at least three different names, as indicated in the Synonyms, but Breder has shown adequately that the three constitute only one species (*22*: 133).

Commercial Importance. This little herring was seen occasionally in the market in Port-au-Prince, Haiti, by Beebe and Tee-Van, who also stated that it is rare in Haiti (*10*: 43). It is not known to be numerous anywhere, therefore its importance as food for man as well as for fishes and other animals feeding on fish is probably slight.

Range. West Indies, from Cuba, Haiti, Jamaica, Puerto Rico, and Trinidad; also from the Atlantic coast of Panama, the Gulf of Venezuela, and Ubatuba, São Paulo, Brazil.

Synonyms and References:

Pellona bleekeriana Poey, Repert. Fisico-Nat. Cuba, *2*, 1867: 242 (orig. descr.; type local. Matanzas, Cuba; cotypes MCZ 17845; one USNM 120426); Poey, Synop. Pisc. Cubens., 1868: 419 (ref. to orig. descr., notes); Poey, An. Soc. esp. Hist. Nat., *5* (2), 1876: 180, p. 148 in separate (common name, ref.); Howell-Rivero, Bull. Mus. comp. Zool. Harv., *82* (3), 1938: 171 (cotypes in bad condition).

Chirocentrodon taeniatus Günther, Cat. Fish. Brit. Mus., *7*, 1868: 463 (orig. descr.; type local. Jamaica, West Indies; types BMNH); Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 435 (descr. after Günther); Norman, Ann. Mag. nat. Hist., (9) *11*, 1923: 21 (descr., *P. bleekeriana* probably not distinct); Beebe and Tee-Van, Zoologica, N. Y., *10* (1), 1928: 43, fig. (refs., diagn., tables, size, local abund., Port-au-Prince, Haiti); Myers, Copeia, 1929: 1 (*C. bleekerianus* and *C. caribbaeus* probably distinct); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 45 (ref.).

Ilisha bleekeriana Jordan and Evermann, Bull. U. S. nat. Mus., 47 (1), 1896: 436 (descr. after Poey); Evermann and Marsh, Bull. U. S. Fish Comm. (1900), *20* (1), 1902: 86 (diagn.); Nichols, N. Y. Acad. Sci., *10* (2), 1929: 204 (distr., diagn., Puerto Rico).

Ilisha caribbaea Meek and Hildebrand, Field Mus. Publ., Zool., *15* (1), 1923: 191, pl. 10, fig. 1 (orig. descr.; type local. Porto Bello, Panama; type USNM 81769); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 45 (ref.).

Medipellona bleekeriana Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67* (11), 1926: 417 (descr. after Poey; relation.).

Medipellona caribbea Jordan and Seale, Bull. Mus. comp. Zool. Harv., *67* (11), 1926: 418 (diagn.).

Chirocentrodon bleekerianus Fowler, Proc. Acad. nat. Sci. Philad., *80*, 1928: 456 (descr., *taeniatus* Günther synon., Haiti); Jordan, Evermann, and Clark, Rep. U. S. Comm. Fish. (1928), 2, 1930: 45 (ref.); Breder, Copeia, 1942: 134, fig. 1 (synon., relation., descr.).

Genus *Dorosoma* Rafinesque 1820

Gizzard Shads, Threadfin Shad

By

Robert Rush Miller

Museum of Zoology

The University of Michigan

Dorosoma Rafinesque, West. Rev. misc. Mag., *2* (3), 1820: 171 (see Fowler, Monogr. Acad. nat. Sci. Philad., 7, 1945: 6, 8); Ichthyol. Ohiensis, 1820: 39; type species by monotypy, *D. notata* equals *D. cepedianum* (LeSueur). Below falls of Ohio River.

Generic Synonyms:

Chatoessus Cuvier, Règne Anim., ed. 2, *2*, 1829: 320, in part; restricted by Cuvier and Valenciennes to *Megalops cepediana* LeSueur.

Signalosa Evermann and Kendall, Bull. U. S. Fish Comm. (1897), *17*, 1898: 127; type species, *Signalosa atchafalayae* equals *D. petenense* (Günther). Atchafalaya River, Melville, Louisiana.

Characters. Body compressed, silvery. The abdomen armed with Bony scutes; total 23–32. Scales cycloid, thin, 40–83 along side. Mouth small to moderate in size, terminal, subterminal, or inferior, the lower jaw included or jaws subequal. Snout short and rounded. Maxillary with two supramaxillary bones. Teeth absent in adult, but a row of fine teeth on upper jaw in young. Dorsal with last ray prolonged into a slender filament (absent or inconspicuous in young), thus resembling *Opisthonema.* Fin rays: dorsal 9–15, anal 17–38, pelvic 8, pectoral 12–17, caudal 19 (17 branched), rarely 17 or 18. Stomach gizzard-like, the Intestine long and much convoluted, with numerous Pyloric caeca. Vertebrae (including urostyle) 40–51.

Remarks. Dorosoma may be readily distinguished from *Opisthonema* in having (1) the ridge of the back before the dorsal fin naked rather than crossed by scales; (2) no bilobed dermal fold on the vertical anterior edge of the cleithrum; (3) an axillary scale, the pectoral fins not folding into a groove; (4) the dorsal origin not well in advance of the insertion of the pelvic fins; and (5) gill rakers 200–400 in *Dorosoma,* only about 65–109 in half-grown to adult *Opisthonema.*

Range. All species except *D. smithi* are confined to the Atlantic drainage of North and Middle America, from Canada to Nicaragua. They are found from southern South Dakota, Nebraska, and Minnesota, from the Great Lakes-St. Lawrence River Basin, and from about 40 to 41° N on the Atlantic seaboard (New York, New Jersey, and southeastern Pennsylvania) southward to Lake Nicaragua, but with a discontinuous distribution from northern Guatemala and British Honduras to Nicaragua. *D. smithi* is known only from coastal streams of northwestern México, in Sonora, Sinaloa, and Nayarit. Only two species, *D. cepedianum* and *D. petenense*, have been taken in brackish and salt water—the former from as far north as Sandy Hook Bay, New York, southward to the vicinity of Tampico, México.

Key to Species of *Dorosoma* Known from Brackish or Salt Water

1a. Mouth terminal; ventral edge of upper jaw smooth; fewer than 50 scales in lateral series, regularly arranged; anal rays 17–27, usually 20–25; prepelvic scutes 14–17 (rare); vertebrae 40–45. *petenense* (Günther) 1866, p. 448.

1b. Mouth subterminal or inferior; ventral edge of upper jaw with pronounced notch (except in young); more than 50 scales in lateral series, irregularly arranged; anal rays 25–36, usually 29–35, where sympatric with *D. petenense*; prepelvic scutes 17–20; vertebrae 48–51. *cepedianum* (LeSueur) 1818, below.

Dorosoma cepedianum (LeSueur) 1818

Gizzard Shad, Eastern Gizzard Shad

Figure 116

Study Material. Seventy-four specimens, 78–247 mm SL, for body proportions, 51–200 for meristic data except as otherwise stated, from various parts of its range, Canada to México.

Distinctive Characters. The comparatively small scales, 52–70 in lateral series and 36–45 around the body, a higher vertebral count (48–51, usually 50), the longer anal fin and greater number of rays (25–36), and preponderantly 18 + 12 ventral scutes, distinguish *D. cepedianum* from its sympatric relative *D. petenense.* Another relative, *Opisthonema oglinum*, may be separated from *D. cepedianum* by features listed in the generic account under *Remarks* (p. 443).

Description. Proportional dimensions in per cent of standard length and head length, with all measurements "stepped off" with a pair of precision dividers; based on *Study Material*, specimens 78–247 mm SL; counts based on 51–200 specimens, the number of specimens counted being given in parentheses.

Body: depth 2.3–3.1 in SL.

Caudal peduncle: length 2.4–3.5 and depth 2.45–3.4 in hl.

Head: length 3.0–3.9 in SL; width 1.8–2.5 in hl.

Snout: length 5.0–6.0 in hl.

Eye: length 3.3–5.4 in hl.

Interorbital: bony width 3.3–4.5 in hl.

Upper jaw: length 3.5–4.2 in hl.

Mandible: length 2.6–3.3 in hl.

Dorsal fin: base 1.85–2.6 in hl; length of filament 3.1–6.5 in SL, 0.8–2.0 in hl.

Caudal fin: length of lower lobe 0.7–1.1 in hl, typically longer than anal base (rarely subequal).

Anal fin: length of base 3.2–3.9 in SL, 0.75–1.25 in hl.

Pelvic fin: length 2.0–2.5 in hl.

Pectoral fin: length 1.15–1.45 in hl.

Distances: predorsal 1.85–2.05; prepelvic 2.0–2.35; anal origin to caudal base 2.4–2.8, all in SL.

Scales: lateral series 52–70, av. 61.06 (67), the first scale counted being the first above uppermost corner of gill opening; between dorsal and anal fins 19–24, av. 21.77 (52); around body 36–45, av. 41.03 (73), beginning with first one just in front of left pelvic fin; around caudal peduncle (slenderest part) 16–20, av. 18.02 (53).

Scutes: prepelvic 17–20, av. 17.99 (196); postpelvic 10–14, av. 11.76 (197); total ventral 27–32, av. 29.74 (196).

Gill rakers: on first arch, >300 at 65 mm SL, *ca.* 350 at 95 mm, and 412 at 157 mm; very numerous and fine (rakers counted *in situ*).

Fin rays: dorsal 10–13, av. 11.61 (197); caudal 19; anal 25–36, av. 31.32 (195); pelvic 8, rarely 7; pectoral 14–17, av. 15.52 (288; 144 fish).

Vertebrae: 48–51, av. 49.83, including urostyle (42).

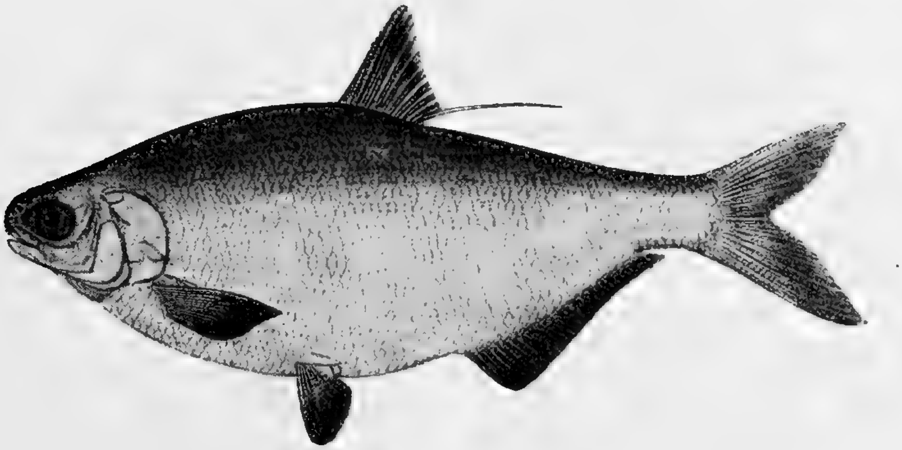

FIGURE 116. *Dorosoma cepedianum*, from Cumberland River, Tennessee, USNM 20034. After Goode, from drawing by H. L. Todd, somewhat emended.

No external characteristics will reliably distinguish the sexes.

Color. In life, body silvery. Bluish over back and upper sides but milky-white on abdomen, often with brassy or golden reflections from scales. About 6–8 horizontal, dark stripes along upper sides above level of middle of shoulder spot, extending from behind head to base of caudal fin. A large, round dark spot behind opercle lustrous purple, prominent in young and half-grown. Dorsal fin of adults nearly uniformly dusky; caudal fin dusky but darkened on its outer third; anal fin with outer 67 % dark, the basal third lighter, with melanophores sprinkled over most of fin; pectorals and pelvics with their outer halves darkened, grading to pale basally. Top of head, snout, upper jaw, and upper part of opercle pigmented in young and adult; the rest of head silvery. In young-of-the-year (up to about 4.5 in. TL), dorsal fin sparsely but uniformly sprinkled with chromatophores; caudal fin similar but with more pigment cells; anal, pectoral, and pelvic fins almost unpigmented.

Size. The Gizzard Shad is known to attain a total length of 20.5 inches but does not commonly grow longer than 10–14 inches. In a letter dated July 14, 1953, Mr.

Alfred Larsen (Fishery Biologist, Pennsylvania Fish Commission) wrote that specimens of *D. cepedianum* killed in Presque Isle Bay, Pennsylvania, early in 1953 ranged from 4 to 19 inches. Fish 10–13 inches long weigh about one pound, individuals 14–18 inches, 1–3 pounds; the heaviest recorded specimen weighed 3 pounds, 7 ounces (Trautman, *126*: 182).

Development and Growth. The prolarvae perform characteristic alternate sinking and rising movements for the first two days after hatching. The larvae are characterized by a long gut, 1.5–2.0 times the total length of the fish, by the retarded development of the single dorsal fin, and by the elongated anal fin with 22 rudimentary rays at 17.5 mm and 30–34 at 19–22 mm TL.

In contrast to the deep-bodied and strongly compressed adults, the very young are slender, cyprinid-like, and nearly cylindrical; the maxillaries have a few teeth on the lower edge which are lost with age, and unlike the adults with a highly specialized digestive tract, the young have an almost straight intestine and no pyloric caeca. By the end of the first summer of life the young possess the specializations of the adults.

At the end of the first summer, an average total length of about 4 inches is attained in Indiana and Ohio, 4.5 inches in the Chesapeake Bay region, and 5.0 inches in Tennessee and Oklahoma. The sizes in two Indiana ponds, after the first year, have been reported as follows: second summer, 7–9 inches, average 7.6; third summer, 9–11 inches, average 9.5; fourth summer, 9–12 inches, average 10.5; fifth summer, 10–13 inches, average 11.3; and sixth summer, 11–15 inches, average 12.8. Although they may live as long as 10 years, the life span is usually not more than seven years. In Lake Erie about 75 % of the annual growth of the Gizzard Shad takes place during the summer; in winter they grow little if at all and lose considerable weight.

Maturity typically occurs in the second or third year of life, at about 7–11 inches, but Vladykov (*127*: 35) has reported a mature female that was only 6 inches (151 mm) TL.

Spawning. Gizzard Shad are known to spawn only in fresh water, from late winter (mid-March) through most of the summer (at least to August 20) in sloughs, ponds, lakes, and large rivers. Spawning generally occurs on a rising temperature, usually between about 50° and 70° F. The creamy-yellow eggs, demersal and adhesive, are about 0.75 mm in diameter when fertilized and fixed. The embryos hatch after 95 hours of incubation at 62° F, or after about 36 hours at 80° F.

Precocious females appear to have few eggs. Those belonging to age-group II have the most, averaging about 380,000 eggs in five females 291 mm long; egg production then declines with successively older groups.

Food. Gizzard Shad are essentially filter feeders. Except for a few weeks after hatching, those in fresh water are almost entirely herbivorous, feeding heavily on microscopic plants, phytoplankton, and algae. After they reach a length of about 20–25 mm TL, the diet is remarkably alike at various sizes. The food habits in salt and brackish water have not been studied.

Habitat and Occurrence. Gizzard Shad inhabit large rivers, reservoirs, lakes, swamps, bays, barrow pits, estuaries, bayous, temporary floodwater pools along large river courses, sloughs, and similar quiet, open waters that may be clear to very silty. The very young apparently do not enter brackish water; in coastal rivers of Virginia the young occur in greatest abundance well upstream. In Chesapeake Bay, Gizzard Shad are common only during the fall months, occurring principally in brackish water near the mouths of freshwater streams, but in the rivers of that region they are common or abundant throughout the year. Along the Texas coast, they frequent the large brackish-water bays where individuals may be taken throughout the year in waters that vary in salinity from 2.0 to 33.7 ‰. Thus Gizzard Shad in this area also prefer brackish water to sea water. In general the smallest fish occur in the freshest water, with size increasing as salinity increases.

Dr. R. D. Suttkus of Tulane University has taken *D. cepedianum* at about 20 brackish and saltwater stations in Louisiana, not including nearly 40 separate captures from Lake Pontchartrain. Most of the 20 records are from along the Gulf of Mexico coast or within embayments connected with the Gulf. I am grateful to Dr. Suttkus for these data.

Range. Atlantic drainage of eastern North America south to Río Pánuco, México.

Synonyms and References:

Megalops cepediana LeSueur, J. Acad. nat. Sci. Philad., *1*, 1818: 361 (orig. descr.; markets of Baltimore and Philadelphia, hence usually given as Chesapeake and Delaware bays).

Clupea heterura Rafinesque, Amer. Month. Mag., 1818: 354 (orig. descr.; Ohio River).

Dorosoma notata Rafinesque, West. Rev. Misc. Mag., *2* (3), 1820: 172 (orig. descr.; type local., falls of Ohio R.).

Chatossus ellipticus Kirtland, Rep. Zool. Ohio *in* Second Rep. geol. Surv. Ohio, Columbus, 1838: 169, 195 (NOMEN NUDUM, Ohio; same as *D. notata*); Boston J. nat. Hist., *4* (2), 1842: 235, pl. 10, fig. 1 (orig. descr.; compar., occur. in Ohio, habits, mortal., Ohio R. and tributaries).

Megalops bimaculata LeSueur *in* Cuvier and Valenciennes, Hist. nat. Poiss., *21*, 1848: 104 (NOMEN NUDUM, synon. with *Chatoessus cepedianus* by Valenciennes).

Chatoessus insociabilis Abbott, Proc. Acad. nat. Sci. Philad. (1860), *12*, 1861: 365 (orig. descr.; habits, "sturgeon pond 2 miles below Trenton, New Jersey").

Chatoëssus cepediana Günther, Cat. Fish. Brit. Mus., *7*, 1868: 409 (descr., based on specimens from New York).

Dorosoma cepedianum exile Jordan and Gilbert, Proc. U.S. nat. Mus. (1882), *5*, 1883: 585 (orig. descr.; Galveston Bay, Texas).

Dorosoma cepedianum Goode, *et al.*, Fish. Fish. Industr. U.S., 1, 1884: 610 (in brackish or sea water, Atlantic coast); Higgins and Pearson, Rep. U.S. Comm. Fish. (1927), 1928: 42 (Pamlico Sound, N. Carolina); Hildebrand and Schroeder, Bull. U.S. Bur. Fish. (1927), *43*, 1928: 106 (Chesapeake Bay, rare in strictly salt water); Fowler, Monogr. Acad. nat. Sci. Philad., 7, 1945: 165 (Cape I. and rice field near Cordesville, S. Carolina); Gunter, Publ. Inst. mar. Sci. Texas, *1* (1), 1945: 30 (brackish and salt water, Texas coast; prefers brackish to sea water); Massmann, Trans. 18th N. Amer. Wildl. Conf., 1953: 439 (young in Virginia estuaries); Bailey, Winn, and Smith, Proc. Acad. nat. Sci. Philad., *106*, 1954: 120 (common in fresh tidewater, Escambia R., Florida); Miller, Fish. Bull. (173) U.S. Fish Wildl. Serv., *60*, 1960 (review of systematics and biol.); Minckley and Krumholz, Zoologica, N.Y., *44*, 1960 (hybrid. with *D. petenense*).

Dorosoma exile Meek, Field Mus. Publ., Zool., *5*, 1904: 94 (descr., lowland tributaries of Gulf of Mexico N. of Veracruz, México, San Juan, Forlón, Valles).

Dorosoma petenense (Günther) 1866

Threadfin Shad

Figure 117

Study Material. Twenty-five specimens, 59–180 mm SL, for measurements, and 186 for meristic data except as otherwise stated, from Florida to Lake Péten, Guatemala.

Distinctive Characters. The terminal mouth and the smooth ventral edge of the upper jaw distinguish this species from the other forms of *Dorosoma.* In addition it is readily separated from *D. cepedianum* in having larger, regularly arranged scales (fewer than 50 in lateral series), only 40–45 vertebrae, a smaller anal fin with 17–27 rays (usually 20–25), a longer and more pointed snout, longer upper jaw and mandible, and usually 16 or 17+9–11 ventral scutes. This species may be confused with *Opisthonema oglinum*, since both have a prolonged dorsal filament, but the latter is distinguished by the features given under *Remarks* in the generic account (p. 443).

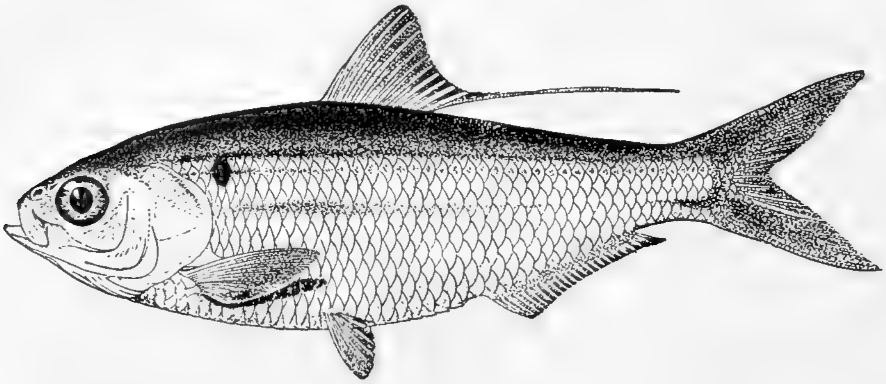

FIGURE 117. *Dorosoma petenense,* from Atchafalaya River, Alabama, USNM 48790. After Evermann and Kendall.

Description. Proportional dimensions in per cent of standard length and head length, with all measurements "stepped off" with precision dividers; based on specimens 59–180 mm SL; counts based on 186 specimens or less, the number of specimens counted being given in parentheses.

Body: depth 2.4–3.0 in SL.
Caudal peduncle: length 2.3–3.4 and depth 2.25–2.8 in hl.
Head: length 2.95–3.7 in SL; width 1.95–2.4 in hl.
Snout: length 4.1–4.85 in hl.
Eye: length 3.3–4.1 in hl.
Interorbital: bony width 3.5–4.5 in hl.
Upper jaw: length 2.8–3.35 in hl.
Mandible: length 2.1–2.5 in hl.
Dorsal fin: base 1.5–2.05 in hl; length of filament 2.7–3.1 in SL, 0.6–1.0 in hl.
Caudal fin: length of lower lobe 0.7–0.9 in hl.
Anal fin: length of base 3.5–4.35 in sl.

Pelvic fin: length 2.05–2.4 in hl.

Pectoral fin: length 1.2–1.35 in hl.

Distances: predorsal 1.9–2.25; prepelvic 1.9–2.25; anal origin to caudal base 2.6–3.1; all in SL.

Scales: lateral series 41–48; between dorsal and anal fins 14–17; around body 28–36; around caudal peduncle 16–20 (all counts based on 25 specimens covering the size range of this species).

Scutes: prepelvic 15–18, av. 16.79 (176); postpelvic 8–12, av. 9.95 (178); total ventral 23–29, av. 26.75 (176).

Gill rakers: *ca.* 300 at 66 mm SL, 330 at 117 mm, 350 at 131 mm, and about 440 at 180 mm; fine and numerous (rakers counted *in situ*).

Fin rays: dorsal 11–14, av. 12.13 (178); caudal 19; anal 17–27, av. 22.38 (179); pelvic 8, rarely 7; pectoral 12–17, av. 14.39 (354, 177 fish).

Vertebrae: 40–45, av. 42.23, including urostyle (30).

As in *D. cepedianum*, there appear to be no reliable external features that will distinguish the sexes.

Color. In life, body bright silvery, especially on sides, opercles, and underparts, but back and upper sides bluish-black or dark olivaceous, washed with gold and overlain with horizontal rows of dark stripes. A conspicuous, jet-black round or oval spot behind upper part of opercle. Caudal with middle portion of each fin lobe bright golden yellow, fading basally and distally, the posterior border dusky; dorsal fin dusky, washed with yellowish olive; anal fin intensely yellow; paired fins yellow basally. A broad golden stripe (often represented only by gilt reflections) in the light band between back and sides, but almost no gilt on sides of head.

Size and Age. The Threadfin Shad is a smaller species than the gizzard shad. In the northern part of its range, the adult generally does not exceed 5 or 6 inches TL; in southern states it may grow to 7 inches, and in Guatemala to nearly 8.75 inches or 180 mm SL (specimen from Laguna de Yalác; UMMZ 143386). The species has a short life-span, for few individuals appear to exceed two years of age.

Variations in Size with Season. In bays along the Texas coast, adults were most abundant in August and October while the young were entirely absent; between August and November the size increased from a mode between 103 and 108 mm TL to 118 mm. In January, only fish with a modal length of 63 mm came into the catch, and in February the same group was present along with a few fish 114 and 117 mm long. Possibly early growth takes place only in fresh water. Water temperatures in the bays of Texas varied from about 48 to 86° F over the year.

Spawning. Threadfin Shad may spawn when they are less than one year old; there appear to be two spawning peaks—spring and fall. Spawning occurs at about 70° F in open waters, near or over plants and other objects. The eggs are slightly adhesive.

Habits. Threadfin Shad are generally pelagic; they often feed and migrate in schools numbering thousands of individuals. The different age-groups usually remain in separate schools. They are known to concentrate at the downstream faces of dams and similar obstructions, and large aggregations are seen at reservoir inlets. Water current obviously attracts large schools; when the electric turbines were reduced or shut off in the Tennessee impoundments, the Threadfin Shad were difficult to find, but when the power was turned on they were present in abundance.

Food and Feeding. Like their close relative, these fish are plankton feeders, the major items of the adult diet consisting of algae (diatoms and unicellular green species), copepods, and cladocerans. Threadfin Shad introduced into the Salton Sea, California, have a preference for the fry of *Bairdiella icistius* (Jordan and Gilbert), which suggests that they may have similar food habits in coastal lagoons and estuaries within their natural range.

Tolerance to Temperature. As in the case of the gizzard shad, sudden temperature changes often produce high mortality among Threadfin Shad. Berry *et al.* have observed a spawning mortality for both species during April in Florida lakes. *D. petenense* cannot tolerate as low temperatures as *D. cepedianum*. For Threadfin Shad in the Colorado River, Texas, temperatures of about 54–58° F may be close to the minimum tolerance. However, among experimental individuals from the lower Tennessee River, subjected to water cooled from 50 and 60° F, there was a high mortality below 45°, with very few fish surviving below 40°.

Habitat and Occurrence. Threadfin Shad seek habitats similar to those of the gizzard shad and are often associated with *D. cepedianum* where the two species are sympatric. They live in bays, large rivers, reservoirs, lakes, estuaries, and other similar situations. Along the coast of Texas they occur in bays having salinities varying from 3.8 to 26.9 ‰, the majority having been taken in waters with salinities between 10 and 20 ‰. Apparently these fish show a preference for water that is neither fully marine nor very fresh, a condition typical in many lagoons along the coast of Texas. Larger fish, approximately 100–150 mm long, occurred in waters of about 15–30 ‰, whereas smaller fish, generally below 100 mm, were taken in salinities below 15 ‰.

Records of Threadfin Shad obtained by Dr. R. D. Suttkus through 1958 indicate their occurrence at nearly 50 brackish and saltwater stations in Florida, Alabama, Mississippi, Louisiana, and Texas, not including about 75 captures from Lake Pontchartrain.

Range. From the Ohio River of Kentucky and southern Indiana westward and southward to Oklahoma, Texas, and Florida, thence along the coast of the Gulf of México to northern Guatemala and British Honduras (Belize River). Their recent invasion of the Ohio River Basin is discussed by Minckley and Krumholz (*94*).

Synonyms and References:

Meletta petenensis Günther, Proc. zool. Soc. Lond., 1866: 603 (orig. descr.; Lake Petén, Guatemala).

Chatoessus petenensis Günther, Cat. Fish. Brit. Mus., 7, 1868: 408 (redescr. of types).

Chatoessus mexicanus Günther, Cat. Fish. Brit. Mus., 7, 1868: 409 (orig. descr.; México, New Orleans, Louisiana).

Dorosoma mexicanum Jordan and Evermann, Bull. U.S. nat. Mus., 47 (1), 1896: 416 (descr., from Günther).

Dorosoma petenense Jordan and Evermann, Bull. U.S. nat. Mus., 47 (1), 1896: 417 (descr., from Günther); Regan, Biol. Centr. Amer., Pisces, *8*, 1906–08: 178 (redescr. of types); Fowler, Proc. Acad. nat. Sci.

Philad., *63*, 1911: 211 ("Panama," obviously in error); Bailey, Winn, and Smith, Proc. Acad. nat. Sci. Philad., *106*, 1954: 119 (range; from fresh tidal waters, Escambia R., Florida); Berry, Huish, and Moody, Copeia, 1956: 192 (spawn. mortal. in Florida, life-hist. notes); Kimsey, Calif. Fish Game, Inl. Fish. Adm. Rep., 58–16 (mimeo), 1958: 1–21 (life hist., proposed introd. into Sacramento–San Joaquin Delta); Shapovalov, Dill, and Cordone, Calif. Fish Game, *45*, 1959: 166 (review introd. into California).

Signalosa atchafalayae Evermann and Kendall, Bull. U.S. Fish Comm. (1897), *17*, 1898: 127, pl. 7, fig. 4 (orig. descr.; Louisiana and Mississippi; use as bait; type local., Atchafalaya R. at Melville, Louisiana).

Signalosa mexicana Meek, Field Mus. Publ., Zool., *5*, 1904: 94 (synon., descr., lowland streams trib. to Gulf of Mexico, México—Valles, Obispo, El Hule, Perez); Regan, Biol. Centr. Amer., Pisces, *8*, 1906–08: 178 (redescr. of types, range); Fowler, Proc. Acad. nat. Sci. Philad., *63*, 1911: 211 (Volusia, Florida); Regan, Ann. Mag. nat. Hist., (8) *19*, 1917: 310 (descr. 9 specimens, includ. types, from Louisiana to Centr. Amer.); Gunter, Publ. Inst. Mar. Sci. Texas, 1 (1), 1945: 31 (prov. ident., size range, temp. range, and salinity, Copano and Aransas bays, Texas).

Signalosa petenensis Regan, Ann. Mag. nat. Hist., (8) *19*, 1917: 310 (redescr. based on types); Hubbs, in Hubbs and Allen, Proc. Fla. Acad. Sci., 6, 1943: 116 (*S. mexicana* and *S. atchafalayae* synon. with *S. petenensis*); Miller, Proc. Okla. Acad. Sci. (1953), *34*, 1955: 33–34 (first rec. for Oklahoma); Riggs and Moore, Proc. Okla. Acad. Sci. (1957), *38*, 1958: 64–67 (Lake Texoma, Oklahoma and Texas); Minckley and Krumholz, Zoologica, N.Y., *44*, 1960 (chars., hybrid. with *D. cepedianum*, range).

Signalosa mexicana mexicana Weed, Field Mus. Publ., Zool., *12* (11), 1925: 142 (synon., char., basin of Rio Papaloapan, Veracruz and Oaxaca, México).

Signalosa mexicana campi Weed, Field Mus. Publ., Zool., *12* (11), 1925: 143 (orig. descr.; compar., type local. Resaca de la Guerra, on or near Media Luna Ranch, Brownsville, Texas).

Signalosa atchafalayae atchafalayae Weed, Field Mus. Publ., Zool., *12* (11), 1925: 144 (synon., char., compar., Louisiana).

Signalosa atchafalayae vanhyningi Weed, Field Mus. Publ., Zool., *12* (11), 1925: 145 (orig. descr.; type local. Prairie Cr., 6 mi. SE of Gainesville, Florida).

Signalosa petenensis vanhyningi Hubbs and Allen, Proc. Fla. Acad. Sci., *6*, 1943: 116 (common name, habits, color, Silver Springs, Florida); Fowler, Monogr. Acad. nat. Sci. Philad., 7, 1945: 266 (synon., refs., Volusia, Florida); Parsons and Kimsey, Prog. Fish-Cult., 16 (4), 1954: 179–181, 1 fig. (distr., review of biol., use as forage fish).

Signalosa petenensis campi Fowler, Monogr. Acad. nat. Sci. Philad., 7, 1945: 22 (Rio Grande).

Signalosa petenensis atchafalayae Fowler, Monogr. Acad. nat. Sci. Philad., 7, 1945: 366, 372 (synon., refs., Avery I., Louisiana; Galveston, Texas); Hubbs, Copeia, 1951: 297 (min. temp. tolerance in Colorado R., Austin, Texas); Chance and Miller, J. Tenn. Acad. Sci., *27* (3), 1952: 218 (first publ. rec. for Tennessee Valley; effect of severe winter, 1950–51); Kimsey, Calif. Fish Game, *40*, 1954: 204 (introd. into California).

Dorosoma petenensis atchafalayae Kimsey, Trans. Amer. Fish. Soc. (1957), *87*, 1958: 331, 332 (forage use in California and Arizona).

Dorosoma petenense atchafalayae Haskell, Copeia, 1959: 298–302 (food habits, Arizona).

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Suborder Salmonoidea

COMPOSITE AUTHORSHIP[1]

Characters and Key to Families

HENRY B. BIGELOW

Museum of Comparative Zoology
Harvard University

Characters. Isospondylous fishes with PELVIC FINS abdominal in position, and with an ADIPOSE FIN between the rayed dorsal and caudal fin.

SCALES. Body and tail sectors of trunk with scales everywhere in most, but naked in some Salangidae;[2] head naked; scales thin, rounded. LUMINESCENT ORGANS (photophores) absent.

MAXILLARY bones as well as PREMAXILLARIES taking part in formation of upper jaw. TEETH of moderate size in most, but those on lower jaw in the form of canines in a few, perforating the upper jaw; teeth present on premaxillaries, maxillaries, palatines, vomer (except in some Salangidae), dentary portion of lower jaw, and tongue in most; teeth small or absent among the Coregonidae.

PECTORAL GIRDLE with a mesocoracoid element in most; lacking in the Salangidae. Last few VERTEBRAE upturned in Salmonidae, Coregonidae, and Thymallidae; a single vertebral centrum turned upward in the Osmeridae, but conditions in this respect seem not to have been reported for the Salangidae.

A SWIM BLADDER in most, connected to the alimentary canal by a permanently open duct; no swim bladder in Salangidae. OVIDUCTS incomplete insofar as known,

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[1] Characters and Key to Families by H. B. Bigelow; Family Salmonidae and Genus *Salmo* by J. R. Dymond; Genera *Salvelinus* and *Cristivomer* by H. B. Bigelow; Family Coregonidae by H. B. Bigelow; Family Osmeridae by H. B. Bigelow and William C. Schroeder.

[2] The Salangidae are described (*46*: 239) as "naked, or with a few exceedingly thin, large, scattered deciduous scales." For illustrations of the salangid dentition, see Fang (*46*: 240, fig. 1; 246, fig. 3; 252, fig. 8; 260, fig. 10).

being represented by a fold of the peritoneum. Stomach with PYLORIC CAECA except in Salangidae.

Remarks. For discussion of the characters that distinguish the Salmonoidea from other Suborders of the Isospondyli, see Key to Suborders (p. 95) and related text.

Families. Of the six families recognized in the following Key, three are represented with detailed accounts in this series: Salmonidae (p. 457), Coregonidae (p. 547), and Osmeridae (p. 553). The Thymallidae (graylings), Plecoglossidae (ayu or sweetfishes), and Salangidae (icefishes) occur in northern waters of western North America, Europe, Siberia, northern China, Korea, and Japan. Many of the species are anadromous, ascending freshwater rivers to spawn.

Key to Families

1a. A fleshy axillary lobe on each side close above base of pelvic fins.
  2a. Rayed dorsal fin, when depressed, shorter than head.
    3a. Teeth well developed on jaws, on roof of mouth, and on tongue; at least 19 scales in a transverse series from origin of dorsal fin to lateral line; parietal bones of skull not meeting in the midline. Salmonidae, p. 457.
    3b. Teeth minute or lacking; not more than 13 scales in a transverse series from origin of dorsal fin to lateral line; parietal bones of skull meeting in the midline. Coregonidae, p. 547.
  2b. Rayed dorsal fin, when depressed, much longer than head.
    Thymallidae.
    Mostly in clear, cold streams, seldom entering salt water; western North America, northern Europe, and Siberia.
1b. No axillary lobe above base of pelvic fins.
  4a. Head only slightly depressed, its depth at eyes 67% or more of body depth at dorsal fin; snout in front of eyes at least no longer than base of dorsal fin; body not transparent; branchiostegal rays 6–10; swim bladder present; stomach with pyloric caeca.
    5a. Jaw teeth firmly and directly attached to jaw bones; tongue not pleated; not more than 10–12 pyloric caeca. Osmeridae, p. 553.
    5b. Jaw teeth arranged on serrated plates on inner sides of jaws, not directly attached to jaw bones; tongue pleated; up to 400 pyloric caeca.
      Plecoglossidae.[3]
      Running up cold streams to spawn; coastal waters of Japan and Formosa.
  4b. Head strongly depressed, its depth at eyes less than 50% of body depth at dorsal fin; snout in front of eyes about twice the length of base of dorsal fin; body transparent; branchiostegal rays only 3 or 4; no swim bladder; no pyloric caeca. Salangidae.[4]
    Ascending rivers to spawn; coastal waters of Japan, Korea, and northern China.

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[3] Only known genus, *Plecoglossus*.

[4] Contains only one genus, *Salanx*.

Family Salmonidae

JOHN R. DYMOND
University of Toronto

Acknowledgment. I am indebted to Henry B. Bigelow for much help in the preparation of the manuscript, especially concerning conditions in New England and in the matter of angling.

Characters. MOUTH large. MAXILLARY reaching to a vertical through the eye or beyond. TEETH well developed on jaws, vomer, palatines, and in a double series on the tongue. PARIETALS not meeting in the midline. ORBITOSPHENOID, BASISPHENOID, and SUPRAOPERCULAR present. Last few VERTEBRAE upturned. DORSAL fin with not more than 16 rays, 12 or less of them branched. ADIPOSE DORSAL fin present. AXILLARY PROCESS associated with ventral fin. SWIM BLADDER connected to alimentary canal by a permanently open duct. OVIDUCTS incomplete, being represented by a fold of the peritoneum. Stomach with PYLORIC CAECA.

Sexual Dimorphism. This phenomenon occurs in the entire family, especially at spawning time, with an extreme condition in *Oncorhynchus* to comparatively little in *Cristivomer*, *Salmo* occupying an intermediate position. The extent to which these changes affect the two sexes is discussed in the account of the Atlantic Salmon (p. 463).

Remarks. For characters that separate the family Salmonidae from other families of the Suborder, see Key to Families (p. 456) and related text.

Range. The Salmonidae, composed of six genera, is an important and widely distributed family of the Arctic and north temperate zones of the northern hemisphere. Many members are anadromous, living in both fresh and salt water, and others are confined to only freshwater lakes and rivers (see Key to Genera, p. 458). The species of *Salvelinus* and *Salmo* are found in both marine and fresh waters of northern North America, Europe, and Asia. The various species of *Oncorhynchus* are confined primarily to the Pacific, but one or two species range through the Bering Strait and then for limited distances eastward and westward along the Arctic coasts of North America and Asia. Three genera are virtually confined to fresh water: *Cristivomer* of North America, *Brachymystax* of Asia, and *Hucho* of Europe and Asia; being essentially freshwater fish, they apparently have never been able to spread through salt water from one continent to another. Members of *Salvelinus* live the farthest north, with *S. alpinus* ranging well within the Arctic Circle. [For the ranges of the species discussed, see pp. 490, 499, 521, 539, and 543.]

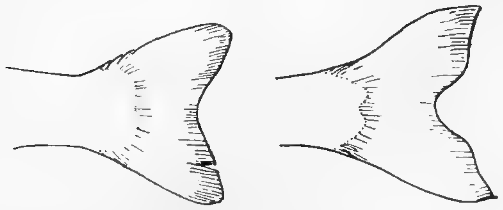

FIGURE 118. Outline of caudal fin: *Salvelinus alpinus* (left); *Cristivomer namaycush* (right).

FIGURE 119. Outline of side of head: *Salvelinus alpinus* (left), *Brachymystax* (right), illustrating difference in shape of lower margin of upper jaw (maxillary bone).

Key to Genera

1a. Lower margin of sides of upper jaw (maxillary bones) weakly and uniformly concave in outline (Fig. 119).

- 2a. Anal fin usually with fewer than 13 rays.
  - 3a. A double or zigzag series of teeth on shaft of vomer along midbelt of roof of mouth, but sometimes lost in adult; sides with black markings. *Salmo* Linnaeus 1758, p. 459.
  - 3b. Teeth absent on shaft but present on head of vomer; sides without black markings.
    - 4a. Teeth on the vomer usually separated from the teeth on the palatines.
      - 5a. Caudal fin only moderately concave (Fig. 118); sides with reddish or salmon-colored spots; not more than 50 pyloric caeca. *Salvelinus* Richardson 1836, p. 503.
      - 5b. Caudal fin deeply concave (Fig. 118); sides with pale whitish spots; about 140 pyloric caeca. *Cristivomer* Gill and Jordan 1878, p. 542.
    - 4b. Teeth on the vomer connected in an unbroken series with the teeth on the palatines. *Hucho* Günther 1860. Rivers of central and eastern Europe, northern Asia, and Japan.
- 2b. Anal fin with 13–19 developed rays. *Oncorhynchus* Suckley 1861. Both sides of northern North Pacific.[5]

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[5] The Humpback Salmon (*O. gorbuscha*) has been introduced in several rivers of Maine and for a time it seemed that it was established there, but it failed to maintain itself. The Silver Salmon (*O. kisutch*) also has been planted in Maine, but without result. For further details see Bigelow and Schroeder (*18*: 131–133).

1 b. Lower margin of sides of upper jaw (maxillary bone) strongly convex in outline (Fig. 119). *Brachymystax* Günther 1860.
Rivers of Siberia.

Genus *Salmo* Linnaeus 1758

Salmon, Trouts

Salmo Linnaeus, Syst. Nat., *1*, 1758: 308; type species, *Salmo salar* Linnaeus, established by Jordan and Gilbert, Bull. U.S. nat. Mus., *16*, 1882: 309. European Ocean.

Generic Synonyms:
Trutta Geoffroy, E. L., Descr. 719 Plantes, 134 Animaux., Paris, 1767: 719.
Fario Cuvier and Valenciennes, Hist. Nat. Poiss., *21*, 1848: 227; *argenteus* equals *trutta*.
Salar Cuvier and Valenciennes, Hist. Nat. Poiss., *21*, 1848: 294; *ausonii* equals *fario*.

Species. *Salmo*, the type genus of the family, contains the species originally named THE Salmon (*S. salar*) and THE Trout (*S. trutta*). In addition to THE Trout, other black-spotted trout closely related to it are included. These occur chiefly in Europe and North America; a few are found in areas that may be regarded as extensions of the main centers of distribution.

Some isolated landlocked populations have diverged so far from the presumed parent stocks as to constitute distinct species. In the case of others, the question of their taxonomic status is still a matter of doubt. This has led to uncertainty as to how many species should be recognized. Three species fall within the scope of this book: *S. salar*, the Atlantic Salmon, which is anadromous and spawns in fresh water (see also *Freshwater Populations*, p. 491); *S. trutta*, the European trout, an introduced species that is anadromous in Newfoundland and is called the brown trout in America (p. 498); and *S. gairdneri*, the rainbow trout, which is indigenous in northwestern America but which has been widely introduced and is well established in the north-eastern United States and eastern Canada, occurring mostly in fresh water but being anadromous locally (p. 499).

Key to Species of the Western North Atlantic

1a. Anal usually with 9 fully developed rays; caudal usually unspotted.
  2a. Vomerine teeth little developed, those on shaft few and deciduous; scales from adipose fin to lateral line, 10–13; maxillary extending to below rear edge of pupil at length of 150 mm, never far behind in large adults; caudal weakly concave in adults; black spots on body small, without halos.
  salar Linnaeus 1758, p. 460.
  2b. Vomerine teeth well developed, those on shaft of bone numerous and per-

sistent; scales from adipose fin to lateral line, 12–16; maxillary extending to below rear edge of eye at 150 mm, farther back in large specimens; caudal truncate in adults; black spots on body large, many surrounded by halos.
trutta Linnaeus 1758, p. 498.

1 b. Anal with 10 or more fully developed rays; caudal spotted.
gairdneri Richardson 1836, p. 499.

Salmo salar Linnaeus 1758

Atlantic Salmon, Sea Salmon

Figures 120–123

Study Material. Ten fresh specimens (7 males, 3 females), about 71–90 cm or 28–35 inches SL, from the Matamek River, Saguenay County, Province of Quebec, caught towards the end of July 1931 (not preserved); also 87 specimens, fry to adult, from New Brunswick, Nova Scotia, Newfoundland, and Quebec (including Ungava Bay).

Distinctive Characters. Salmo salar is distinguished from all species of *Oncorhynchus* of the Pacific in having fewer than 13 rays in the anal fin (13–19 in *Oncorhynchus*).

It is readily distinguished from *Salvelinus alpinus* and *fontinalis* (Arctic charr and brook trout) and from *Cristivomer namaycush* (lake trout) by its black spots (light-colored in charrs) and by its larger scales (so small as to be readily overlooked in charrs).

It is separated from *Salmo gairdneri* (rainbow trout) by the absence of black spots on its caudal fin (many spots on caudal of *gairdneri*).

Separation of *Salmo* salar from *Salmo trutta* (brown trout) is more difficult than from the above species, for both *salar* and *trutta* lack spots on the caudal fin. However, in *salar* the tail is more constricted at the base of the caudal fin than in *trutta*, so that in *salar* the anterior caudal rays form more of a shoulder; consequently, an Atlantic Salmon does not slip through one's fingers when grasped round the caudal peduncle as a brown trout usually does. This difference is reflected in the number of scales in an oblique row from the posterior edge of the adipose fin (downwards and forwards) to the lateral line: 10–13 (usually 11) in *salar*, 13–16 (rarely 12) in *trutta*. Other differences include: dorsal fin rays 10–13 (usually 11) in *salar*, 13–16 (usually 14, rarely 12) in *trutta*; pyloric caeca 50–80 in *salar*, 30–60 in *trutta*. The caudal fin of *salar* is more widely spread and is more deeply emarginate than that of *trutta*. Finally, *salar* has a smaller mouth, the maxillary in the adult extending scarcely, if at all, beyond the eye (well beyond the eye in *trutta*).

Jones (77) has tabulated the differences between the young Atlantic Salmon and brown trout as follows:

	YOUNG ATLANTIC SALMON	YOUNG BROWN TROUT
Body	Usually thinly spotted.	Usually much spotted.
Caudal peduncle, depth	One-tenth of length of body.	One-eighth of length of body.
Operculum	Rarely more than three spots.	Usually more than three spots.
Maxilla, at length of:		
4 inches	To center of pupil.	To posterior edge of pupil.
6 inches	To posterior edge of pupil.	To posterior edge of iris.
Dorsal fin	Usually weakly spotted.	Usually well-defined spots.
Adipose fin	Rarely edged with red.	Usually edged with red.
Paired fins	Generally grey.	Generally orange-yellow.
Tail	Deeply forked; middle rays not more than 0.6 of length of longest rays.	Shallowly forked; middle rays 0.6 or more of length of longest rays.
Parr marks	Usually 11–12.	Usually 9–10.

It is possible that hybridization may occur between *salar* and *trutta*, in which case the hybrids probably would not possess the distinguishing characters of either parent.

Description. The adult Atlantic Salmon is a graceful fish, deepening rearward from a small pointed head to the deepest point under the dorsal fin, then tapering to a slender caudal peduncle which supports a spreading and slightly emarginate caudal fin. The mouth is moderately large, with the posterior end of the maxillary extending to, or slightly beyond, a vertical through the posterior margin of the eye.

Proportional dimensions in per cent of standard length (averages, followed by ranges in parentheses) of the 10 fresh specimens listed in the *Study Material*, 28–35 inches (*ca.* 71–90 cm). *Note*: Shape and length of head and depth of body varying with stage of sexual maturity.

	MALES	FEMALES
Body: greatest depth	21 (20 –22)	22.6 (21.4–24)
greatest width	12.2 (11.4–13.3)	12.4 (11.3–13.2)
Caudal peduncle: depth	7.9 (7.6– 8.6)	8.0 (7.0– 8.6)
Head: length	23 (20.8–25.9)	20.7 (20.0–21.2)
Snout: length	9.2 (7.2–11.1)	7.2 (6.7– 7.5)
Eye: diameter of eyeball	2.9 (2.7– 3.0)	2.8 (2.7– 2.9)
Maxillary: length	12.5 (10.7–14.4)	10.5 (10.0–10.8)
Dorsal fin: longest ray	11.7 (10.5–13.5)	11.6 (11.3–11.9)
Anal fin: longest ray	10.6 (10.2–11.0)	10.5 (10.1–11.1)
length of base	9.5 (8.9– 9.7)	9.2 (8.0–10.4)
Pelvic fin: length	11.0 (9.9–11.6)	10.7 (10.5–11.2)
Pectoral fin: length	13.3 (12.1–13.8)	12.7 (12.5–13.1)

BOTH SEXES

Scales: diagonal rows to end of vertebral column 113 (110–118).
Branchiostegals: 11 or 12.
Gill rakers: 18 (17–20).
Dorsal rays: Usually 10 branched rays preceded by one full-length unbranched ray and one (occasionally two) shorter unbranched rays.
Anal rays: 8 or 9 unbranched rays preceded by one full-length ray and one (occasionally two) shorter unbranched rays.

FIGURE 120. *Salmo salar*, 37.8 inches long, probably from Delaware Bay. After Goode; posterior outline of fleshy caudal peduncle somewhat emended.

Pyloric caeca: 55.4 (40–74) for Salmon taken in or near the mouth of the Miramichi River, Quebec (*14*).
Vertebrae: 58.5 (58–61) for 23 specimens from the Moose River, N.S.

Color. The color of an adult Atlantic Salmon depends on whether it is in salt or fresh water. When it is at sea, its back is blue-green overlaid with a silvery coating, the sides are silvery, and the belly is pearly white. There are scattered black, x-shaped, and round spots on the sides, usually above the lateral line and occasionally below it anteriorly; a few round black spots are present on the sides of the head. The dorsal fin is dusky, with the lower half lighter. The caudal is dusky (darker posteriorly), usually without spots; and the anal is gray with whitish rays. The pelvics (ventrals) are light-colored, with a few of the anterior membranes dusky, especially above; the pectorals are dusky with a whitish base.

When the Atlantic Salmon re-enters fresh water, it loses the silvery guanin coat and becomes greenish, or reddish brown mottled with red or orange (more especially in the male), and has large dark spots edged with whitish color.

The parr of this species (p. 467) is bluish or purplish above and has a series of 8–11 or 12 vertical dark crossbars or "parr marks" along each side; also there are blackish spots chiefly above the lateral line anteriorly and on the sides of the head, a red spot between each pair of parr marks, and usually a few other spots.

The smolt (p. 467) is silvery due to the deposition of light-reflecting spicules of guanin in the epidermis, covering the bars and spots of the parr so that it resembles the adult Salmon at sea.

Changes in Spawning Fish. As spawning approaches, the head (snout and lower jaw particularly) elongates, and the lengthening of the lower jaw is greater than that of the skull itself; and in the male the tip of the lower jaw turns upward to form a prominent hook that fits (when the mouth is closed) into a hollow of the upper jaw. These changes are more pronounced in the male than in the female, and in both sexes they are relatively much greater in large specimens than in small ones (*127*). After spawning is completed, in those that live, these changes gradually disappear and the features of the head resume their normal shape and proportions.

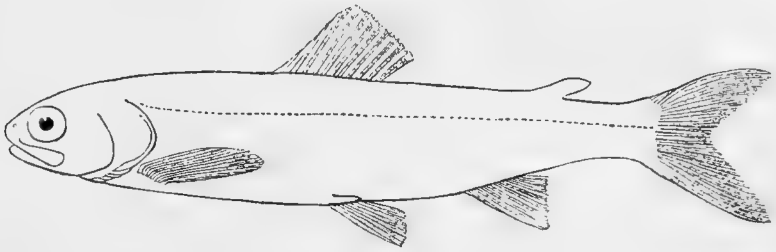

FIGURE 121. *Salmo salar*, smolt stage, 140 mm TL, from Margaree Harbor, Cape Breton, Nova Scotia, ROMZ 9462. Drawn by Jessie H. Sawyer.

The teeth also undergo very marked changes with each breeding period (*126*). The "feeding teeth" are replaced by special "breeding teeth" when the fish moves inshore towards the river. These are relatively shorter and broader at their bases than the feeding teeth, and on some bones they are strongly curved; when fully grown in large males, the breeding teeth are securely fastened to the bones. When spawning is completed they are apparently replaced again by feeding teeth. In specimens of equal size, the number of breeding teeth on the maxillaries is higher than the number of feeding teeth. In the large breeding males examined, the vomerine teeth on the anterior part of the shaft were in a transverse row. Tchernavin's observations are supported by those of Rushton (*118*), who found that well-mended kelts (p. 467) had large teeth, with small teeth beginning to grow between them. The large teeth showed signs of decay at their bases and looked as though they would drop out before long. In addition to the striking changes in head and teeth, the skin of the back becomes thick and spongy and the scales are embedded.

Size. This species grows larger in European waters than in the western Atlantic, where very few reach 50 pounds (p. 478). The largest ones that have been caught in America by angling were a 55-pound fish taken in the Grand Cascapedia River, Quebec, on July 27, 1939; and two 54-pound fish, one taken there on June 20, 1886 (*135*: *50*), and the other in 1921.[6] In some of the larger rivers of Newfoundland and in

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[6] See photo in Atlantic Salmon Journal, Sept. 1959: 24.

those emptying into the Gulf of St. Lawrence, fish of 40 pounds were not uncommon years ago, but today an Atlantic Salmon of that size is rare.

The record recognized by the International Game Fish Association as the heaviest Atlantic Salmon taken by rod and line is a 79-pound 2-ounce fish caught at Tanalev, Norway, in 1928; also, in 1921, a 74-pound fish was taken in Norway on a fly (*135*: 3,4). An 83-pound fish has been reported as being netted in England (*18*), and an 84 3/4-pound fish in Ireland in 1881 (*83*). There are reports also of "a one-hundred-and-three pound, two ounce salmon taken in a net on the Devon River in Scotland" (*148*: 23), and of others weighing over 100 pounds (*133*: 56); however, records such as these are to be accepted only with extreme caution.

Size-Weight Relationship. The accompanying graph (Fig. 122), based on records for specimens from several localities, both American and European, is presented as a rough over-all average of length and weight for the species. A curve for any one locality would probably differ to some extent from that for any other.

Spawning and Number of Eggs. Atlantic Salmon, following their early growth in the river and one or more years at sea (see also *Spawning Survival*, p. 479), return to fresh water to spawn (p. 473), the spawning time usually occurring in fall or winter according to locality. In Canada generally, actual spawning occurs in late October and early November, but in Greenland, near Kapisigdlit in Godthaab Fjord, it is said to occur in early spring (*52*). In northern Europe they may spawn as early as September (in Iceland still earlier) or as late as January, or even later; thus in some Scottish rivers they do not spawn in numbers until after New Year's Day (*100*), while in southern England spawning has been observed as late as the third week in March, mainly in the lower reaches (*122*). See also *Coastal and River Spawning Runs* (p. 475).

Any place where the conditions are favorable may be used as a spawning site—from just above tidal waters to the upper reaches of a river, sometimes as much as 200 miles or more from the sea. The depression, or so-called "redd," in which the eggs are deposited, is made in shallow sections of the stream where the current is swift. The most suitable bottom is a coarse gravel, with many stones from two to eight inches in size, that allows well-aerated water to penetrate. Loose gravel or sand is unsuitable because of its shifting nature (*10*).

The spawning act has been described repeatedly, but the most careful observations are those by Jones and King, first made in 1947 and confirmed by them in 1948 (*79*; *80*; *78*). For their studies they built a glass-sided observation tank on the banks of the River Alwen, a tributary of the Welsh Dee. From this they made lateral observations and took photographs that could be studied later.

Before depositing her eggs, the female cuts a depression in the gravel with her tail and feels the bed with her anal fin. The male takes no part in making the bed and is often not present, but he courts the female and drives away all other fish.

Just before the spawning act, the female drops into the bed, opens her mouth, erects her fins, and bends her tail upwards. Upon this the male immediately joins her and settles alongside, quivering, with his mouth agape. At this instant the pair spawns almost simultaneously. The complete operation, observed in the case of a nine-pound female and a five-pound male, consisted of eight emissions in different beds prepared by the female. After each spawning act, the female moved upstream of the bed and cut vigorously with her tail, thus covering the eggs with gravel. Each spawning act took place in 10–15 seconds, and the eggs were completely covered about 30 seconds later.

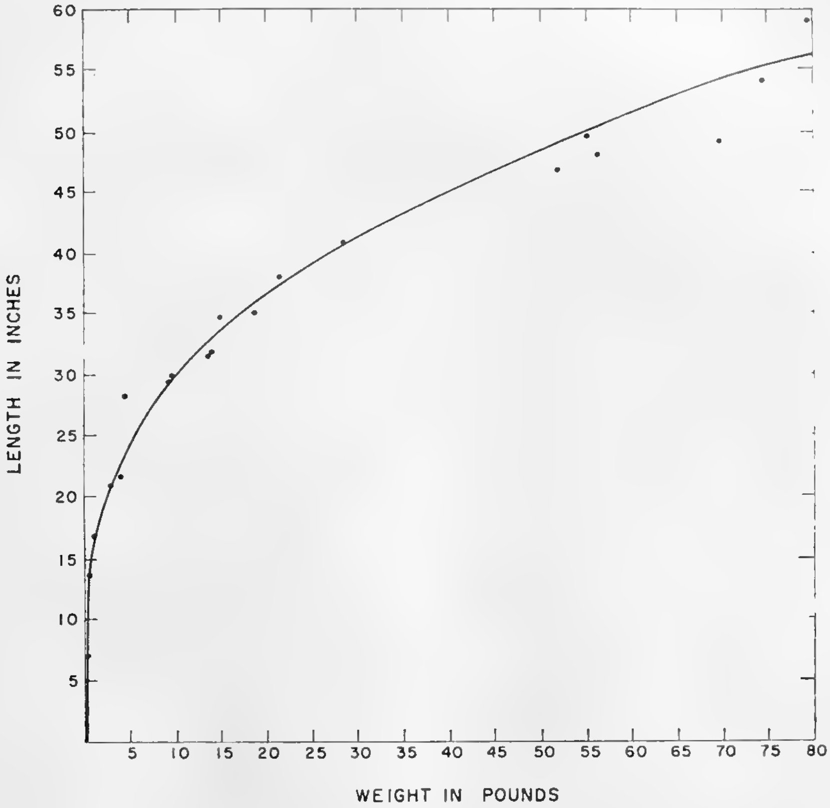

FIGURE 122. Length-weight relationship for Atlantic Salmon.

In the experimental tank, spawning took place at temperatures varying between 36–42° F. Of the eggs collected from 12 nests, 97.6 % had been fertilized.

An interesting feature of the spawning of the Atlantic Salmon is the participation in it of male parr. That some parr become sexually mature before they leave the river has long been known. As early as 1686, Willughby wrote that while female parr (salmolus) never have ripe eggs, male salmolus fertilize the eggs of the adults (*146*). These early observations have been amply confirmed in recent careful studies by Alm (*3*) and others (*80*; *81*; *82*; *111*). According to Jones, 75 % of the male parr become sexually mature during river life (*78*: 128). Their sperm is as effective in artificial fertilization of the eggs as is the sperm stripped from adults. Eggs fertilized by parr sperm produce normal progeny, and male parr under natural conditions may be responsible for fertilizing a considerable fraction of the total number of eggs that develop. It has been suggested furthermore that the presence of parr is a safety factor. The spawning males may fail to get their vent deep enough into the bed to have their sperm fertilize most or all of the eggs. Under such circumstances, the parr are of importance since their sperm, released very close to the eggs, have a good chance of reaching them.

The number of eggs produced varies with the age and size of the females, as shown in Table 1. Menzies has given a range of 600–1000 eggs per pound of spawning female (*100*). Jones and King estimated from the number of eggs recovered from redds made by their nine-pound experimental female that she had laid 700 eggs per pound of body weight (*79*). Large females usually have larger eggs than small ones (*14*), but they are fewer (*100*).

Table I. Average Number of Eggs Produced by Canadian Atlantic Salmon*

	First Spawning After		Salmon That Have Spawned Before
	2 Years at Sea	3 Years at Sea	
Number of females	503	15	16
Average weight of female (pounds)	10.51	19.13	16.68
Total number of eggs	8,848 ± 68	13,883 ± 483	12,313 ± 648
Eggs per pound of fish	834 ± 5	723 ± 13	738 ± 34

* From Belding (*14*).

Although Belding found a definite but slight difference in the number of eggs per pound of fish between females of the Miramichi River (817 fish) and coastal females of the Bay-of-Chaleur type (854 fish), this difference was not sufficient to warrant its use in identifying river varieties of Atlantic Salmon at sea (*14*).

After being deposited and during incubation, the eggs of the Atlantic Salmon are subject to many vicissitudes, such as being dislodged by other spawning Salmon in overcrowded streams, being washed out by floods, and being frozen in the winter at times of low water.

Incubation Period. The large, thick-shelled eggs, about 6–7 mm in diameter, develop slowly over the winter and hatch in the spring at various times depending on the temperature and on other conditions at the spawning sites. In hatching experiments with eggs from specimens of different ages taken in or close to seven rivers of the three Maritime Provinces of Canada, Belding, *et al.* (*16*) found that the date of hatching varied from March 15 to May 4 and that the location of the hatchery in which the eggs were incubated seemed to be an important factor, for it took place on III/15 at Prince Edward Island, on III/21 and IV/25 at Middleton, N. S., on IV/11–19 at Margaree, N. S., on IV/20 at St. John, N. B., on IV/23 at Bedford, N. S., on IV/26 at Antigonish, N. S., and on V/2–4 at Restigouche and Miramichi, N. B. They observed further that the water temperature "between 34 and 41° F. is not a prominent factor in determining the length of the incubation period," whereas temperatures above that decrease the incubation time markedly; also the water temperature at the end of the incubation period may determine the hatching date, since the temperatures in the early hatcheries were only slightly lower at hatching (35°–38° F) than in the late hatcheries

(41°–43° F). In another hatchery experiment, hatching occurred much sooner at 42° F (88 days) than at 33° (191 days).

Names Applied to the Successive Life Stages. The Atlantic Salmon at various stages of growth has been given the following distinctive names:

ALEVIN: the stage from hatching to absorption of the yolk sac, which occurs at a length of about one inch; often called the yolk-sac stage.

FRY: the stage between absorption of the yolk sac and acquisition of the parr marks.

PARR: the young stage spent entirely in fresh water when it has 8–11 or 12 dark vertical bars or parr marks on each side, acquired soon after the disappearance of the yolk sac. Some male parr mature during this stage but the females do not, so far as is known.

FINGERLING: same as parr.

SMOLT: A young fish that has acquired a coat of guanine that hides its parr marks and gives it a shiny, silvery appearance. This change usually occurs after the fish has spent one to four years, and exceptionally as much as seven years, in the natal river. Following this transformation the young Atlantic Salmon migrates to the sea (pp. 468–470).

GRILSE: a mature fish that returns to fresh water to spawn after one complete year at sea; distinguishable from the older fish by its more deeply forked caudal fin and its smaller size; its average length in Canada is 18–24 inches, its weight 3–5 pounds, with extreme ranges of 2–14 pounds reported.

SALMON: a mature fish that has spent two or more years in the sea before returning to fresh water to spawn for the first time; its weight with two years of sea-life, 6.5–16 pounds (usually 10–12 lbs.), and with three years, 20–35 pounds or more; most of the large fish, 40–50 pounds, are females that have been at sea a long time and have spawned only once or not at all.

KELT: a thin adult that has spawned and still shows the dark color assumed during its freshwater stay; often called a black salmon.

MENDED KELT: a fish that has recovered from the kelt period by regaining its silvery color and a more normal plump form.

The Alevin Stage. The newborn alevin, 15–20 mm long, are hatched with a mass of yolk which nourishes them but which also weighs them down and keeps them from maneuvering freely; during this time they usually remain on the river bed. The yolk-sac period for hatchery-reared alevin varies between 29–65 days (usually 39–53 days), with temperature the controlling factor; as in the hatching of the eggs, the higher the temperature the shorter the yolk-sac period (*16*). Vibert's studies (*131*) have confirmed earlier conclusions that alevin hatched under gravel are hardier than those reared in a hatchery, are better developed, and average 15 % heavier. With the disappearance of the yolk, the little Salmon must begin to seek their own food. They are then gregarious (*78*), resting on the stream bed with others and rising to take prey, either individually or with a group.

From Parr to Smolt. Soon after the disappearance of the yolk, which marks the end of the alevin stage, the young fish develop the characteristic crossbars along each side that distinguish them as parr (p. 467), and they begin to acquire scales. As they grow, they seek a new habitat, since the area that provided them with food and shelter when they were younger is no longer adequate. Thus each one establishes a more or less definite territory of its own as described by Katteberg (*85*). The behavior pattern has been described by Huntsman as follows (*70*): "salmon . . . may become related to particular local environments which may be called their homes. Such relation may involve having a place or places for rest on the bottom, for stationing in a current, and for cover, with more or less roaming as well as precise dashes in taking food."

That parr move about in the parent stream now seems established. Huntsman (*67*: 399) found that freshets may greatly alter or destroy their home, and that this and other factors induce or force the parr to descend from their spawning area to lower waters of the parent stream, there to populate lakes as well as estuaries that have fresh or brackish water (but not full sea water, which kills parr; *74*: 409). Some may reascend varying distances upstream and populate places that are accessible; falls as low as one foot seem to stop parr less than a year old.

Subject as they are to many vicissitudes and to different environmental conditions throughout their range, the populations of young vary widely at all times in abundance as well as in size and growth relative to age (dependent mainly on food and temperature) and hence in time of smoltification, not only from one general area to the next and from one river to another in the same general area in different years, but even from year to year in the same river. Such data as are available indicate that parr throughout the Atlantic Salmon's range may spend anywhere from one to seven years in the river before they become smolts, and that, generally, parr life is longer in northern than in southern regions (Table 11). Most of the parr in America spend two or three years in the river, but longer northward. In England and Scotland one- or two-year smolts are the rule. In southern Norway it is usually three years, but northward, five-, six-, or even seven-year smolts are common.

In general, the fastest growing parr develop the soonest into smolts, but little is known about the factors that initiate and control smoltification. According to Pyefinch (*116*: 9):

> Smoltification is in some way connected with size, but the nature of this relationship is by no means direct. . . . It seems possible that rate of growth may be more important than the mere attainment of a critical length. Reference has already been made to the observation that growth during the first year is an index of growth later in life. Therefore, assuming that the internal changes which occur during smoltification are seasonal in their incidence, a rapidly growing fish may have developed far enough for these changes to take place when it is only a little more than a year old, whereas a fish which grows more slowly is not sufficiently well-developed for these changes to take place then and so must wait until the following spring.

Elson concluded that, as a general rule, parr that have reached or exceeded a certain size towards the end of one growing season are likely to become smolts at the next season of descent (*43*: 5). Those that have nearly but not quite reached a length of 10 cm at the end of the summer will, if they grow fast, reach a much greater length, say 14–16 cm, at the end of the following summer, and make big smolts. Those that

Table II. Percentage Composition of Smolt Population Based on Years Spent as Parr in Fresh Water

	Age in Years						
	1	2	3	4	5	6	7
NORTH AMERICA							
Penobscot R., Maine (*87*)	...	majority	few	...	...	...	...
Pollett R., Petitcodiac R. system, N. B. (*43*: 3)	...	90–95	5–10	...	...	...	...
Margaree R., N. S. (*12*)	4	68	25	3	...	...	...
Miramichi R. system, N.B. (*43*: 1).	...	*ca.* 33	*ca.* 67	...	...	...	...
Miramichi R., N.B. (*19*)	...	15.1	78.1	6.6	0.2	...	...
Grand Cascapedia R., Que. (*29*)	...	6	58.8	34.1	1.1	...	...
Moisie R., Que. (*104*)*	0.35	34.45	61.3	3.9	...	...	...
Six west coast rivers of Newfoundland (*11*)	...	7.1	57.4	29.8	5.4	0.3	...
East coast rivers of Newfoundland, including Labrador (*20*)	...	3.4	26.0	39.1	25.3	5.7	0.5
Greenland (*53*)	...	...	...	42.8	52.4	4.8	...
EUROPE							
Avon R., Hampshire, Eng. (*100*)	60	...	...	...	...	...	...
Shannon R., Eire (*136*, *137*)†	12.8	79.1	8.1	...	...	...	...
Scotland (*100*)	few	mostly 2–3 years		few	rare	...	...
Rivers of southern Scotland (*100*)	some	90 or more	some	...	...	...	...
Tweed R., Scotland (*100*)	...	97	...	...	...	...	...
Norway – Kristiansund distr. (*35*)††	...	25.8	64.5	9	0.7	...	...
Trondhem district (*35*)††	...	9.8	69.5	20	0.7	...	...
East Finmarken (*35*) 1909	...	2.5	47	43.5	7	...	...
Repperfjord R.**	...	...	...	18.2	45.4	31.8	4.6

* Average 1923 and 1924 collections.
† Average 1944–1947.
†† Average 1908 and 1909.
** Skr. Norske Vidensk., *16*, 1941.

have barely attained the required 10-cm size at the right time will, if slow growing, make small smolts, perhaps only 12 cm long. But Elson has clearly pointed out that this hypothesis "definitely does not specify that young Atlantic salmon become smolts as soon as they reach a length of 10 cm, but rather that they transform after reaching this length in the smolt-running season immediately following."

Smolt lengths have been reported to be as follows, south to north: rivers tributary to the Gulf of Maine, 5–6 inches (*18*); average for the rivers of Canada, 5–7 inches; the Little Codroy River, Newfoundland, 5–9 inches; George River, Ungava Bay, 8.5 inches (*115*).

Only a small percentage of the numerous alevins that are hatched survives the freshwater stage as parr to become smolts and go to sea, nor is this astonishing when all the dangers that threaten their continued existence are taken into account: predators, competitors, disease, food shortage, abnormal water temperatures, and others. For discussion of survival at different stages, see *Length of Life* (p. 479).

Downstream movements of smolts result from a change in their behavior associated with the physiological changes involved in smoltification. According to Huntsman, when they assume the smolt condition they tend to leave the bottom, come nearer the surface, and go or are carried downstream (*64*). While the resulting downstream movement is facilitated by freshet conditions and although the peak of the run is usually associated with a freshet, there is evidence to suggest that some other factor may be responsible for the initiation of the migration. As long ago as 1926, Bull produced evidence suggesting that floods did not provide the departure stimulus (*25*). However, his suggestion that the initiation of the run was not associated with rainfall has not been accepted. Swain has recently concluded that the immediate stimulus is either a rise in temperature or some factor associated with a rise in temperature (*125*). Huntsman has suggested that freshets appear to affect migration not only through carrying fish downstream but through breaking up their "homes" (*67*: 399; *70*: 257).

Normally the main smolt migration occurs in the spring or early summer, chiefly at night, with minor seaward movements at other times of the year. In the rivers of the Maritime Provinces of Canada, the main migration takes place in May and June. In the Little Codroy River, Newfoundland, the run during 1955 took place from May 11 to July 22, with the peak during June 1–15 (*5*: 63, 64). In the northerly part of their range, in rivers flowing into Ungava Bay, most of them migrate in June and July, though smolts may be taken there at all seasons (*115*). It is evident from the foregoing that all members of a year-class do not migrate in the same year, nor at the same time in any year.

Life at Sea. After moving into salt water, the smolts apparently spend some time in the estuaries and river mouths and descend to deeper water with the onset of winter (*18*). The length of time they remain at sea before returning to fresh water on their first spawning migration varies from one to four years, and in some areas up to five years. As in river life, there is variation in growth and size at sea brought about by various factors. Thus fish of the same age from different rivers often grow at different rates while at sea, and members of one year-class may reach weights that are different from those of another year-class from the same river with the same length of sea-life. Generally, the longer they continue to feed at sea, the larger they are when they return, growing more rapidly in summer than in winter. Those that spend two or more continuous years at sea before spawning will in most instances be larger fish than those of a similar age from the same river that have survived the ordeal of spawning, since the growth of the latter has been interrupted by fasting for a longer or shorter time, depending on how long they have been in fresh water before spawning.

Salmon develop rapidly during their sea life. Thus smolts may grow from only one or two ounces to as much as six or seven pounds and a length of 16 inches or more in their first year at sea.

There is comparatively little certain knowledge about the habits of Atlantic Salmon when they are in salt water. Most of what we know about their movements in the sea is derived from data on fish caught in nets set by commercial fishermen. Since such nets are fished only in certain restricted areas, there is little knowledge of this species in places where no fishing has been carried on. We have no knowledge, for instance, as to whether or not they are to be found in midocean, far from any shore, because there has been little or no fishing there. In Canada, except for limited offshore fishing by surface drift nets, commercial fishing is practically restricted to fixed traps and gill nets operated near shore, nowadays only in tidal waters. Occasionally Salmon are taken in herring weirs, in trawling for ground fish on offshore banks, and in line fishing, for instance in the Gulf of Maine and the Bay of Fundy (*18*).

Even when they are taken in salt water there is no way of telling how far they have traveled or from where they have come unless they bear a tag or mark and unless the previous whereabouts of an individual fish so identified has been recorded. (Tagging consists of attaching numbered tags to the fish; marking is the clipping of a fin or a combination of fins.) In America, tagging and marking of specimens have been carried out mainly in Canada, and to a lesser extent in Maine. Although river fish, both kelts and smolts, have been used in most cases, some Atlantic Salmon caught at sea have also been tagged.

Numerous specimens tagged in their river of origin have been recaptured there later, and although it is usually assumed that they return to their natal river, it is known that they sometimes enter and subsequently leave rivers other than their own. If tagged specimens are recaptured in the sea at some distance from the place of release, it is usually assumed that they are returning to their river of origin; this may be true if they have the ability to direct their course; otherwise they may be merely wandering.

Studies indicate that some of them remain relatively close to their river of origin, whereas others travel various distances to feeding grounds, often hundreds of miles away. Such a variable pattern of dispersal has been shown by results from the tagging and release of nearly 12,000 kelts by the Canada Department of Fisheries between 1913 and 1936 in 12 localities of the Maritime Provinces. Of those recaptured, some, notably those of the St. John River, N.B., were recaptured within or close to the estuary, and others were taken at various distances from the point of release, even as far as Newfoundland and Labrador (*62*: 96; *67*: 311; *58*). The meaning of these results is not clear. We can only guess how many of those found in or near the streams in which they had been tagged may have been to some distant point (such as Newfoundland) and returned. That not all had undertaken far journeys is suggested by the fact that none of the St. John fish was recaptured more than 50 miles from the St. John River mouth.

A wide distributional pattern has also been shown by the marking of smolts from a number of rivers and by their subsequent recapture at sea as adults. Thus Atlantic Salmon that developed from hatchery stock planted in the Pollett River (Petitcodiac River system at the head of the Bay of Fundy) were taken in quantity by fishermen over a wide area, including trap nets around Newfoundland, and drift nets off Miramichi, northern New Brunswick.

Based on smolts marked in the Miramichi River, N.B., and recaptured as adults, it has been estimated from one experiment that approximately one-third of the total catch of Miramichi stock was taken off Newfoundland and Labrador in commercial nets, about three-fifths in the Miramichi area in commercial nets and by freshwater anglers, and the remainder elsewhere in the Maritime Provinces in commercial saltwater nets. However, more were taken in the freshwater section of other rivers than in that of the Miramichi (C. J. Kerswill, personal communication).

A considerable number of marked fish originating in the Port Daniel River, Quebec, has also been taken around Newfoundland (*4*), as have specimens marked in Maine rivers (*45*).

In contrast to the wide distribution of Atlantic Salmon from these rivers, only one out of 31,359 Margaree River smolts was recaptured on the east coast of Newfoundland; they were taken mostly in the waters of western Cape Breton and the neighboring mainland of Nova Scotia (*66*: 381).

Specific examples of results from taggings at sea are as follows:

Off Bonavista on the coast of eastern Newfoundland (*21*):
  Of 386 grilse tagged, 140 were recovered—93 % in Newfoundland waters, 7 % in Canadian mainland waters.
  Of 68 older specimens tagged, 28 were recovered—about 57 % in Newfoundland waters, 40 % in Canadian mainland waters, and somewhat less than 4 % off Labrador.
In Cabot Strait between Newfoundland and Nova Scotia (*14*):
  Recaptured along the eastern part of the north shore in the Gulf of St. Lawrence and in waters off the northern part of western Newfoundland.
In the eastern end of Belle Isle Strait (*14*):
  Recaptured in parts of the Gulf of St. Lawrence where fish tagged in Cabot Strait did not go.
The results of the Cabot Strait and Belle Isle taggings were interpreted by Belding (*14*) as indicating two distinct stocks.

Since Atlantic Salmon do not originate in Massachusetts rivers, specimens taken from time to time off that coast probably come from the rivers of eastern Maine or even from the St. John River. Other examples of rather extended movements are afforded by the capture of Salmon by trawlers 90–100 miles seaward from the outer coast of Nova Scotia, and 100 miles from the nearest land, on Georges Bank (*18*).

European findings also support the conclusion that some of them make extended journeys (up to 1,600 miles), while others appear to move relatively short distances (*102*). Especially definite are Alm's observations (*2*). Young fish from rivers tributary to the Baltic and Gulf of Bothnia migrate to the southern part of the Baltic, where they feed and then return to their rivers as grilse or older fish. Smolts from the rivers of western Finland and from the northern and middle parts of Sweden move down the Swedish coast to the southwestern corner of the Baltic or travel across the mouth of the Gulf of Bothnia and then down to the Polish and Pomeranian coasts. Fish from Estonia and Latvia find an adequate quantity of food comparatively close to their native rivers.

Apart from the capture of one Scottish fish in Greenland waters, there is no evidence that Atlantic Salmon travel from one side of the Atlantic to the other. This fish, tagged at Loch na Croie, Blackwater River, Ross-shire, Scotland, on November 23, 1955, was recaptured in Eqalug Fjord, south of Sukkertoppen, Greenland (64° 56.5′N, 52°02′W) on October 15, 1956 (*105*). It is a matter of speculation whether Atlantic Salmon from Europe and eastern North America intermingle in the mid-Atlantic, as do salmon of Asian and North American origin over a broad area of the Pacific high seas, at least between 160°W–170°E (*6*).

The farthest any American Atlantic Salmon is known to have traveled is from the Annapolis River on the Bay coast of Nova Scotia to Ramah in northern Labrador, a journey of about 1,900 miles accomplished in nearly two years (*62*: 105); there are also many other records, though not as spectacular, of fish traveling hundreds of miles both here and in Europe (*18*). Blair has reported a distance of 792 miles for a grilse and of 785 miles for an older Salmon tagged at sea off Bonavista, Newfoundland (*21*). In Europe, two fish from Norway swam impressive distances of 1,600 and nearly 1,200 miles round the North Cape to the White Sea and to the Pechora River (*102*), which is believed to be the eastern limit for the distribution of *Salmo salar.* In the Baltic, Atlantic Salmon cover as much as 800 miles from their native rivers to their feeding grounds (*102*). The one tagged in Scotland and recovered in Greenland had traveled 1,730 miles in less than one year.

There appears to be general agreement that Atlantic Salmon feed in the mid-depths (*18*); that is, the bulk of them is neither on the bottom nor at the surface; however, some have been taken in both situations. In February and June 1948, 130 full-grown Salmon averaging 11 pounds were netted by mackerel fishermen about 100 miles west of Land's End, Cornwall, England, within 10 fms. of the surface (*22*). Evidence of their occurrence on bottom is found in reports that trawlers have taken strays on offshore fishing banks at depths of 50 fms. (*18*) and 70 fms. (*13*). Dr. Huntsman was told by a fisherman of Sandy Cove, Digby Neck, Nova Scotia, that he once caught an Atlantic Salmon at 35 fms., on a handline, when he expected to take a pollock. Menzies has reported the capture of smolts in 65–70 fms. of water by trawlers off Scotland (*100*). There is no factual support, however, from fish actually taken, for Roule's belief, often quoted, that Salmon pass their growth period at sea, deep down the continental slope.

Huntsman says that after Atlantic Salmon have become fat and when the water is not too cold, they roam to and fro near the surface; it is during these movements that they are taken in drift nets (*69*).

Return of Salmon to their Natal Rivers. The belief that Salmon return to their natal river is very old. Isaac Walton reported that many in his day believed that 'every salmon usually returns to the same river in which it was bred.' Scheer (*119*) has concluded: "The hypothesis most compatible with these facts is that anadromous salmon hatched and reared in a particular region will, when seeking freshwater, seek out and return in the great majority of cases to the same region, even from considerable distances." From what distance, under what conditions, and to what extent Atlantic Salmon find their way back to their home stream is an aspect of their sea-life about which a great deal more information is needed before definite conclusions can be reached. That most of those that actually spawn do so in the river where they have spent their early life appears to be accepted by most observers who have investigated their life history. Some investigators, however, believe that Atlantic Salmon that go to distant places in the sea do not usually get back and thus may be regarded as lost (*61: 18*).

That Atlantic Salmon are able to return to their natal stream from a distant place is proved by finding one in the Margaree River that had been marked there two years before; in the interval, this fish had been caught, identified, and released at Bonavista on the coast of Newfoundland; the return of this fish involved a round trip of about 550 miles (*66*). Whether the performance of this one fish was exceptional or whether it is usual for Salmon to undertake such migrations and even longer ones and get back to their home stream must await the results of further research. In studies carried out on the Miramichi River, N. B., over a five-year period, it was found that smolts produced in two tributaries and marked at two-way counting traps returned as adults to the trap of their natal stream with over 98 % accuracy (C. J. Kerswill, personal communication). It is also known that Atlantic Salmon often wander in and out of estuaries other than their own and that marked fish are occasionally caught in strange rivers.

Views as to the means by which Salmon return to their river of origin tend in two extreme and opposite directions. One extreme view pictures them as going unerringly from their river to a predetermined feeding place from which, on the approach of sexual maturity, they return unerringly to their river of origin, as if drawn by a magnet. According to the other extreme view, they are carried to feeding grounds by ocean currents, and the only ones that find their natal rivers again are those whose wanderings, with cessation of feeding on the approach of sexual maturity, perhaps aided by currents, take them to the coasts, which they follow until they find themselves within the guiding influence of their home stream.

Huntsman's studies have led him to believe that Salmon, when outside of the influence of their natal river, find their way back, if they do, through a process of wandering until they come within the influence of the native river (*73*). Homing, he says, is the end of wandering rather than a directive factor. He believes that the shore or sea coast and transportation by currents are definitely directive factors for Salmon movement (*71*).[7] Toner, who has reached a similar conclusion, says that "salmon approach the Irish coasts in a haphazard fashion and only when they are close inshore do they make a definite search for the river of their origin" (*128*). Nearly a hundred years ago, Austin's observations led him to a somewhat similar view (*8*). He wrote:

> A prominent feature in the migration of these fish to and from the sea is, that they always . . . hug the shore on their way up and down. They do not, asserts Mr. Russell in his work on the salmon, lie off in mid-ocean, and then as with a needle and compass, steer right into the river's mouth; but they feel, or, as Sir Humphrey Davy expressed it, scent their way along the shore for many miles and follow closely the indents of the land.

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[7] For a discussion of the relation of currents to Salmon movements, see Bigelow and Schroeder (*17*: 970).

There is a good deal of evidence that these fish in some way, probably through their olfactory sense, are able to recognize the water of the river in which they spent the early part of their life. Hasler has reviewed the results of observations and experiments on the perception of pathways by fishes in migration (*54*). He concluded that there is in river and creek water some characteristic odor to which the young become conditioned while they are in the stream and which they recognize and to which they orient upon coming in contact with it. Hasler, *et al.* (*55*) have carried out experiments that support the theory that fish, when out of touch with the shore or of the water of their natal stream, have a sun-compass mechanism for direction-finding similar to that found in birds (*97*) and in bees (*49*).

Coastal and River Spawning Runs. A spawning run usually occurs in two stages, the first being the coastal run, the second the river run. During the coastal run, the fish enter the river mouth or estuary and remain there for varying lengths of time before they actually enter the fresh water on their river run. The river run may take place shortly after the coastal run, or the two stages may be so widely separated that "early running" and "late running" have little meaning as applied to a particular lot of fish. If the fish appear early off the river mouth they may be referred to as "early running" by the commercial fishermen who catch them there, and if their actual entrance into the river is long delayed, they may be "late running" to the anglers who take them in the river.

With reference to the coastal run, no Atlantic Salmon move in from the sea off Canadian rivers when the water is coldest, from January to April, with the probable exception of the southern outer coast of Nova Scotia. Most of the fish that are heading for the rivers of the Maritime Provinces (New Brunswick, Nova Scotia, and Prince Edward Island) appear in coastal waters sometime between late May and July. In Newfoundland, where there is a major and minor coastal run each year (*95*), the fish of the major run appear in the latter half of May off St. John's (in the southeast) and progressively later northward, with the fish appearing at Cartwright (Labrador) late in June; this coastal run in the spring is short, and profitable fishing can be pursued for only about three weeks in any one locality; the minor run in the winter is much more restricted, and evidence of it is confined almost entirely to the Avalon Peninsula in the southeast, where some fish are taken in November and December. To the south, in the St. John River, N.B., it has also been observed that some fish, mostly large female grilse, enter the estuary in November and December, where they remain until the following May before ascending the river; however, they do not spawn until October (*59*).

Two of the conditions that determine how long Atlantic Salmon remain in or near the river mouth before beginning their ascent of the river appear to be water temperature and volume of river discharge, with high temperatures and the absence of freshets being nonconducive to their movement (*89*). The Margaree River in northern Nova Scotia presents a striking case of the action of these two factors (*63*). The Northeast Margaree, which has cool spring water that travels from high land through a deep gorge, provides angling from the time the fish start to wander in the adjacent sea, from June onwards through the summer and fall. But the Southwest Margaree, which arises from the large shallow Lake Ainslie in relatively low country, has warm water and, in contrast to the Northeast Margaree, is populated by alewives, eels, and white perch; here Atlantic Salmon sometimes provide a little angling at the beginning of the season; otherwise they are not seen ascending the river until the water becomes cool in the fall, toward spawning time.

It has long been known that runs of certain stream fishes are more or less definitely associated with floods, freshets, or spates; sometimes artificial freshets have been used to bring Atlantic Salmon up from the sea. For example, in 1888, in the Grimersta River, Scotland, water from Loch Langabaht was held by a six-foot dam at the mouth of the lowest of a series of four lochs. For a long time the fish had gathered at the head of tide (in a very dry season), and when the dam was broken they swarmed up the river (*27*). In the Moser River (Nova Scotia), during the dry summer of 1942, sharp but not large artificial freshets brought double the expected number of Atlantic Salmon and brook trout from the sea (*70*: 257). Artificial freshets,[8] however, have not been used regularly, for this procedure is rarely feasible.

The spring runs in the Maritime Provinces of Canada are usually at their height in June.[9] Most of the rivers tributary to the Bay of Chaleur and around the Gaspé Peninsula have early runs, as do those on the northern shore of the St. Lawrence, although the runs there are slightly later.[10] The Miramichi in central New Brunswick "has both early and late runs. The small rivers of the coast of eastern New Brunswick, the Nova Scotia rivers of the Northumberland Straits and the rivers of Prince Edward Island have fall runs only" (*15*: 225–230). In the Koksoak River, tributary to Ungava Bay, northern Quebec, a summer river run has been reported as occurring sometime between July 25 and the end of August, and sometimes there is a late run in September (*39*). At or near their northern limit in the western Atlantic, they enter a river near Kapisigdlit (inner Godthaab Fjord) in southwestern Greenland in both July and October (*53*). In England, gravid females may ascend rivers from late autumn until after Christmas, and some of them may remain in ice-free rivers for 12 months or more prior to spawning (*121*; *122*).

The distance they run upstream to spawn depends on a number of factors such as the length of the river, presence of insurmountable falls and man-made obstructions (p. 485), available spawning sites, etc. The fish that enter the river the earliest usually go the farthest upstream before spawning. In large rivers, as in the St. John system, this may mean an upstream run of more than 200 miles and of many months spent in fresh water before spawning. Fish entering later travel lesser distances, and very late

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[8] Hayes (*56*) has discussed the results of observations and experiments on artificial freshets and other factors as controlling the ascent and populations of Atlantic Salmon in the La Have R., Nova Scotia.

[9] It has been reported that, in the latter part of the eighteenth century, when Atlantic Salmon were still running in the Connecticut River, the river migration began about April 1 and was at its height in May, though occasional fish were taken as early as mid-January (*23*).

[10] The early-run fish are much more desirable for the angler than the late-run fish, both because they rise more freely to the fly and because they are much more desirable on the table.

fish often spawn only a short distance above the head of tide. It has also been observed that most of the rivers having only fall runs are small, with their spawning grounds relatively short distances from the river mouth. The Miramichi is the only large Canadian river that has a fall run.

As they gradually work their way upstream, from one resting place to another, they assemble in the deeper and stiller parts; these are known as salmon pools to anglers. In some rivers they must ascend through long stretches of turbulent rapids, some of which culminate in falls. Whether or not the fish can surmount falls depends on the configuration and height of the falls and on the amount of water at the base; the deeper the water the higher they can leap, but 10–12 feet seems to be the maximum. Salmon leap[11] not only in attempting to surmount falls but in the quieter stretches of the river, and at sea.

Differences and Changes in Composition of River Runs. Salmon entering each river system have certain characteristics, such as smolt age, size, length of sea-life, and time of running (early or late), that distinguish them from those of other rivers; and these characteristics, with minor variations from year to year (*9*: 304), tend to persist over long periods of time. For Newfoundland waters it has been demonstrated (*95*) that there are no fewer than 25 classes of fish with different life histories, and 33 types are listed as likely to be found in these waters. According to the laws of permutations and combinations, a very large number of types could and possibly do occur, some of them rarely.

Spawning runs consist of both grilse and older Atlantic Salmon of all sizes and ages with two to four or more years of sea-life behind them; and, whether grilse or older fish, those returning early in the season are generally smaller than those returning later because their growth period at sea has been shorter. Grilse, ready to spawn, return to fresh water during their second summer at sea, and these are mostly males; for example, in the Little Codroy River, Newfoundland, only 15 % of the spawning grilse taken were females, and in Norway only 19 %. But in certain localities of Scotland, females may constitute more than 50 % of the grilse (*100*: 79).

In some rivers grilse are the more numerous in a run and in other rivers the older fish predominate.[12] Rivers reported as having a high proportion of grilse include: The Minas system, northern Bay of Fundy, 89 % (*59*); the Little Codroy, southeastern Newfoundland, 64 % in 1954, 74 % in 1955 (*106*). For grilse in other rivers, the following percentages have been reported: six western Newfoundland rivers, 34.3 % (*11*); an unidentified Greenland river, 33.4 % (*53*). In the Moisie and Grand Cascapedia (north shore of the Gulf of St. Lawrence and Chaleur Bay, respec-

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[11] It is from its habit of leaping that the Salmon gets its Latin name. Both *Salmo* and *salar* are apparently from the same root, salire, to leap.

[12] Estimates of the composition of a catch or population of fish may be subject to large error, as in the case of estimating the proportions of grilse and older Salmon. In commercial fishing, the gear used may take a selective rather than a representative sample of the run, being designed to take only the larger individuals. Often the fishing effort is concentrated on the main run and is not carried on throughout the year. Even in experimental fishing, a good representative sample can be obtained only if the fishing is continuous and is done with gear designed to sample accurately the various sizes.

tively) and in New England rivers, grilse have been reported as being seldom seen (*101*; *104*; *29*) or rare (*7*).

Rivers having a high proportion of fish that have been at sea for three years are known as "large salmon" rivers, two of the most notable being the Moisie and Grand Cascapedia rivers, for which the following percentages have been given for two- and three-year sea-life fish, respectively: 18.3 and 58.8 for the Moisie (*12*); 6 and 58.8 for the Grand Cascapedia (*29*). The tabulated data to the left, giving the percentage of Atlantic Salmon of 30 pounds and over in the Moisie run, suggest that there has been a decline in the proportion of heavier fish in that river (*12*).

1900–04....	11.78
1905–09....	5.86
1910–14....	3.96
1915–19....	5.69
1920–24....	2.44
1925–29....	2.33
1930–34....	5.68

The average weights (in pounds) of Atlantic Salmon reported for various rivers are: for those two years at sea—10.8 for the Restigouche in New Brunswick, 8.9 for the Godbout in Quebec, and 11.2 for the Wye in England, averaged from records of more than 20 years (*9*); 11.7 for the Grand Cascapedia, 10 for the Miramichi,[13] and 11.4 for the east coast of Newfoundland, including Labrador (*20*); for those three or more years at sea—Grand Cascapedia, 23.6 and 37 for 3 and 3 + fish, respectively (*29*); Miramichi, 19.5 for 3 and 3 + fish combined;[13] and the coast of eastern Newfoundland, including Labrador, 19.5 for 3 and 3 + combined (*20*).

It has been suggested for Newfoundland Atlantic Salmon that those having a short river life tend to stay longer at sea before they return to spawn (*95*). On the other hand, the opposite suggestion is implied in Dahl's statement that findings in Norway do not appear to support the idea that the longer parr remain in the river the less time they will spend in the sea (*37*). For Scotland, Calderwood found that smolts that matured rapidly and well in the river were likely to stay away from fresh water for some years after leaving it, while smolts that remained in the river for more than two years and developed slowly were likely to return to it soon. However, he found that this relationship did not apply to the Grand Cascapedia, Quebec. A tabulation of the characteristics of Atlantic Salmon from various sections of the Gulf of St. Lawrence does not show a consistent relation between those factors (*12*).

There is no agreement from either observations or experiments concerning the relative extent to which heredity or environment affect the early or late running characteristics of fish of the different rivers (*144*; *26*: 22), or the marked changes that have sometimes occurred in the proportion of grilse running to a number of streams, or other differences. The nature and extent of these changes are indicated in the following examples.

A serious and almost catastrophic decline in the stock of grilse along the coast and in the rivers of Scotland during the present century (*100*: 79), more especially after about 1908, has prompted the question as to whether selective fishing or some other factors may be responsible for these changes.

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[13] Blair, M. A. thesis, University of Toronto (1932).

Following construction of a hydroelectric plant on the Shannon River, Ireland, there was a marked change in the composition of the incoming runs (*138*: 789). Taken as representative of the pre- and post-period of hydroelectric operation, about 27.5 % of the total run occurred in June of 1928 compared with 70 % that month in 1941; in 1928, 24.7 % of the run consisted of grilse, and in 1941, 75 %. The age of the fish in 1941 averaged approximately one year less than in 1928, and of course the average size was smaller. This change, due to a proportionate rather than an actual increase in the number of grilse, arose from a reduction in the number of age groups spending two or more years feeding at sea. Hydroelectric operations resulted in a reduction of the Atlantic Salmon stocks in the river to about 30–40 % of those of prehydroelectric days. The Mulcair River, which was the major spawning ground for the smaller fish, became the major spawning tributary for both large and small fish.

In the Miramichi, regulations to restrict fishing to the early run and encourage reproduction of the late run (natural as well as artificial) have not succeeded materially in either reducing the early run or increasing the late run, although this unconscious experiment had been carried on for more than 80 years (*58*).

Length of Life and Spawning Survival. During all stages, from egg to fry, fry to smolt, smolt to adult, and after spawning, there are wide differences in the number of Atlantic Salmon that survive, not only from river to river but in the same river from year to year, depending on meteorological conditions, population density of Atlantic Salmon as well as other species, abundance of predators, disease, and man's activities. In considering these differences, factors responsible for discrepancies in estimates of the composition of the runs should be kept in mind (ftn. 12).

Kerswill has found in experiments in progress on the Pollett River, N. B., that survival of fry from egg deposition (three light seedings) had averaged 6 % in July (1957 MSS.). "Under favourable conditions, each 100 square yards of stream is capable of producing 5 or 6 smolts.... These will arise from 10 or 12 large parr, and they in turn from 30 to 40 hatchery fingerlings planted in late summer." About 200 eggs, it was estimated, should produce this number of fish (*5*: 49). Another estimate of survival from fingerling to smolt stage, based on observations for five successive years, is 8 % (*90*).

Percentage survival from smolts to returning adults is difficult to determine; the following figures are not all directly comparable. For example, it has been estimated from the counting and marking of descending smolts and from the trapping and counting of returning adults in several rivers of the Maritime Provinces that "about 8 % of the smolts survive the rigors of life in the sea and return to fisheries and rivers as mature salmon" (*43*: 25; *91*: 825). On the other hand, the contribution to various fisheries by the rivers was found to be about 2 % of the marked descending smolts (*5*).

The following figures on smolt survival have been published: Little Codroy River, Newfoundland, 3.3 % (*107*); Pollett River, 0.5 % (*88*); Great Britain, 1 % (*116*); Tay River, Scotland, nearly 2 % (*100*); Sweden, 5–10 % (*32*).

Data on survival after spawning—more adequate than data on survival during earlier stages of life history—show that the percentage of Atlantic Salmon that survive spawning is usually rather small but is higher in North America than in Europe. The strain of spawning leaves the fish thin and exhausted. Although some of the spawned-out kelts descend to the sea in the autumn after spawning, others winter in the river and migrate downstream the following spring, sometimes along with the migrating smolts. That comparatively few are seen dead in the rivers suggests that most of those that die regain salt water first. The high death rate probably results chiefly from a combination of exhausting travel up the river, prolonged fasting en route to the spawning site, and production of the spawning products.

The percentage of fish that survive after spawning to the stage when they are ready to spawn again is reflected in the percentage of such fish in the catch of adults participating in the run to a given area or river. The following are examples of such percentages: for all the Canadian rivers investigated to 1934, 3–26 % of the total spawning populations of the rivers concerned (*10*); Grand Cascapedia, Quebec, 34 % in 1926, and 22 % (*29*; *13*); Miramichi, N. B., 12.8 % (*19*); Upsalquitch, N. B., 5 % (*13*); Moisie, Quebec, 16.7 % for 1922 and 1923 combined (*101*), and 22.3 % (*12*); Little Codroy, Newfoundland, 6 % for 1954, 5 % for 1955 (*106*); eastern Newfoundland, including Labrador, 16.5 % (*20*); Greenland, 14 % (*53*); rivers on the east coast of Scotland, about 4 % (*100*); two rivers on the west coast of Scotland, 11 % and 34 % (*116*); all rivers of Ireland, about 5 %, or a range of 1–15 % (*129*); Adour River, France, 3.8 % (*130*).

Of 6,475 kelts tagged and released, only 2.12 % were subsequently recaptured (*10*: 221).

Of those that spawn a second, third, or more times, Menzies observed that in one year, of 63 previous spawners in the Moisie River, 35 had spawned once before, 11 twice, 16 three times, and one four times (*101*). On the coast of eastern Newfoundland (including Labrador), in 1939, 15.9 % had spawned once, 0.5 % twice, and 0.08 % three times (*20*). In six small rivers on the coast of western Newfoundland, of 70 previous spawners, 15 had spawned twice or more, two had spawned three times, and one had spawned four times (*11*).

In Ireland, among nearly 50,000 fish, the scales of which were examined, 3 % had two spawning marks, but only six fish had three marks (*129*). In Scotland only 0.2 % and 0.1 % of fish from Spey and Aberdeenshire Dee, respectively, on the east coast, had spawned twice before capture. In the Add River, 6.5 % had two spawning marks, 2.9 %, three. A fish with four spawning marks was taken in the Add in 1914, and another was taken in the Conon in 1920 (*100*).

The percentage of Atlantic Salmon that survive spawning is higher among females than among males. A male that returns to spawn a second time is a rarity. According to Menzies, there is no record of a male spawning three times (*101*: 338), in spite of a report that six of the 16 Moisie fish that had spawned three times were males; Menzies was inclined to question the identification. However, if they were males it suggests the possibility that males may live longer in the western Atlantic than in the eastern Atlantic.

Fourteen years is the greatest age reported for an Atlantic Salmon. A fish from the Moisie River, Quebec, that had spawned in four consecutive seasons is reported to have attained that age (*28*). Another Moisie River Salmon weighing 38.5 pounds, which had also spawned four times, is reported to have been 13 years of age (*101*). Menzies has also referred to a 13-year-old Scottish Atlantic Salmon (*100*). All of these very old fish were females.

Tolerance to Temperature. It is evident, from their northerly range, that Atlantic Salmon prefer cool waters, and from their observed behavior in streams, that water temperature is certainly one of the most influential of environmental factors, as is illustrated in the two branches of the Margaree River (p. 475). Egg development, incubation time, and the rate of growth of fry are definitely linked to temperature conditions (p. 466).

The lethal temperature for any given individual varies with its thermal history. Experimental fingerlings that had been living at 25° C began to die when exposed for any length of time to a temperature of 28.5° C; and planted fingerlings died when the stream temperature reached 30.5° C (*98*). Parr tolerate temperatures as high as 28–29.5° C (82–85° F), at least temporarily, but they die under experimental conditions at temperatures of 32.9 and 33.8° C (90.2 and 91.8° F). The older fish die when the water temperature rises as high as 28–29.5° C, which happens in some of the smaller streams of New Brunswick and in some of the rivers of outer Nova Scotia during periods of very low water resulting from deficient rainfall and protracted hot weather (*65*: 485; *67*: 476).

The success or failure of commercial fishing and of angling is closely associated with the temperature of the water, and it is common knowledge among anglers that Atlantic Salmon do not rise freely to the fly if the water is warmer than about 70° F.

Food. Studies of specimens from many parts of their range indicate that the same items—May fly nymphs, caddis larvae, and particularly chironomid larvae—usually predominate in the food of parr; all live in the bottom. However, as the fish grow, surface food assumes greater importance. Allen has given a comprehensive review of the feeding habits of young Atlantic Salmon (*1*: 47–76).

Studies in eastern Canada have shown that chironomid larvae consitute the chief food of parr that are beginning to feed (*139*: 499–506); later, especially during midsummer, May fly nymphs become important. Toward the end of the summer growing season, caddis larvae are taken in increasing numbers. Some Plecoptera (stone flies) as well as simulids and tipulids have been found in small or limited quantities in the stomachs of parr examined in early summer and in the fall.

The feeding by parr in the River Dee was found to be indiscriminate. A single meal might include representatives of a dozen or more species taken at random from under stones (insect larvae), in open water (Cladocera and small beetles), or from surface driftage (aerial and terrestrial arthropods); the large number of dipteran flies (uniform in species) sometimes found in a single fish suggests that it might have snapped at swarms in the air (*33*).

Because adults do not feed while they are in fresh water and have usually ceased feeding by the time they reach inshore waters, where most of them are caught commercially, comparatively little is known about what they eat when they actively feed at sea. Among the food items most commonly mentioned are herring, capelin, and sand launce; small mackerel are also frequently mentioned.

Many of those taken in traps inshore are empty, probably because they share with many other fishes the habit of disgorging their food out of fright, or digesting it before they are removed from the traps (*84*: 165–166). In spite of this, there are numerous records of the Atlantic Salmon's diet inshore, where they have been reported as preying on small fishes of various kinds as well as crustaceans. For example, many of those from the north shore of the Gulf of St. Lawrence, opened by Comeau, contained herring, small mackerel, and sculpins (cottids), and some had gorged on capelin (*34*: 184–188). Kendall found alewives (*Pomolobus*) in specimens from the St. John River, New Brunswick, and smelts in Penobscot River fish (*87*: 32, 34). Ungava Bay specimens have contained Arctic cod (*Boreogadus saida*) and sculpins (*39*).

Stomachs of this species from off Norway are sometimes packed full of herring; these as well as launce are common food in the Baltic; Day saw 22 entire sprats (*Clupea sprattus*) up to seven inches in length taken from the stomach of a 12-pound fish caught in the tidal portion of the Severn River, England (*38*). Haddock, eels, small trout (*Salmo trutta*), flatfishes, and other species have also been found in Atlantic Salmon. A hook-and-line fishery using herring as bait is (or was) carried on in the Baltic, and hooks baited with launce (*Ammodytes*) or with pieces of mackerel sometimes catch them in British waters. Trout, charr, and salmon parr have been reported as being taken from stomachs of Salmon caught by anglers in Scotland (*30*: 73).

Atlantic Salmon from the Penobscot, Maine, have been full of "shrimp" (probably euphausiids),[14] and grilse have been described as feeding on euphausiid shrimps and pelagic amphipods (*36*). Sand fleas (gammarid crustaceans) rank with launce and herring as food in the North and Baltic seas; crabs have also been found in Salmon.

In Iceland, and in Great Britain and elsewhere in Europe, they are caught by anglers using natural bait (prawns, angleworms) and artificial minnows, not only in the estuaries and lower reaches of the rivers, but also in lakes near the sea; no doubt this would be the case in Canada also if bait-fishing were allowed there.

Adults normally eat very little, if at all, after they have run up well beyond the head of tide. Accordingly, their stomachs seldom contain anything except a little yellowish fluid. Of the numerous fish from fresh water on the north shore of the Gulf of St. Lawrence that were opened by Comeau (34), only four contained recognizable items: two taken by anglers had eaten insects; one speared in November had parts of a mouse in its stomach; and a kelt contained organic fragments, apparently of some

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[14] For a survey, with references, of the diet of Salmon in general and in the Gulf of Maine in particular, see Kendall (*87*: 33–34); for diet lists for the Baltic and North Sea Salmon, see Eichelbaum (*41*).

bird. The energy to maintain them during their stream life when they return to spawn and the resources for the development of either eggs or milt have been built up and stored in their bodies during the feeding stage in salt water.

Why Atlantic Salmon in fresh water so often rise freely to artificial flies has been widely argued and still is. An experienced angler has suggested verbally that on sighting the fly an occasional fish suffers an attack of temporary insanity; this explanation is perhaps as satisfying as any other that has been proposed.

Predators. Atlantic Salmon are preyed on throughout their life, in both stream and sea, and this factor, probably as much as any other, is generally responsible for the small percentage that survives to spawn (pp. 479, 480). Most of what we know about this subject is confined to reports for fresh water; as Pyefinch has aptly observed (*116*): "The depredations of birds and other fish in fresh or estuarine waters may be impressive only because they are visible and are noticed, they may actually be much less significant than the effects of other predators present, for example, in the sea." The extent of predation today relative to that under primitive conditions is not known (*142*; *143*).

Atlantic Salmon are probably preyed on throughout their range by one or another of the predatory fish that cohabit the same waters. In fresh water, birds (mergansers, cormorants, gulls, and herons) destroy significant numbers of young. In the Maritime Provinces of Canada, mergansers (especially *Mergus merganser*) and the belted kingfisher (*Megaceryle alcyon*) are often destructive; control of these in the Pollett River (Petitcodiac R. system) is believed to have increased smolt production eightfold. Following control of mergansers[15] on the Northwest Miramichi (but not on the Dungarvon which is also tributary to the Miramichi system and has a similar run of adults), production of large parr increased more than fourfold (*44*). Mergansers are also serious predators on young Atlantic Salmon in Sweden (*93*). *Salvelinus fontinalis* (brook trout) in America and *Salmo trutta* in Europe eat young Atlantic Salmon in the streams; and in some areas eels reduce their number (*43*: 15).

In marine situations, both harbor seals and gray seals are reported as frequently preying on Atlantic Salmon when these gather near river mouths. Indeed, depredations by seals, chiefly gray seals, cause substantial losses to the fishermen who operate traps and drift nets in the estuary of the Miramichi and within the mouth of the river (*47*: 28). Very little information is available about the predation that obviously must occur at sea. Ten Salmon, 10–12 pounds each, are reported to have been found in the stomach of a shark about 25 feet long, caught eight miles east by south of Peterhead, Scotland. One has also been reported from the stomach of a shark taken in Greenland (p. 490).

An inspection in both 1956 and 1957 of adults caught in the estuary of the Miramichi River, N. B., showed that 0.46 and 0.66 %, respectively, either had small living lampreys attached to them or bore lamprey scars; the corresponding figures for those in fresh water in the Northwest Miramichi were 0.15 and 0.25 %; no fish were found with large adult lampreys attached. These records indicate that lampreys are not

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[15] White has also studied the feeding by mergansers on Salmon fry (*139*, *140*, *142*, *143*).

a serious menace to adult Atlantic Salmon in the Miramichi (M.H.A. Keenleyside, personal communication).

Parasites and Diseases. Numerous parasites and a few diseases[16] have been reported for Atlantic Salmon, but it is not known to what extent they affect the population. For the most part, ways and means of controlling them have not been found. Among the external parasites, sea lice (*Lepeophtheirus salmonis*) and gill maggots (*Salmincola salmonea*) are common and widespread, and five others have been reported as sometimes occurring. Of the diseases, "Salmon disease" and furunculosis are the more common.

Sea lice, which occur on Atlantic Salmon throughout their range in both North America and Europe,[17] are parasitic copepods frequently found attached to fish that have recently entered fresh water from the sea. Sea lice usually die within a week of being brought into fresh water, but sometimes they live longer. Most of those attached to Atlantic Salmon are females about three-quarters of an inch long. White observed that some of the fish that entered the Moser River in 1939 were so heavily infested with them and had so much of the skin in the occipital region eroded away that the fish died after entering fresh water (*141*). The large fish were not so heavily infested as grilse, some of which had an almost complete layer of lice extending over the dorsal part of the body from the posterior edge of the eyes to the caudal peduncle, and a few lice around the anal and ventral fins. Before the skin sloughs away there is a distinct white area over the regions affected; White believes this is the condition described as "white spot."[17]

Gill maggots (*Salmincola salmonea*) are smaller than sea lice (0.25–0.33 in.), and most of those on Atlantic Salmon are females. Although they are able to breed only in the river, numbers survive in salt water. Maggots attach themselves to the gills of the fish in fresh water, only after the latter have been in salt water and have returned. They are not found on young that have remained in fresh water (*31*: 16). Maggots have been found on fish that have been in fresh water for as much as a year and in salt water for two additional years.

Internal parasites of Atlantic Salmon are reported under more than a hundred names, but until careful taxonomic studies have been made it is impossible to say how many of these represent valid species. Twenty-five names, for example, have been reported for trematodes or flukes, 38 for cestodes or tapeworms, 25 for nematodes or round worms, 22 for acanthocephalous or thorn-headed worms, and 8 for Protozoa.

Furunculosis, the ulcer or boil disease, caused by the bacterium *Bacillus salmonicida*, has occasionally assumed epizootic proportions in hatcheries, whence it has spread to natural waters; it has also reached similar proportions at times in southern England. A second bacterial disease (Salmon disease), caused by *Bacillus salmonis pestis*, has occasionally assumed serious proportions in southern England.

[16] Lists of parasites reported for the Atlantic Salmon were provided by the Parasitology Division, Ontario Research Foundation; Animal Disease and Parasite Research Division of the U.S. Department of Agriculture; and Institute of Parasitology, McGill University.

[17] Sea lice also affect brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), Dolly Varden (*Salvelinus alpinus malma*), and two Pacific Salmon (*Oncorhynchus tshawytscha* and *O. gorbuscha*) (*120*; *51*; *147*).

Decline in Abundance. Atlantic Salmon were extremely abundant in early colonial days from New England northward to the northern shores of the Gulf of St. Lawrence and Labrador in every river that was not barred to them by impassible falls and where spawning conditions were suitable. The few taken by the natives merely reduced overcrowding at the spawning sites; and the waters ran clear and clean, deeply shaded by virgin forest growth down to the stream and river banks. The advances in colonization and expansion, however, with concomitant increases in man's exploitation of both the land's resources and the fishery, soon began to deplete the Salmon population.

In 1849, Perley (*112*) wrote:

> The quantities of salmon in the River Restigouche and Miramichi, at the first settlement of the country were perfectly prodigious; although many are yet taken annually, the supply diminishes from year to year. And this is not surprising when it is considered that many of the streams formerly frequented by salmon are now completely shut against them by mill dams without "fishways"—that in the branches of the large rivers, as also in the smaller rivers, nets are too often placed completely across the stream, from bank to bank, which take every fish that attempts to pass—that "close time" in many of the rivers is scarcely, if at all, regarded—and that, besides the improper use of nets at all seasons, fish of all sizes, are destroyed by hundreds in the very act of spawning, by torchlight and spears at a time when they are quite unfit for human food.[18]

Perhaps the most destructive practice in the early days, especially in New England, was the construction of dams in connection with the production of power through water wheels, as typified in the Connecticut and Merrimack rivers. The Connecticut River, extending 407 miles northward into northern New England, supported a large run until the end of the eighteenth century. In four years, however, following the construction of a dam 16 feet high across the river at Miller's Run in 1798, there were few fish left, and in 12 years there was none (*23*). The fate of this species in the Merrimack River in northeastern Massachusetts (110 miles long and extending into New Hampshire) also typifies the history of Atlantic Salmon in New England rivers from which they have been barred (*18*). They spawned plentifully in this river's upper reaches as late as 1793; in 1790, for example, 60–100 fish a day was the usual catch with a 90-yard seine, near the river's mouth; but the completion in 1847 of a dam at Lawrence, Massachusetts, completely barred the spawning areas of the river to them. For some years thereafter those that had been produced in the upper reaches gathered below the dam in spring and summer, "vainly endeavoring to ascend." There has been no run in the Merrimack since 1859 or 1860, when the last fish hatched above the dam had lived their span of life, and there has been no spawning there except by a few that may have been lifted over the dam.

The spawning areas in only a few of the numerous rivers in New England that supported Salmon runs in the early days were still open to them by the end of the past century, and by 1925 only two of the Maine rivers, the Dennys and the Penobscot, saw regular runs, aided in part by the artificial propagation carried on by the U.S. Bureau of Fisheries. Since then, however, the situation has improved slightly in Maine.

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[18] See also *108*; *92*; *7*.

Canada has always had more Atlantic Salmon than New England, and the area occupied by the Canadian fishery has seen less industrial development than the area originally frequented by Atlantic Salmon in New England. It was stated in 1931 that depletion in the Maritime Provinces of Canada was particularly evident in rivers emptying into the Bay of Fundy, and in some cases it had progressed to total extinction (*59*). The Petitcodiac River system in New Brunswick afforded an example of a stop just short of extinction. However, in 1958 it was reported that Atlantic Salmon in fluctuating numbers occur in 300 rivers of Canada's Atlantic provinces (*45*: 19), with 75% of the population being restricted to six principal river systems of New Brunswick and Newfoundland.

The largest recorded commercial catch in Canadian waters, exclusive of Newfoundland, was taken in 1873 and amounted to 6,698,200 pounds. The largest for United States waters was 205,679 pounds in 1888. At present the total Canadian catch, including Newfoundland, totals up to 3,000,000 pounds a year, one-half to two-thirds of which comes from Newfoundland, including Labrador. U.S. commercial production is now less than 1,000 pounds. From the 1888 high in New England, the catch declined so that about 50 years later (1932–1938) it varied between 16,000 and 40,000 pounds; and during the next ten years it averaged only 3,600 pounds, less than 2% of what it had been about 60 years before.

The total Canadian angling catch in recent years has been 75,000 Salmon per year. Of this, the Miramichi River, N.B., reputed to be the greatest salmon river in the world, contributed 30,000, followed by the Restigouche with 3,000; all the Newfoundland rivers combined yielded 20,000 fish, and the Quebec rivers 12,000 (*91*). In Maine, the combined angler's catch for 1956 was only 278 fish (*148*: 212).

Lumbering and agriculture, by removing natural soil cover, have exposed large areas to erosion, thus creating several conditions detrimental to this species, including silting of stream beds, floods, and summer low water. Floods wash out nests and eggs and destroy the homes of the fry and fingerlings. Low water not only enables predators to more readily see and capture the young, but it results in higher summer temperatures that sometimes reach the lethal point for Salmon. Spraying forests with DDT and other chemicals to control insects (such as the spruce bud-worm and others) has recently created another danger. Not only is DDT harmful to many of the insects on which the young feed, but it is directly destructive to the fish themselves (*4*; *86*; *75*). Pollution of stream waters by poisonous chemicals and other wastes has also been injurious, sometimes directly, and sometimes indirectly through the removal of oxygen from the water.

The more recent use of rivers for the development of hydroelectric power has added other destructive conditions; either the spawning grounds are eliminated through the creation of large lakes, or the young are destroyed in going over the spillway or through the turbines. Irrigation projects involving dam construction and creation of storage basins also obstruct their ascent and eliminate spawning grounds.

Whether Salmon predators, for example mergansers and kingfishers, are more or less destructive today than under primitive conditions has not been determined. Their relative effect on Atlantic Salmon populations now as compared with those in earlier times may be due to either or both of the changes that affect the ability of the predators to reproduce or to prey on the fish (*142*; *143*).

Overfishing has often been blamed for the decline noted. Anadromous fish are more vulnerable to overfishing than species that remain at sea throughout their entire life because they concentrate within a small area when they run up rivers to spawn; thus it is much easier for fishermen to take a high percentage of the stock. The high price that Atlantic Salmon command encourages intense exploitation of the fishery. However, present evidence indicates that the fishery as now permitted by law does not reduce the spawning population below what is necessary to provide all the young that the streams, in their present condition, can support (*42*). In other words, the decline of the fishery has been due to the creation of unfavorable conditions in streams rather than to overfishing (see also *Maintenance and Restoration of the Fishery*, p. 488–490).

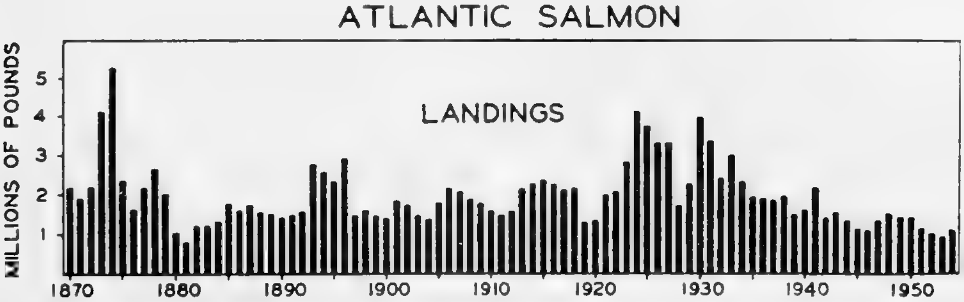

FIGURE 123. Commercial landings of Atlantic Salmon from the Gulf of St. Lawrence area (Cape Gaspé to Cape Breton) for the period 1870–1954 (Elson and Kerswill, *44*).

Fluctuations in Abundance. It is reasonable to assume that the Atlantic Salmon population has always fluctuated more or less in abundance, but it is only for recent years that it has been possible to estimate with any degree of certainty from the catch statistics the extent and nature of the fluctuations. Although catch cannot be regarded as an accurate measure of actual population, it is the only available measure we have. On the basis of such statistics it must be concluded that populations not only have fluctuated widely from time to time but have declined seriously since 1930. However, since 1955 there has been evidence of some improvement.

The extent and nature of these fluctuations, illustrated in Fig. 123, show three important features: (1) the great difference between neighboring highs and lows, for instance between 1873 and 1881 and between 1924, 1928, and 1930; (2) the over-all steady decline since 1930, with recent low catches persisting much longer than in earlier years; and (3) the tendency of the peaks of production to occur about every 10 years. This periodicity was noted almost simultaneously around 1930 by several investigators. Griswold's discovery was based on a study of the records of the Cascapedia and Restigouche Salmon clubs and of New Brunswick and Quebec fishery statistics (*50*). Phelps and Belding corroborated Griswold's findings from the records of the Restigouche Club, noting a periodicity of nine or ten years extending back to 1879 (*114*). Huntsman used for his study the fishery statistics of the Maritime Provinces of Canada, which extended back to 1869 (*58*: 9–14). Huntsman attributed periodicity in Atlantic Salmon to periodicity in rainfall (*60*: 17–28; *72*: 43–53). Griswold related it to a nine-year cycle of tides, believing that coastal currents move offshore and onshore in cycles of nine years. Phelps and Belding believed that an oceanic—or possibly a river—condition affected the migrating smolts periodically. What connection, if any, there may be between such periodicity and the nine- or ten-year periodicity in terrestrial animals such as the varying hare (*Lepus americanus*), ruffed grouse (*Bonasa umbellus*), and some others is not known (*40*: 1–34).

Atlantic Salmon catches in Great Britain and Ireland also fluctuate and show a striking similarity to those in America (*88*). Svardson, while noting a tendency toward parallel trends in the yields of Atlantic Salmon fisheries in Great Britain, Norway, Sweden, and Holland, has pointed out that they are not parallel every year (*124*: 226–262). He believes that he found a statistically significant positive correlation between the area of ice cover in the Baltic and the Atlantic Salmon catch five years later, suggesting, in explanation, that severe winters cause the death of large numbers of the common porpoise, which preys on them. Lindroth, however, questioned Svardson's conclusions, arguing that the short-term fluctuation is only an artifact created by the long-term fluctuation, which is dependent on climate (*94*).

Maintenance and Restoration of the Fishery. The problem of maintaining or restoring the species is largely one of assuring that conditions necessary for successful spawning, hatching, survival, and growth in fresh water are maintained or restored. There are no reasons for believing that the sea could not support as large populations today as it did hundreds of years ago; therefore it is in the rivers that remedial action is necessary.

Salmon thrive best under the primitive conditions of northern regions. They require cold water and, for reproduction, clean gravel. The changes incidental to settlement and industrial development that destroy these conditions have already been mentioned under *Decline in Abundance*. The problem of preserving Salmon is that of halting these injurious forces and, when possible, of restoring favorable conditions. The failure of experiments to reintroduce Atlantic Salmon into a stream flowing into Lake Ontario where they formerly spawned illustrates the detrimental effects of man's activities (*98*). Apart from mill dams that formerly barred the fish from reaching the spawning grounds, the changes brought about in the conditions of this stream were due to lumbering, which removed the tree cover, and to farming, which exposed the soil to erosion. High lethal temperatures eliminated the planted fry from some sections, and over the balance of the planted part, the greatest mortality occurred soon after planting when heavy predation by other species of fish occurred. The extent of predation was related largely to the amount of suitable shelter for the fry. This was limited generally to gravelly ripples where the degree of bottom silting determined the amount of shelter.

Measures necessary to improve streams for Atlantic Salmon include: better land-use practices to reduce erosion, floods, and low summer flow; overcoming pollution and the detrimental effects resulting from measures undertaken for the benefit of other resources (e. g. spraying forests to control injurious insects); and means of assuring reproduction in streams used in the development of hydroelectric power or irrigation. The cost involved in adopting remedial measures will determine the extent to which suitable streams will be saved for Atlantic Salmon production. If society values this species highly enough, its future can be assured through wise management based on research. Overcoming pollution, for instance, is largely a matter of deciding on the relative importance or value of Atlantic Salmon compared with the value of industries that cause pollution. If the cost of disposing of polluting substances by means other than putting them into streams will be greater than the value placed on the fishery, then the latter will be sacrificed; and, in considering the worth of this species, values other than those of economics must be considered, such as the sports value.

In the past, relatively too much emphasis has been placed on restricting the catch and too little on maintaining suitable stream conditions. Recent studies indicate that, in many streams, enough spawners escape capture to provide all the young that can survive and grow in the streams in their present condition (*42*). That this number is not large is shown by the results of studies in four streams of the Maritime Provinces, where it was found that between 40 and 50 pounds of adult females per mile of stream 10 yards wide are enough to maintain stocks (*43*: 23).

The role of hatcheries in maintaining Salmon populations is not as great as it once was believed to be, but hatcheries have an important place if the young fish produced in them are used intelligently. If the eggs normally deposited by the adults at the spawning grounds are adequate to produce all the young that can survive and grow in the stream, the planting of more young is not only wasteful but may actually be harmful by increasing the competition for limited living room and food. However, in streams that lack suitable grounds but where conditions are suitable for the survival and growth of young to the smolt stage, the planting of hatchery-reared young may be beneficial. Also, in streams barred by dams over which it is not practical to pass spawning adults, the planting of hatchery-reared young may be advantageous if means can be provided for them to reach salt water. Where the use of streams by adults and young has been made impossible, a fishery may be preserved by raising young to the smolt stage under artificial conditions and planting them directly in an estuary or in the sea. Another promising method of providing artificial propagation is in creating artificial spawning beds to replace those eliminated by power development or other detrimental factors.

In Sweden the experimental planting of marked smolts has given a return of 5–10 % in adults, a higher percentage than is usual; this suggests that artificial propagation may be sound both biologically and economically (*32*). Efforts to rehabilitate this species in Maine have met with some success; at least seven rivers there (versus two in 1925) now have Salmon populations, with sizable runs in four or five of them (*45*).

Relation to Man. The Atlantic Salmon has long been highly esteemed as a table fish; in fact, its bones have been found commonly in caves occupied by prehistoric man in western Europe. Ausonius, a Latin poet of the fourth century, was the first to describe fishing for this species—in the Moselle River, a tributary of the Rhine.

Since the Atlantic Salmon is prized as a game fish as well as a commercial species, it is difficult, if not impossible, to estimate its true monetary value. Angling is one of the most popular of outdoor recreations, and the Atlantic Salmon's value is indicated by the relatively large sums of money that sportsmen are willing to spend to fish for it. Salmon fishing ranks with the higher satisfactions of life for which some men are willing to pay handsomely after their physical needs have been satisfied. The value of the Canadian commercial catch is in the neighborhood of a million dollars a year, and it has been estimated that the angling fishery is worth more than this amount (*44*).

Range of Sea-going Populations. The general range of *Salmo salar* includes the coasts of northern Europe and North America, from the Arctic to Portugal in Europe and to New England in America. In Europe the northern limit is the Tschernaja River, which flows into the White Sea east of the Pechora. The southern limit is the Miño River at the boundary between Spain and northern Portugal; perhaps a few reach the Douro River midway of Portugal (*123*: 18; *24*: 35; *109*: 354; *110*: 355; *96*: 155).

There are many good Atlantic Salmon rivers in Iceland.

The Atlantic Salmon is relatively scarce in Greenland; it is known mainly from the southwest coast. Before the 1920's it was known from small numbers at only Kapisigdlit (Godthaab Fjord, 64°10′N) and Amerdlok Fjord (near Holsteinsborg, just within the Arctic Circle). However, during the 1920's, according to Jensen, it increased off western Greenland with rising sea temperatures (*76*: 17, 18). Towards the end of that decade a migration occurred in October and November in the Sukkertoppen district (65°22′N), and later, especially in 1935 and 1936, the Salmon occurred in large numbers at several places in the same district from October on into December. In 1952 is was reported for Amerdlok Fjord, Ikerasak (Sukkertoppen district), and Kapisigdlit (*39*: 92). In 1951 an Atlantic Salmon was found in the stomach of a shark taken in the Umanak River (about 70°20′N), north of Disko Island; it must have been devoured only a short time before the shark was caught because the Salmon was so fresh that the natives ate it. The northernmost river in which the Atlantic Salmon was known to spawn in 1953 was near Kapisigdlit (*53*: 79–81).

On the North American mainland the Atlantic Salmon ranges north to Hudson Strait. There was a commercial fishery in Ungava Bay from 1881 till the early 1930's (*39*), and there still are spawning migrations into the larger rivers on the eastern half of the Bay between and including the George and Koksoak rivers. The latter is at present the western limit of its normal distribution in this area. According to native report, it is occasionally taken as a stray in the Leaf River, farther west; and a fishing camp for anglers has recently been established on the George River (*148*: 215).

The northernmost Salmon rivers on the Atlantic coast of America are "just north of Hopedale, about 350 miles north of the Strait of Belle Isle; the Adlok near Hopedale has a run of salmon which will average well over ten pounds" (*148*: 216).

Southward there are regular spawning runs in all the larger rivers of Newfoundland, including outer Labrador, Quebec as far into the Gulf of St. Lawrence as Bay St. Paul and Kamouraska (*132*), Prince Edward Island, New Brunswick, and Nova Scotia. The northern limit of intensive commercial exploitation for it is Indian Harbor on the north shore of Hamilton Inlet, about 54° N (*18*).

In New England during colonial days the Atlantic Salmon occurred in every suitable stream southward to Connecticut, but after the early part of the past century, dam construction (p. 485) was responsible for the elimination of the Atlantic Salmon from many of the rivers. In the decade 1850–1860 it still entered the St. Croix, Dennys, East Machias and Machias, Penobscot, Sheepscot, Kennebec, and Androscoggin. At present the St. Croix, Dennys, Machias and East Machias, Narraquagus, and Pleasant rivers alone have regular runs large enough to attract some anglers, and a few still enter the lower reaches of the Penobscot, where a Federal hatchery is in operation. Southward, enough Atlantic Salmon to yield a supply of eggs for artificial hatching continued to enter the lower reaches of the Merrimack until 1896 at least (doubtless wanderers from the north), and while none has been reported for the Merrimack since 1901, it is not unusual for some, straying from the north, to be reported off Massachusetts. Thus in 1928, 1,600 or so fish (16,050 pounds) were taken offshore there (on long lines and in otter trawls), while in 1937 the floating traps along the north shore of Massachusetts Bay picked up 4,400 pounds. A few are taken in Cape Cod Bay in most years; there are records for the Woods Hole region, as well as for New Jersey; and in April 1893, one of 16 pounds was taken with a school of mackerel off Delaware, where it is said to have been introduced (*48*). However, it no longer runs in any river south of Maine.

Freshwater Populations. In addition to anadromous populations, there are in both Europe and North America populations consisting of fish that spend their entire life in fresh water; the counterpart of the anadromous Salmon's sea phase is passed in some lake. They are sometimes referred to as "landlocked," but this term is not accurately descriptive, for they could all go to sea, but many of them could not return to their natal rivers because of impassible falls. However, the Shubenacadie Lake population (Nova Scotia) can freely pass to and from salt water. Lake Salmon is a more appropriate name than landlocked Salmon for these nonmigratory populations (*68*: 289).

There is no agreement as to whether their habit of remaining in fresh water is hereditary or not. Rounsefell has found that various species of salmonid fishes are characterized by different degrees of anadromy (*117*). Several species besides the Atlantic Salmon, notably *Salmo gairdneri* and *Salvelinus alpinus*, have given rise to lake populations. In experiments with marked young of both native Lake and Atlantic Salmon planted in Lake Shubenacadie, Huntsman observed no differences in their migratory behavior; however, the fish used were too few to provide final conclusions. Wilder has suggested that the observed differences in coloration, spots, and flesh color in Lake and Atlantic Salmon result solely from environmental differences (*145*).

Some of the lake populations were once regarded as being composed of distinct species, but they are now generally considered subspecific. Instead of being distinguished from anadromous Atlantic Salmon by the scientific names *Salmo sebago*, *S. ouananiche*, and *S. hardinii*, they are usually referred to now as *Salmo salar sebago*, etc.

Lake populations in North America are now found in Vermont, New Hampshire, Maine, New Brunswick, Nova Scotia, Quebec, Newfoundland, and Labrador, and formerly in Lake Ontario. They occur also in Norway, Sweden, and Russia.

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[19] References to the Atlantic Salmon are so numerous that only part of them are included here. Those listed provide information about the Salmon in the western North Atlantic and in fresh water of North America, but some European contributions dealing with taxonomy, distribution, and life history that are of particular importance are also included. Publications repeating essentially the same information or results have been omitted for the most part. References to Salmon are also included in most natural histories and in many annual reports or documents on fish or fisheries by government departments of the United States, Canada (particularly the Fisheries Research Board of Canada), and European countries where Salmon occur.

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Salmo trutta Linnaeus 1758

Brown Trout (North America); the Trout, Lochleven Trout (British Isles); European Trout (Continental Europe)

Figure 3

The Brown Trout, introduced from Europe to North America, is similar in general appearance to the Atlantic Salmon (*S. salar*) but is distinguished from it by the characters given on pp. 459–461. It is easily separable from the brook trout (*Salvelinus fontinalis*) and from the Arctic charr (*Salvelinus alpinus*) by its much larger scales, its black-spotted sides, and the presence of one zig-zag row (or two alternating rows) of sharp, well-defined teeth (easily felt) along the shaft of the vomer in the midline of the roof of the mouth. As in other salmonids, the Brown Trout in the sea is silvery in color. In Europe, where this species is indigenous, anadromous populations were formerly

[20] The reference in Neaves Nomenclator to Geoffrey, 1764, is erroneous, based on a mistake of Sherborn's. The work was in fact by Garsault, and is not binomial; this information is contributed by Dr. E. Trewavas of the British Museum (Natural History), who is preparing a note about it for Bull. Zool. Nomencl.

considered specifically distinct from the strictly freshwater type, but no specific difference is now recognized.

The Brown Trout is believed to have been first brought to North America in 1883. In that year eggs were sent from Germany to New York. The next year a shipment was sent from England. In 1884, the Lochleven trout, now considered to be the same as the trout in other parts of Great Britain and continental Europe, was introduced in Newfoundland. Another variant known as the German Brown Trout was brought to Newfoundland in 1892.

Anadromous populations are well established on the Avalon Peninsula in southern Newfoundland, where this species has spread through salt water to many streams, some as far as 60 miles from the four original centers of introduction. H. W. Walters, Director of the Wildlife Division of the Newfoundland Department of Mines and Resources, believes that the native brook trout (*S. fontinalis*) is declining in numbers in streams resorted to by the Brown Trout and that the latter will continue to spread to still more rivers around Newfoundland. The anadromous Brown Trout is also reported for the Guysborough River watershed, Nova Scotia, where it is taken chiefly in the 10–12 mile long estuary (information from James Cott), and a few are taken in some streams and rivers of Maine, Massachusetts, Connecticut, New York, and New Jersey.

Salmo gairdneri Richardson 1836

Rainbow Trout, Steelhead Trout

This species has been transplanted artificially from western to eastern North America. In the west there are both anadromous and freshwater populations. Some of the latter have diverged far enough from the parent stock to be regarded by some as specifically distinct while the taxonomic status of others is still in doubt. The only evidence that the Rainbow resorts to salt water in eastern North America is based on its presumed natural extension from Crooked Creek, New Brunswick, to a few neighboring streams, apparently by way of the Shepody River estuary into which Crooked Creek flows. The sea-going individual is silvery when in salt water, but upon returning to fresh water it becomes greenish with a pinkish or reddish band along the side, hence the name "Rainbow."

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Genus *Salvelinus* Richardson 1836

By

HENRY B. BIGELOW
Museum of Comparative Zoology
Harvard University

Salvelinus Richardson, Fauna Boreal.-Amer., 3, 1836: 169; first use in the singular (by implication) of the group name Salmones salvelines of Nilsson, Prod. Ichthyol. Scand., 1832: 7; type species, *Salmo salvelinus* Linnaeus, Syst. Nat., ed. 10, *1*, 1758: 309, Austria, designated by Jordan, Genera Fish., 2, 1919: 186.

Generic Synonyms:

Salmo (in part) Linnaeus, Syst. Nat., ed. 10, *1*, 1758, for *S. alpinus* Linnaeus 1758: 309, Lapland, Alpine lakes in England; *S. salvelinus* Linnaeus, 1758: 309, Austria; *S. salmarinus* Linnaeus, 1758: 310, "Habitat tridente in fluviis frigidis"; and *S. umbla* Linnaeus, 1758: 310, Switzerland.[1]

Baione, DeKay, Zool. N. Y., Fishes, 4, 1842: 244; type species, *B. fontinalis* DeKay 1842; Rockland County, New York.

Umbla, von Rapp, Jheft. Ver. Vaterl. Naturk. Württemberg (1854), *10*, 1856: 171; type species, *Salmo umbla* Linnaeus, Syst. Nat., ed. 10, *1*, 1758: 310; Lakes of Switzerland and Italy.

Not *Cristivomer* Gill and Jordan *in* Jordan, Manual Vert. north. U. S., ed. 2, 1878: 356, 359; type species, *Salmo namaycush* Walbaum, P. Artedi Genera Pisc., Ichthyol., Emend., 3, 1792: 68, by ref. to "the Namaycush," Pennant, Arctic Zool., *1*, Introd., 1784; cxci; lakes far inland from Hudson Bay.

Characters. Essentially as in the genus *Salmo*, but with: SCALES very small, scarcely visible—at least 195 rows and commonly 200 or more (120–130 in *Salmo*); TEETH lacking on shaft of vomerine bone along midline of roof of mouth (one or two more or less complete rows in the young of all species of *Salmo*, persisting throughout life in some); the teeth on premaxillaries usually forming a continuous series around front of mouth (for exception, see Fig. 127). CAUDAL fin only moderately concave. Bone above vomer (ETHMOID of Kendall, MESETHMOID of Regan, PROETHMOID of Starks) more than 38 % as wide as long. FRONTAL AREA OF SKULL not flat, usually with a median longitudinal ridge. Not more than 50 PYLORIC CAECA.

Sexual Dimorphism. Normally, in the mature male the head is noticeably larger than in the female, as is the mouth, the teeth are somewhat larger, and the pectoral and pelvic fins are somewhat longer. In the male at spawning time the lower jaw becomes slightly hooked, as in Fig. 124 (less so than in the salmon), a thick mucous layer develops, nearly or quite concealing the scales, and the colors intensify, especially the reddish hues, with the white margins of the pectoral and pelvic fins standing out more conspicuously. These seasonal characters disappear soon after spawning has been completed (*45*: 85; *62*: 7; *9*: 8).

Remarks. The restriction of the genus *Salvelinus* to species having a nearly truncated

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[1] *Salmo lacustris* Linnaeus, 1758: 309, appears to have included more than one species. For an early discussion, see Heckel (*31*: 353, pl. 7, figs. 4, 5).

caudal fin (at most a moderately concave one), a relatively broad bone in the ethmoid position, a more or less rounded frontal region in the skull, not more than 50 gastric caeca, and various skull characters as well as differences in the caudal skeleton,[2] excludes *namaycush* Walbaum (North American lake trout), for which Gill and Jordan founded the genus *Cristivomer*. Vladykov has revived *Baione* DeKay as a subgenus of *Salvelinus* for the species *fontinalis* (67: 928), which, according to him, is characterized by a "little forked tail, black stripe on lower fins, the absence of hyoid teeth, and an uninterrupted row of vomerine and palatine teeth." But Walters has found that in some specimens of the companion species *alpinus* the vomerine and palatine teeth also form an uninterrupted row (70: 258, 260, fig. 14). Neither do small differences in color seem to me to provide a sufficient basis for subgeneric separation in a genus where local populations vary as widely in this respect as they do in *Salvelinus*; nor does the presence or absence of hyoid teeth serve any practical purpose in this case, whatever the phylogenic implication of differences in this respect.

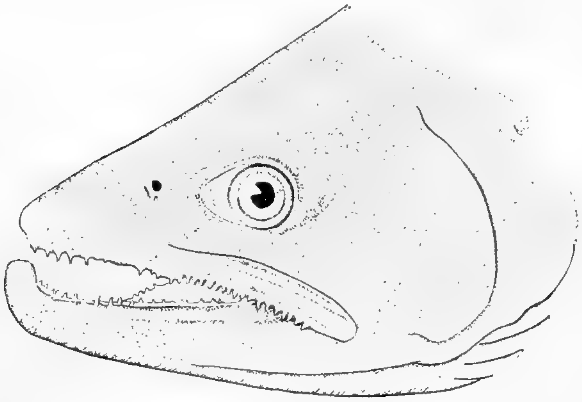

FIGURE 124. *Salvelinus alpinus.* Head from a male about 600 mm long, from Kungmiut, western Greenland. After Jensen.

Species. The species remaining in *Salvelinus* after *Cristivomer namaycush* is excluded fall in two divisions, the one typified by what may be termed the "*fontinalis* complex," the common brook trouts of North America (p. 525), the other by the "*alpinus* complex," the Arctic-subarctic charrs (p. 507). Regan characterized these two divisions as follows (55: 408):

S. alpinus division: head of the vomer with posterior process little developed. No dark spots or markings. Circumpolar.

S. fontinalis division: head of the vomer with posterior process well developed. Blackish or dark olivaceous markings on back and on dorsal and caudal fins. North America.

The shape of the head of the vomer, however, is not a convenient aid for identification, for careful examination of the lower surface of the anterior part of the skull is required. But the color pattern does afford a reliable field mark, not only for freshwater populations of *alpinus* and *fontinalis* but even for those taken in brackish or salt water; specimens of *S. fontinalis* always retain some trace of the wavy dark markings on the dorsal and upper part of caudal, even though similar marks may disappear entirely from the back and sides when the fish leave fresh water, or shortly before. Further, the *alpinus* division, compared to the *fontinalis* division, has the smaller

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[2] For further details, including the history of the case, see Kendall (46: 78–81), and especially Vladykov (67: 932).

mouth and the less blunt snout; although the maximum numbers of dorsal and anal rays and of gill rakers average more in *alpinus* than in *fontinalis*,[3] the overlap here is too wide for these numerical differences to serve as a reliable basis for separation. Neither is the shape of the caudal fin a safe clue to identity, for while the concavity is somewhat less deep on the average among *fontinalis*[4] than among sea-run *alpinus*, it is deeper in some freshwater trout from Labrador (seen by me) than in some *alpinus* from eastern Greenland.

Both the *fontinalis* complex and the *alpinus* complex include populations that spend their entire life in fresh water, as well as populations that spawn in fresh water but spend a part of the year in brackish or salt water, just as salmon do. It is with these migratory populations alone that we are concerned here.

Both complexes tend to vary widely in color and body proportions and in the sizes to which they grow in different localities, as is reflected in the names under which they have appeared in scientific literature (see Synonyms, pp. 523, 541). In the case of *fontinalis*, these local varieties seem so clearly to be a result of environment that only one of the forms in question, *agassizii* Garman 1885, has been recognized as a separate species, by Jordan, *et al.* (*43*: 60), but doubtfully so in my opinion.

"The various forms of charr allied to *Salvelinus alpinus* (Linnaeus) present a ... confused picture to the systematist, for a myriad of forms, described and undescribed, exist" (Walters, *71*: 274); views have differed widely as to how many of these deserve recognition as distinct species or as subspecies. On the one hand, six separate species were listed for North America by Jordan, *et al.* (*43*: 60–61), 15 for the British Isles by Regan (*54*: 82–85), and 16 for the Soviet Union and adjacent countries by Berg (*in 71*: 274). On the other hand, Goode (*26*: 501), following von Siebold's lead (*59*: 285–288) and finding it "difficult to believe that every little lake or group of lakes in Europe possesses a well characterized species of fish," tentatively regarded the charrs of Europe as representing a single highly variable species. This viewpoint is further exemplified by Smitt's union of all charrs of Scandinavia, from both fresh and salt water, in the single species, *umbla* Linnaeus, with *alpinus* Linnaeus and *salvelinus* Linnaeus rated as synonyms (*61*: 841).

In view of this diversity of opinion as to the systematic status of the freshwater charrs of the *alpinus* complex from different parts of the world, it is fortunate for present purposes that sea-going populations of the western North Atlantic appear clearly to represent a single species that seems to be identical to the common sea-run charr of Greenland. This was described by Fabricius in 1780 as *Salmo carpio* (*22*: 170); but this name had been previously applied by Linnaeus to one of the European freshwater charrs (1758: 309). To replace *carpio* for our fish, Kendall (*44*: 507),

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[3] *S. fontinalis*: dorsal rays 9–14, anal rays 8–12, gill rakers on first arch 4–8 + 7–9; *alpinus*: dorsal rays 9–15, anal rays 8–14, gill rakers usually 6–8 + 12–16, with a total of 13–22 reported. For meristic counts for sea-run trout of the Moser River, Nova Scotia, compared with several populations of freshwater *fontinalis*, see Wilder (*78*: 186, tab. 8); for *fontinalis* compared with *alpinus*, see Vladykov (*67*: 909–912).

[4] The anglers' name, Square-tail Trout, is based on the contrast between *fontinalis* and *Cristivomer namaycush* (p. 453).

following Regan (*55*: 408), proposed *alpinus* Fabricius 1780 (*22*: 173) on the assumption that Fabricius' *alpinus* is not separable specifically from his *carpio*, an assumption that seems fully justified, so closely do Fabricius' accounts of the two agree. The name *alpinus* has accordingly been used for the sea-run Arctic charr by a majority of the authors who have studied it within the last few years. In this connection, see especially Vladykov (*67*: 929) and Walters (*71*: 274).

The name *stagnalis* Fabricius 1780 (p. 175) has sometimes been applied to the sea-run Arctic charr (for instances, see *References*, pp. 523, 524), but it is not an appropriate choice, for as Kendall has emphasized (*44*: 507), Fabricius gave this name to a large Greenland trout (17.3 in.), of remote mountain waters, that never descends to the sea. If Fabricius was correct in using for his Greenland charr the name *alpinus* of Linnaeus (1758: 510), it follows further that the charr with which we are dealing here is not separable specifically from the Arctic charr of Lapland or perhaps from the charr (or one of the charrs) of England. Indeed, a specimen about 215 mm TL from Novaya Zemlya does not differ from my smaller specimens from Greenland and Labrador in any evident respect that might be regarded as specific, unless perhaps it differs in a more slender trunk and in a wholly plain coloration with blue-gray back, bright silvery sides, and white lower surface. Present indications are that the red-spotted charr of the *alpinus* group, named *malma* by Walbaum in 1792 (*69*: 66) and which is sea-run along both coasts of the northern North Pacific, deserves recognition as at least a subspecies of *alpinus* (Dymond, *17*: 39), if not as a separate species, as it is classed by Delacy and Morton (*12*: 81–90).

The freshwater populations of northeastern continental America have been given separate specific names, i. e. *oquassa* Girard 1854 for those of the Rangeley Lakes region in northern Maine, *aureolus* Bean 1887 for those of the cold lakes of northern New England in general, and *marstoni* Garman 1893 for those known in similar situations in northern Quebec. It remains an open question, however, whether any of these named forms, based chiefly on color and size, differ consistently enough from the typical sea-running *alpinus* to call for specific or subspecific recognition in zoological nomenclature; this applies equally to the names that have been proposed for the freshwater populations of Arctic Canada and northward; for a list of these, see p. 524.

Key to Species of *Salvelinus*, Taken in Brackish or Salt Water, in the Western North Atlantic

1 a. Dorsal fin and upper corners of caudal with dark wavy or vermiculated markings; color pattern on back, if visible, in the form of darker and paler marblings; length of head from tip of snout to rear margin of gill cover about 3.8–4.4 in SL; anterior contour of head bluntly rounded; pectoral fin broadly rounded (Fig. 128).
fontinalis (Mitchill) 1815, p. 525.

1 b. Dorsal and caudal fins with no dark markings; back without darker and paler marblings; length of head from snout to rear edge of gill cover 4.6–5.3 in SL,

but 4.5 in larger males where heads are relatively larger; anterior contour of head more narrowly tapered; pectoral fin pointed (Figs. 125, 126).
alpinus (Linnaeus) 1758, below.

Salvelinus alpinus (Linnaeus) 1758

Arctic Charr

Figures 3, 118, 119, 124–127

Study Material. I. Sea-run populations. More than 31 specimens: 15, 78–*ca.* 600 mm SL, from eastern Greenland, Thule in northwestern Greenland, and Godthaab in western Greenland; 3, from the Fraser River near Nain, Labrador (*ca.* 56°37′N); 2, from Novaya Zemlya, and others from the northwestern coast of North America and from Sakhalin Island, MCZ; 11, 305–*ca.* 600 mm SL, from Baffin Island, Ungava Bay (Turner Coll.), and Island Harbor near Mokovik, Labrador, USNM.

II. Freshwater populations. Numerous specimens of the *alpinus* complex from various freshwater lakes in northern New England, northern Quebec (Lac de Marbré, and a lake near Lake St. John), Norway, Switzerland, and Austria.

Distinctive Characters. The only saltwater fishes for which *Salvelinus alpinus* might be mistaken in eastern North American waters or around Greenland are *Salmo salar* (Atlantic salmon) of corresponding sizes, *Salvelinus fontinalis* (sea-run brook trout), or possibly *Cristivomer namaycush* (lake trout), which have sometimes been known to stray out into brackish or salt water;[5] nor is there much danger of confusing *alpinus* with any one of these. It is readily separated from *fontinalis* by its wholly plain color, or at most by its faintly spotted dorsal and caudal fins, by the spotted (not vermiculated) color pattern (if any) on its back, and by its noticeably more pointed head. It is set apart from *Salmo salar* old enough to have dropped some of the vomerine teeth by its very much smaller scales and the lack of black markings on its sides; and the toothless nature of the shaft of its vomer is an additional point of distinction between *alpinus* and a very small *S. salar.* Neither, I fancy, would anyone at all acquainted with the salmon-like fishes be likely to mistake *alpinus* for *C. namaycush*, so much more deeply forked is the caudal fin and so much longer relatively is the head of the latter (cf. Figs. 125, 129).

Description. Based on six sea-run specimens, 360–600 mm SL, from Mokovik Bay, Fraser River, and Ungava Bay, Labrador; Baffin Island; Godthaab, western Greenland; and eastern Greenland; in USNM and MCZ; and on other available data.[6]

TRUNK fusiform, its maximum thickness about 11–16 %, its maximum depth about 22–26 %, of SL, depending on the fatness of the specimens; dorsal profile weakly and about equally convex both forward from dorsal fin to snout and rearward to adipose fin. Depth of CAUDAL PEDUNCLE between 0.33 and 0.5 of length of head. SCALES present

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[5] In northern Labrador, in the northern part of Hudson Bay, and in Bathurst Inlet, Arctic coast of Canada. For a recent list of such happenings, see Walters (*71*: 275).

[6] For proportional dimensions and meristic counts for sea-run *alpinus* from various localities in Arctic-subarctic Canada and western Greenland, see Garman (*25*: 80–81), Dresel (*14*: 255–258), Henn (*32*: 2), Vladykov (*67*: 909–913), and Backus (*3*: 288–293).

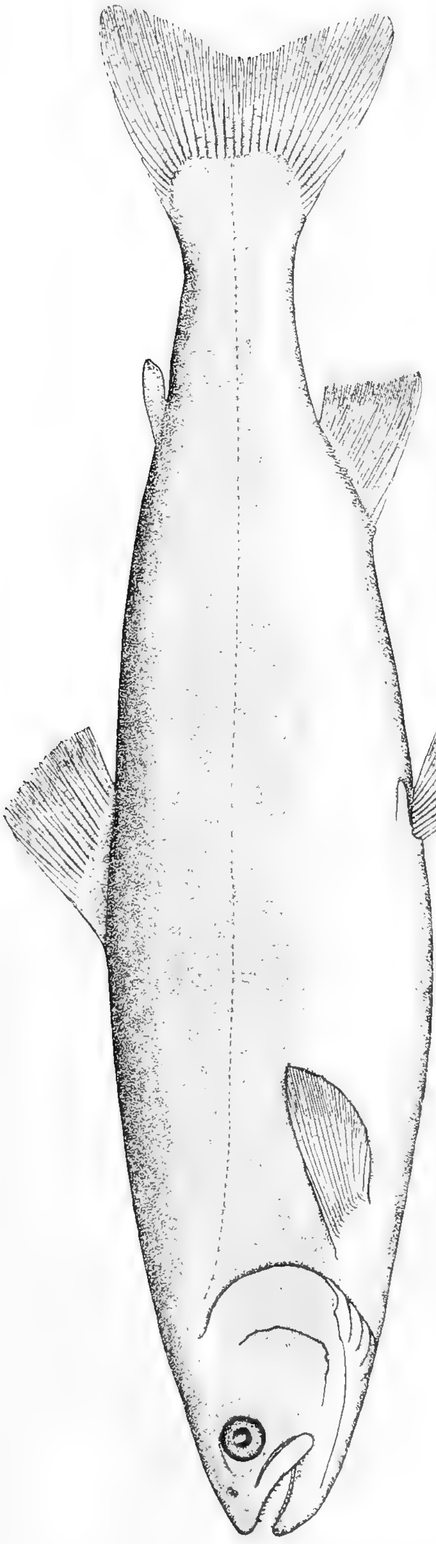

FIGURE 125. *Salvelinus alpinus*, 400 mm, female, from east coast of Greenland, USNM 35336.

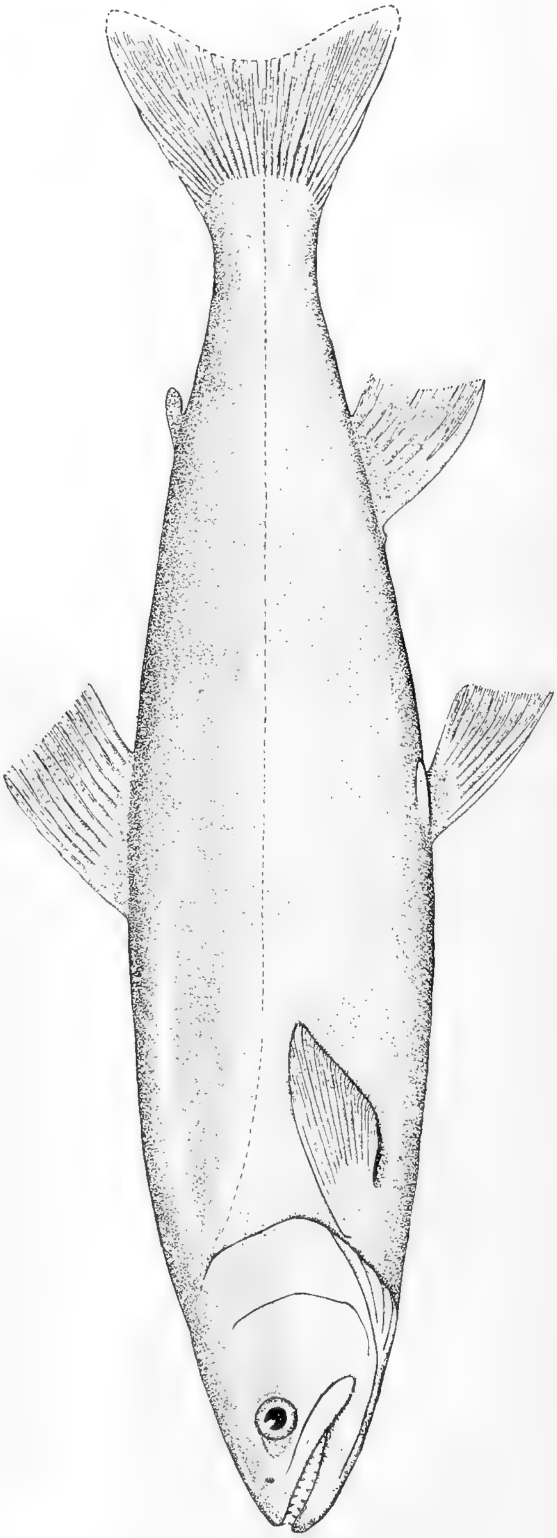

FIGURE 126. *Salvelinus alpinus*, male, from Ungava Bay, USNM 34239 (Turner Collection).

on body and tail sectors of trunk; head and fins naked; scales minute, as is characteristic of the genus *Salvelinus*; 200–235 reported. Lateral line represented as having 120–130 scales perforated.

Head 22 % of SL, noticeably less blunt anteriorly than in *fontinalis* (Fig. 128). Snout narrowly rounded, its length in front of eye 29–30 % of head. Tip of Lower jaw about even with tip of Upper jaw, or extending slightly beyond it; rear end of upper jaw reaching to a perpendicular varying in position from about abreast of midpoint of pupil to slightly behind eye in young specimens and in larger females (Fig. 125), and to behind eye by a distance about equal to length of eye in mature males (Fig. 126). Rear edge of Eye about 35–43 % of distance rearward from snout to rear margin of gill cover. Branchiostegal rays 10–11 reported. Gill rakers 13 and 16 on lower limb and 10 and 10 on upper limb on two fish—from western Greenland and eastern Greenland; 11–18 reported on lower arch and 6–10 on upper limb; the total number in nine fish from northern Canada 17–27, average 23.2 (67: 910, tab. 4).

Teeth. Premaxillaries, maxillaries, palatines, and dentary portion of lower jaw each with a single series of sharp, slightly recurved teeth, smaller on the whole and hence less conspicuous than in *fontinalis*; a patch of similar teeth on head of vomer anteriorly on the midroof of mouth; a single row around the tongue; also a patch of minute but sharp teeth on the bones at base of tongue (no teeth there in *fontinalis*), one such patch farther rearward below, in the pharynegeal region, and two such patches in pharyngeal region above, one of these along the base of each fourth gill arch.[7]

Rayed Dorsal fin rhomboid, its corners angular or very slightly blunted, its base 1.7–2.0 in head, its origin a little less than midway rearward (about 47–48 %) from tip of snout to upper origin of caudal fin, with 10–12 rays[8] (9–15 reported), the first 1–3 not branched, the longest ray 0.9–1.1 times as long as base. Dorsal Adipose fin with shape and relative size as shown in Figs. 125, 126, its origin 56–61 % of distance rearward from rear end of rayed dorsal base to upper origin of caudal. Caudal with upper and lower margins very weakly convex, the upper and lower corners abruptly rounded, the rear contour weakly concave, the breadth of fin, when widespread, about 1.5 times length of its upper and lower margins. Anal rhomboid, with angular corners, of the shape shown in Figs. 125, 126, its base about 84–95 % of base of dorsal, its origin about midway between a perpendicular at midpoint of dorsal and lower origin of caudal, with 11–12 rays (8–14 reported), the first 2 not branched, the longest ray about 0.88–1.2 times longest dorsal ray. Pelvics with midpoint of base about at a perpendicular at midpoint of base of rayed dorsal or a little anterior thereto, the longest ray about

Table I. Frequency Distribution of Dorsal (17 fish) and Anal Rays (18 fish) in Sea-run *alpinus* from Arctic Canada*

Number of rays	9	10	11	12
Dorsal, no. of fish	1	4	6	6
Anal, no. of fish	8	7	3	0

* From Vladykov, 67: tables 8, 9.

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[7] For photographs of the tongue teeth, hyoid teeth, and pharyngeal teeth of the *alpinus* species-complex (as represented by the freshwater *S. marstoni* and *S. aureolus*), of *S. fontinalis*, and of *Cristivomer namaycush*, see Vladykov (67: 920, 924, figs. 6–11).

[8] Precise counting is made difficult by the thickness and fleshy nature of the anterior basal part of the fins.

as long as longest ray of rayed dorsal; the fleshy appendage beside base of pelvics a little longer than eye. Pectorals noticeably narrower and with more acute tip than in *fontinalis*, their shape, when spread, as shown in Figs. 125, 126, their origin a little anterior to rearmost edge of gill cover (as in *fontinalis*, Fig. 128), the longest ray a little longer than longest ray of rayed dorsal.

Table II. Number of Vertebrae in 558 Arctic Charr from the Northeastern Labrador Coast*

	63	64	65	66	67	68	69
Number of fish..	6	26	151	213	125	31	6
Percent of total..	1	5	27	38	22	6	1

* From Andrews and Lear, *2*: 854, tab. 8.

Vertebrae 61–69 recorded; see Table II for their relative frequency. Pyloric caeca, average 39.1 reported.

Sexual Dimorphism. See p. 503.

Color.[9] While the young *alpinus* sojourn in fresh water, their back and the upper part of their sides are of some shade of brown or blackish green with about ten well-marked darker crossbars, the so-called "parr marks." These bars are conspicuous until the little fish have grown to a length of at least 150 mm, and they continue discernible up to 240 mm or so, i. e. until after the fish have moved out into brackish or salt water on their first seaward migration.

While they are in salt water and until the time arrives for their return to fresh water, their back and the upper part of their sides have been variously described as metallic blue, greenish blue, sea green, or steel grey, with metallic reflections; the dark of the back extends forward onto the head and downward there to the tip of the upper jaw. The sides as a whole are pale yellowish, tinged with a fleshy color in some, and marked with a basic pattern of many small spots, yellow or faintly pinkish, and indistinctly outlined; the spots vary widely in size from specimen to specimen—in regularity of distribution, in color, and especially in intensity—being so faint in some as to be scarcely, if at all, distinguishable; they are the most numerous above the lateral line anteriorly, but below the lateral line posteriorly; and they are confined to the upper part of the sides above a line extending from the base of the pectorals to the origin of the lower side of the caudal fin. In salt water, the lower part of the sides becomes overlaid in some specimens with a silver coating so dense that these areas are as silvery as in Atlantic salmon (pp. 462, 463); but others show hardly a trace of silver; the reasons for this difference still remain a subject for speculation. The lower surface is white, sometimes tinged faintly with yellow, without luster. The dorsal fin ordinarily is either colorless or of a pale shade of the back color, sometimes tinged posteriorly with yellowish red or in some cases with purplish black (see below). The caudal is either dusky, purplish black (see below), or colorless, with the outermost rays (below as well as above) yellowish red; and an occasional fish may show irregular dark spots on both dorsal and caudal. The pectorals and pelvics are creamy white. The anal is either creamy white or somewhat dusky centrally, tinged with red both anteriorly and posteriorly.

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[9] I have no color notes from life. This color account is based on the *Study Material*, in comparison with published descriptions; see especially Richardson (*56*: pl. 8), Garman (*25*: 81, fig. 19), Kendall (*44*: 505), Johansen (*40*: 671, pl. 45, figs. 6, 7), Weed (*72*: 133), Jensen (*39*: 68, 69), and Backus (*3*: 289, 290).

The following description of the color of *alpinus* from the Gander River, Newfoundland, contributed by G. B. Wiggins, is especially instructive, because it was based on specimens that were still alive when removed from the gill net:

> The fish had indistinct flesh-colored spots on the sides only and there were no red or blue spots. The flesh-coloured spots were almost completely obscured by a purplish-black metallic colour all over the sides. There were no markings on the back, the colour there being a solid purple-black like the sides. The abdomen was white with greyish blotches. The dorsal and caudal fins were solid purple-black and had no markings. The anal, abdominal and pectoral fins had a pink tinge. The anal and abdominal fins had a distinct white border, while the white border of the pectoral fins was less distinct.

Table III. Percentages of Fish with White, Pink, and Red Meat among 597 Arctic Charr from Representative Localities, South to North, along the Northeastern Labrador Coast, 1953*

Locality	White	Pink	Red	No. of Fish
Adlok.......	9	84	7	89
Nain No. 1..	7	43	50	31
Nain No. 2..	0	39	61	117
Okkak Bay..	23	49	29	120
Hebron.....	0	56	44	120
Ramah......	0	64	36	120

* From Andrews and Lear, *2*: 856, tab. 10.

When Arctic Charr re-enter fresh water, the silvery sheen disappears from their sides, their back changes to a neutral greenish brown, the color pattern of their upper parts becomes greatly accentuated, the spots on their sides assume a stronger whitish yellow or orange-red shade, their ventral fins become more or less suffused with a reddish color, and the color of their bellies changes to a strong orange yellow. The alteration is much more spectacular for maturing males than for immature specimens or for maturing females.

In northeastern Greenland, and presumably elsewhere also, the nuptial livery of Arctic Charr is at its height in November, but the brilliant red-orange hues have entirely faded once more by the time the fish move downstream again during the following May or June. We have yet to learn whether their sides turn silvery again just before they actually re-enter salt water, or just afterward.

Color of Flesh. The color of the flesh of *alpinus* ranges between white and red, with recorded percentages as given in Table III.

In western Greenland the commercial catch is sorted similarly into white and red meat, with the latter fetching the higher price (*39*: 71). But the mutual percentages at a given locality may differ considerably from year to year, as demonstrated in Table IV.

Table IV. Percentages of Arctic Charr with Pink, White, and Red Meat in the Commercial Catches at Okkak Bay, Labrador, during the Seaward Migrations, 1944–1949*

Flesh	1944	1945	1946	1947	1948	1949
White....	8	23	31	15	18	27
Pink......	27	28	25	26	29	55
Red......	65	49	44	59	53	18

* From Andrews and Lear, *2*: 857, tab. 11.

General experience with other salmonids suggests that its food determines whether a given fish will be white-fleshed, pink-fleshed, or red-fleshed, with a crustacean diet favoring the last state; no definite evidence, however, seems yet to have emerged in this regard for *alpinus*.

Size. The averages given in Table V show roughly the relationship between length (mm) and weight (lbs) at four localities. It appears from Table V that the Arctic Charr of Hudson Bay, of northeastern Labra-

Table V. Averages (in pounds) Showing the Relationship between Length and Weight of Arctic Charr from Northern North America and Spitsbergen

	Weight (lb)			
Length (mm)	Frobisher Bay Baffin Island†	Northeastern Labrador††	Western Hudson Bay*	Southern Spitsbergen**
250–295	0.5	–	–	–
300–345	0.6	–	–	–
350–395	1.1	1.5	1.5	1.5
400–445	1.7	1.9	2.4	2.2
450–495	2.4	2.7	3.3	3.3
500–545	3.3	3.8	3.75	3.5
550–595	4.4	5.1	5.2	4.8
600–645	5.8	7.7	7.0	5.5
650–695	7,2	6.9α	8.3α	–
700–745	8.4	–	–	8.8
750–795	10.2	–	11.7	–

† Grainger, *28*: 351. †† Andrews and Lear, *2*: 853, tab. 7. * Sprules, *62*: 6, tab. 1. ** Dahl, *11*: 6.
α One fish only.

dor, and of Spitsbergen average slightly heavier at equal lengths than those of Baffin Island. The general run, as caught, is reported as averaging about 4.3 pounds for the northwestern coast of Hudson Bay, with 56 % of the catch falling between 3–4 pounds. In Ungava Bay, the most common size is between 2–8 pounds. For southern Baffin Island the average is about 3.5 pounds. The bulk of the catch for northeastern Labrador runs from a pound or two up to eight or even ten pounds per fish; spawning fish in poor condition, caught in a brook tributary to Anatalek Bay, weighed close to five pounds. Most of the western Greenland fish weigh between 5.5–7.7 pounds.

The maximum weights (in pounds) that I have found reliably recorded have been 16 (7.3 kilo) for Hudson Bay; 9 for the south coast of Baffin Island and 11.9 for Frobisher Bay; 10 for northeastern Labrador; 8.5 for western Greenland; and 8.8 (4 kilo) for Novaya Zemlya. However, occasional *alpinus* grow much larger than the majority; specimens of 20 and even 26 pounds have been reported for the northwestern Hudson Bay area (*62*: 5; *35*: 24), and a giant of 35 pounds (16 kilo) has been reported for southern Novaya Zemlya (Yessipov, *79*: 70), though not on wholly conclusive evidence.

Development and Rate of Growth. The young fry under hatchery conditions have been reported as averaging about 17 mm in length at hatching. At room temperature (at Östanbäck, Sweden) they averaged 27 mm after 19 days, a rate of growth no doubt more rapid than that for "wild" fish exposed to considerably lower temperatures in nature; for example, Nystrom reported that fry artificially hatched in January in Sweden grew so slowly thereafter in the cold spring-fed fish ponds that they were only a little more than an inch (about 25 mm) long the following August (*in 61*: 847). Average lengths for hatchery fish have been reported as 97 mm at the end of their first year, 123 mm at the end of their second year, and 137–216 mm at the end of their third year (*61*: 847). These lengths seem somewhat greater (thanks to warmer

Table VI. Average Lengths (mm)* of *S. alpinus* at Different Ages for Localities in North America, Greenland, and Spitsbergen

Ages**	Northwestern Hudson Bay†	Labrador (Hebron to Ramah)††	Herschel I. Arctic Canada[α]	Frobisher Bay Baffin Island[α]	W. Greenland Localities[⊿]	Spitsbergen[β]
5........	382	—	246+	130	201–224	369
6........	408	—	362+	139	237–258	412
7........	446	412–449	407+	172	275–310	483
8........	468	423–557	425+	302	268–525	533
9........	494	442–576	421+	337	430–546	611
10........	524	472–584	524+	363	480–554	670
11........	567	478–626	557+	414	489–571	700+
12........	597	495–626	—	425	519–550	—
13........	638	503–656	—	484	530–606	—
14........	636	608+	—	510	—	—
15........	—	671+	—	553	—	—
16........	682+	764+	—	557	605	—
17........	791	—	—	559	—	—
18........	750+	—	—	600	—	—
19........	—	—	—	613	—	—
20........	—	—	—	649	—	—
21........	—	—	—	642	—	—
22........	822+	—	—	655	—	—
23........	—	—	—	678	—	—
24........	—	—	—	678	—	—
24+	—	—	—	685	—	—

* Measurements for Labrador and Frobisher Bay fish were given as fork length (snout to fork of caudal fin); those for Herschel Island, originally given as standard length, have been adjusted here to fork length by adding 9% of the standard length given. The standards of measurement were not stated for either western Greenland or Spitsbergen.

** Ages for Hudson Bay, Labrador, western Greenland, and Spitsbergen were given in years, those for Frobisher Bay and Herschel Island in "winters." Those for Labrador, Frobisher Bay, Herschel Island, and western Greenland were derived from studies of the otoliths, those for Hudson Bay and Spitsbergen from studies of the scales.

† Sprules, *62*: 8, tab. 2. †† Andrews and Lear, *2*: 851. α Grainger, *28*: 341–348. ⊿ Hansen *in 28*: 354, 369. β Dahl, *11*: 1–12. + One fish only.

water and to a more abundant food supply) than those to be expected among the anadromous populations with which we are immediately concerned.

The average lengths reached at equal ages by the Arctic Charr at different localities are summarized in Table vi. Although the data are not strictly comparable (see Table vi, footnotes), it seems evident from these data, added to other available information, that: (1) "the char[r] grow very slowly and may reach an age of more than 24 years" (*28*: 327); (2) the rate of growth varies widely from place to place, even within short distances, both for Labrador and for the western Greenland coast; and (3) sea-run Arctic Charr grow considerably faster along the Atlantic coast of Labrador, in the Hudson Bay region, near Herschel Island, along the coast of western Greenland, and at Spitsbergen than they do in Frobisher Bay, Baffin Island. Grainger has pointed out also that those within a given age class may vary widely in size, irrespective of locality (*28*: 348). Fish of 600 mm, "for example, are found in all age groups between 13 and 24 winters." The over-all picture for the western North Atlantic area as a whole, and for Hudson Bay, is of a very long-lived and slow-growing fish, with the relationship between age and size averaging roughly as shown in Table VII.

Table VII. Approximate Average Lengths of 4- to 16-year-old *S. alpinus*

Age (years)	Fork Length (mm)	Age (years)	Fork Length (mm)
4.......	90–201	11	414–626
5.......	130–382	12	425–625
6.......	123–408	13	484–656
7.......	172–449	14	510–636
8.......	268–557	15	553–571
9.......	337–570	16	557–767
10.......	363–584		

Dahl's observation that such of the *alpinus* of Spitsbergen as run down to the sea after four years in fresh water grow larger than those that remain in fresh water for two or three years (Table VIII) suggests that the longer an *alpinus* is a parr, the more rapid is its subsequent growth in the sea.

The populations of *alpinus* that remain permanently in fresh water grow more slowly than those of the same region that go to sea. Sprules (*62*: 9), for example, has pointed out that landlocked *alpinus* in the northwestern Hudson Bay region average only about 12.3 inches and about nine ounces when ten years old, whereas the sea-run Arctic Charr of that same age average about 20.6 inches and 3.75 pounds. In western Greenland, similarly, the landlocked fish found above falls are smaller than those that are sea-run (*52*: 294; *39*: 74).

Table VIII. Lengths (mm) of Sea-run *S. alpinus* of Different Ages, as Related to the Number of Years Spent in Fresh Water Previous to their First Migration to Salt Water*

Years in sea	Age at First Migration 2 yrs.	3 yrs.	4 yrs.
2......	340	361	390
3......	—	377	403
4......	446	450	487
5......	516	538	570
6......	590	603	610

* After Dahl, *11*: 7.

Survival Rate and Longevity. The great majority of sea-run *alpinus* of northeastern Labrador are between 7+ and 12+ years old, with a pronounced peak at 8+ to 11+ years and a rapid falling off after 13+ years, as appears from Table IX. Also, the mean age (in years) of the samples studied showed an increase from south to north as follows: Adlok, 8.5; Nain, 8.9; Okkak, 10.2; Hebron, 10.5; Ramah, 10.5.

In Spitsbergen waters, according to Dahl, 84 ⁰/₀ of the fish examined were between about 4–6 years old and about 7–9 years old, including 2–4 years passed as parr in fresh water (*11*: 6); and an occasional fish had even spent as much as eight years in fresh water. In Frobisher Bay, Baffin Island, ac-

Table IX. Number of Arctic Charr of Different Ages among 487 Fish from the Coast of Labrador, Adlok to Ramah Combined†

Age (years)* ...	7+	8+	9*	10+	11+	12+	13+	14+	15+	16+
No. of fish.....	47	69	108	99	66	44	30	5	5	2
Percentages	10	14	22	20	14	9	6	1	1	0.3

† From Andrews and Lear, *2*: 849, tab. 3.

* Based on a study of the otoliths.

cording to Grainger's age determinations (*28*: 341), the great majority of 1,566 specimens measured during 1948, 1950, and 1951 were 300–350 and 650–695 mm long, with a few longer than 795 mm; these sizes correspond roughly to ages of 9–10 and 19–24 years, respectively, with a few somewhat older still. A similar picture emerges for the northwestern part of Hudson Bay, where only seven fish among 96, for which Sprules determined the ages, were less than seven years old whereas 70 % were between 8 and 11 years old (*62*: 6, tab. 1); and while the survival rate dropped off abruptly after 11 years, one of the specimens was 22 years old and weighed 16 pounds. Thus, the sea-run *alpinus* are not only much longer-lived than the sea-run *fontinalis* but their rate of survival is much higher.

Spawning and Reproduction. Spawning may take place either in streams or in lakes, at depths ranging from within a foot or two of the surface down to 15 feet or so. Sprules reported that, in lakes, the eggs are deposited on gravel beds in 6–15 feet of water (*62*: 12). In rivers they are laid in shallow pools below rapids in about two feet of water, where the current is strong and the bottom is covered mostly with "round stones just too large to be carried along by the water." Here the fish lie "apparently motionless, ... and ... return to the same places almost immediately after being frightened away" (Weed, *72*: 132). The females of the landlocked fish of Lake Windermere, England, have been described as making shallow depressions for the reception of their eggs in the gravel or stony bottom (Jackson *in 61*: 847), as other salmonids commonly do, but this habit has not been recorded for the sea-running populations.

Normally, *alpinus*, like *fontinalis*, spawn in fresh water, but Weed has written that "the fishermen along the Labrador coast believe that some of the sea trout spawn in the sea" (*72*: 132); and he reports the capture in salt water of females with free eggs in the oviducts. There seems to be no reason, however, to believe that any eggs would survive that might be deposited in salt water.

Arctic Charr have been described as spawning for the first time in Spitsbergen when they are 5+ years old (*11*: 8), in Icelandic waters probably at about 6 years (Saemundssen *in 28*: 363), and around Novaya Zemlya at 6 or 7 years of age (*79*: 69, 70), but not until about their 12th year or later in Frobisher Bay, Baffin Island (*28*: 363). Thus, if these estimations are even approximately correct, *alpinus* is very much slower than *fontinalis* in reaching sexual maturity (p. 531). It appears also from evidence assembled for Baffin Island by Grainger (*28*: 363) that spawning may not be a regular annual event for every adult, though it seems hardly likely to be a biennial one regularly, as has been suggested for Arctic Charr of Novaya Zemlya (*79*).

Labrador females of 465–665 mm contained 2,173–7,223 ovarian eggs in different stages of development, a western Greenland female of 520 mm contained 4,620 (*28*: 364; *39*: 69), and Novaya Zemlyan fish averaged about 3,500 eggs (*79*: 69–70). The eggs of freshwater Arctic Charr of Scandinavia are 4–5.5 mm in diameter. I have found no record of the size of naturally spawned eggs of the sea-run populations of *alpinus*.

Under hatchery conditions, incubation of the eggs of freshwater Arctic Charr has been found to occupy between 60–70 days at a temperature of 40°F (4.4°C) (*in 61*: 847). Eggs that were artificially fertilized at Baldernäs in Dalsland, Sweden, at the end of October did not begin to hatch until the beginning of the following March (Malm *in 61*: 847). In the northwestern Hudson Bay area "the eggs are still visible at break-up [of the ice] in the following spring, probably hatching soon after open water appears" (Sprules, *62*: 12).

Migrations. The migratory schedule of the sea-running populations of *alpinus* consists of a downstream movement early in summer out into brackish or salt water; a sojourn there until late summer or early autumn, during which time they make most of their year's growth; a return movement in late summer or early autumn to fresh water, with the immature fish participating as well as those that are maturing sexually; and a sojourn in fresh water until the following June or July, the early part of which covers the spawning period.

Arctic Charr of Frobisher Bay, Baffin Island, are reported as carrying out their first downstream migration after they have spent 5–7 winters in fresh water, those of Spitsbergen migrate after 2, 3, or 4 years, and those of Novaya Zemlya after 3 or 4 years. Those of northeastern Labrador, however, may descend after only 2 or 3 years to judge by the presence in the bays there of fish not more than three or four inches long, sometimes several miles away from the nearest spawning stream (*72*: 132).

The spawning migration into fresh water takes place between late July and the last half of September, according to locality, with the precise date governed to a considerable degree by the height of the water in the streams. Heavy rainfalls, for example, swell the streams so that Arctic Charr can ascend falls that would otherwise bar their passage, for they do not have the leaping powers of salmon and often are "stopped by falls with a vertical drop of not more than a foot" (Weed, *72*: 132). For this same reason also, their ascent is much easier during periods when the tides are at their highest (spring tides) than when they are at their lowest (neap tides).

Along Southhampton Island they congregate at the head of tide by late August, to ascend either with the first spring-tide period or during the first heavy rainfall, whichever comes the first. In Ungava Bay, in both the George River region and the Koksoak River, Arctic Charr enter fresh water by the latter part of July in most years and during the early part of August in others, with the height of the run lasting from eight to fifteen days (Turner *in 16*: 99, ftn.). In the vicinity of Nain, on the coast of northeastern Labrador, in the one year of record (1928), they had entered the streams by August. In the Sylvia Grinnell River, Frobisher Bay, Baffin Island, the mouth of which is barred to them by falls that are passible by fish only at the time of spring tides, the fish were ascending by the last week of July, in 1950; in 1948, however, few ascended until August. In western Greenland they have been described as ascending from late July through August until the streams freeze once more; in northeastern Greenland (Denmark Bay) the run continues from August until about mid-September, when the local rivers freeze; and the run covers about this same period in Novaya Zemlya.

It seems that the fish generally tend to continue upstream until they meet some obstacle that bars their further progress. In the larger streams or rivers this is likely to be the first waterfall; in many cases, however, the governing factor lies in the length of the stream in which they spawn. In western Greenland, for example, the narrowness of the ice-free belt limits the maximum distance of their upstream migrations to 25–30 miles. For more extreme cases it seems sufficient to refer the reader to Dunbar and Hildebrand's report of spawning fish taken in the lowest half mile of a stream tributary to the estuary of the George River (Ungava Bay, northern Quebec), beyond which further progress is barred by falls (*16*: 99); and to Weed's account of *alpinus* spawning about five miles up a brook tributary to Anatalek Bay, near Nain, Atlantic coast of northern Labrador (*72*: 131, 132). Turner, on the other hand, reported the presence of *alpinus* more than 110 miles up the Koksoak River, tributary to Ungava Bay, and farther still up a tributary of the Koksoak (*in 16*: 99, 100, ftn.)—if indeed the fish in question were *alpinus*, not Atlantic salmon, which run up the Koksoak regularly in considerable numbers (p. 476).

The descent to salt water usually takes place at about the time the river ice breaks. At Southhampton Island, northwestern Hudson Bay, for example, the descending fish have congregated within the mouth of Brooks River by the last part of June, and catches have been made in salt water nearby as early as July 8 in some years (e. g., 1934) but not until after July 15 in other years (*47*: 128, 129). In Frobisher Bay, Baffin Island, in 1951 (the only year of record), the river ice broke on June 10 and Arctic Charr were caught outside the mouth of the river in salt water shortly thereafter (*28*: 355). I find no definite information as to the date of the downstream migration for Labrador. Local ice conditions suggest, however, that it may fall at about the same time there as in Frobisher Bay, though in western Greenland the outlets of the freshwater lakes remain frozen until July, when there is a rush of *alpinus* to the sea (McMillan *in 32*: 1). Similarly, in northeastern Greenland, where the river ice persists late into the season, it was not until the first week of July that Johansen's nets, set in the outlet of a lake tributary to Denmark Harbor, took this species (*40*: 669). Arctic Charr in Novaya Zemlya are described as moving out into salt water during June and the first half of July (*79*: 69, 70).

It is not yet known whether every adult returns to fresh water to spawn every year, whether every fish that has spawned in a given autumn invariably returns to sea the following summer, or whether any of them winter in the sea with any regularity in any given locality.

The few accounts that have appeared concerning the distribution of *alpinus* while they are in salt water, based on their numerical distribution there, are unanimous to the effect that they remain for the most part close to the mouth of their native rivers, or at least within the bays into which these open. Perhaps the most definite evidence in this regard is Manning's observation that, while they are regularly caught at Igloolik Island, three miles off the mainland of Southampton Island, nortwestern Hudson Bay, none was caught "at Walrus Island, 30 miles off Southhampton Island, although a net was kept out there for a week in early August 1936" (*47*: 128). It seems well established, also, that their wanderings along shore are so brief that but little intermingling takes place between local populations. The supporting evidence for this is of two sorts: (1) the development of an intensive fishery has, in at least two documented instances, been followed within a few years by a precipitous decline in the number of fish taken; (2) it has been found by Andrews and Lear that the number of fin rays and of vertebrae average progressively higher from south to north along the northeastern Labrador coast (*2*: 854, tab. 8, 856, tab. 9, 860), which would not be the case if much intermingling took place between the populations that are produced in the various rivers along this stretch of coast.

Food. Sea-run Arctic Charr, like the closely related sea-run *fontinalis* (p. 536), feed on active organisms; to all intents and purposes this limits the diet to fishes smaller than themselves and to crustacea, supplemented on occasion by nereid worms. In Ungava Bay, for example, *alpinus* have been reported as feeding chiefly, if not exclusively, on the crustacean genera *Gammarus* and *Pseudaliprotus*, fish not having been mentioned at all (*16*: 100). On the coast of southern Spitsbergen also, large gammarids (*Gammarus locusta*) as well as mysid shrimps provide their chief sustenance, with fishes (capelin, small cottids, small liparids) of secondary importance (*11*: 8). Similarly, in Frobisher Bay, Baffin Island, the gammarid genera *Pseudaliprotus* and *Gammaracanthus*, together with liparids, were dominant items in their diet; among the 34 food species listed was a variety of small crustaceans (copepods, euphausiid shrimps, cladocerans, and decapod larvae), nereid worms, and fishes (such as *Eumicrotremus spinosus*, small cottids, liparids, launce, and *Boreogadus saida*, together with young of their own); even a few insects were included (*28*: 366, 367).

In Hudson Bay and along northeastern Labrador the recorded diet has been divided in varying proportion between fish (chiefly launce, *Lumpenus*, capelin, cottids, and *Cyclopterus*) and amphipods and euphausiids. Table x, showing the percentages of different items in the stomach contents, illustrates the variation to be expected from place to place.

Table X. Percentages, by Volume, of Different Species in the Stomach Contents of Arctic Charr Taken at Successive Localities from South to North along the Coast of Northeastern Labrador*

Locality	Fish			Amphipods and Euphausiids
	Capelin	Launce	Sculpins	
Adlok	88.0	3.0	0	0
Nain, specimen 1	75.2	10.7	0	13.5
Nain, specimen 2	15.0	12.7	61.2	11.1
Okkak Bay	99.3	0.2	0	0.5
Hebron	2.9	0.3	14.9	81.3
Ramah	3.9	13.5	24.7	56.2

* From Andrews and Lear, *2*: 858.

Finally, Yessipov's report (*79*: 69, 70) that the sea-run Arctic Charr of Novaya Zemlya, where 75 % of their food consists of crustaceans and worms, eat the young of the Atlantic cod (*Gadus morrhua*) in greater amount than any other fish is especially interesting, for young cod are not mentioned at all in any of the other diet lists that I have seen.

Parasites. Sea-run *alpinus* of northeastern Labrador have been reported as being heavily parasitized by the tapeworm *Eubothrium*, and lightly so by the round worm *Philomena* (*2*: 858, 859). It seems astonishing that none of the accounts of this species has mentioned any infestation by the so-called sea lice (parasitic copepods, genus *Lepeophtheirus*) that are so often found clinging to the sides of Atlantic salmon (p. 484) and sea-run brook trout (p. 537) when they re-enter fresh water.

Variations. Variations have been reported in the colors of sea-run *alpinus*, the size of the mouth, the length of the pectorals, the average number of vertebrae, the number of fin rays, and dentition. However, the relative degree of "silveryness" of the Arctic Charr caught during their marine sojourn together with the distinctness of their color pattern seems clearly to be associated with the relative salinity of the water where they are taken combined with the length of time since they last left fresh water. The difference in the relative length of the pectoral fins between sexually mature freshwater *alpinus* of Labrador (average 17–19 % of TL) and those taken in salt water (not in breeding condition) does not bear directly on the racial problem of saltwater fish (*3*: 290).

The south-to-north increase in the average number of both fin rays and vertebrae that has been reported for the coast of northeastern Labrador (*2*: 854–856) evidently is a function of latitude, a relationship paralleled among sundry other coastal fishes of boreal-Arctic waters; thus it is environmental, not genetic. The small-mouthed fish reported by Weed for the vicinity of Nain, Labrador (*72*: 131), doubtless represented the female portion of the population, the very large-mouthed ones "with strongly hooked jaws" the mature males. While the sea-run Arctic Charr from Collinson Point, Alaska (*70*: 258, fig. 14), included some that had an upper pattern of dentition that is generally characteristic of *Salvelinus* (p. 527, Fig. 127 A), others had a pattern characteristic of the genera *Hucho* and *Brachymystax* (pp. 458, 459, Fig. 127 B, C); in this case there can be no question of regional varieties, since both types were taken at the one locality.

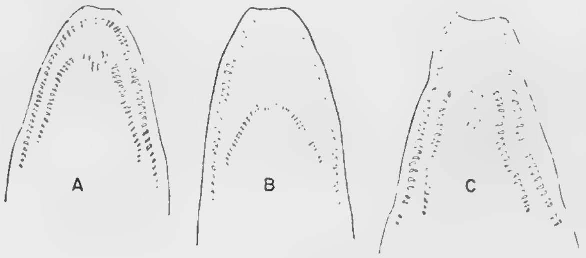

FIGURE 127. *Salvelinus alpinus* dentition.

In short, the regional differences reported thus far for the populations of sea-run *alpinus* do not seem either wide enough or consistent enough to justify their formal recognition in systematic nomenclature for *alpinus* anywhere between Novaya Zemlya in the east and northwestern Alaska in the west. Farther westward the typical *alpinus* is replaced, at least predominantly, by the red-spotted form *malma*, which probably does represent a separate subspecies (p. 519).[10] Neither has my own rather cursory examination brought to light any differences that seem taxonomically significant between my Spitsbergen, Greenland, and North American specimens of *alpinus* and others from Sakhalin Island, Gulf of Tartary, with which I have compared them.

Numerical Abundance and Relation to Man. Attention has been called repeatedly to the great abundance of the Arctic Charr off the stream mouths in Arctic America. The famous explorer, Capt. James C. Ross, reported in 1835 the capture of 3,378 fish ranging from 2 to 14 pounds in weight and averaging something more than 4 pounds, off a stream in the Boothia Peninsula (*58*: lvi, ftn.). Bryant described the "sea trout" similarly as being so numerous in Komaktorvik Bay, northern Labrador, that "you could almost walk across the rivers without wetting your feet.... They were only about one or two feet apart all over the shoal places" (Kendall, *44*: 503); and Welch has recently reported "incredible numbers" in the Sylvia Grinnell River, Frobisher Bay, Baffin Island (*73*: 14).

In northeastern Labrador, 264,000 pounds of salted fish were marketed in the Hopedale-Hebron district in 1948, and 224,620 pounds in 1953, corresponding to something like 62,000–71,000 fish if these averaged between three and four pounds each; and a single schooner took 79,200 pounds, or something like 20,000–26,000 fish, in Nachvak Bay between early July and mid-August in 1948 (*2*: 845). On the coast of western Greenland, in 1914, about 24,250 pounds of Arctic Charr, or about 6,000 fish if these averaged four pounds, were netted at the head of one of the fjords near Godthaab; and for Denmark Harbor, northeastern Greenland, they were described by Johansen as being so numerous that "as many as 50–100 could be taken in one net in one day" (*40*: 669).

It is no wonder that an excellent food, so abundant locally and so readily available close inshore, should be an important item in the economy of the native inhabitants, not only for human consumption but for dogfood as well. The reported catch, for example, averaged about 125,620 pounds (salted) for the Hopedale-Hebron section of Labrador for the 10-year period 1944–1954, with maximum catches of 264,000 pounds and 224,620 pounds in 1948 and 1953, respectively (*2*: 845). On the northwestern Hudson Bay coast, gill nets yielded an average of about 150 pounds per 100 yards at a locality about 150 miles north of the Churchill River (*62*: 2). A yearly commercial catch ranging between 100 and 800 barrels (2,200 and 176,000 pounds, assuming the weight of a barrel to have been 220 pounds) has been reported for western Greenland (*39*: 71). And Yessipov reported a yearly catch ranging between 14 and 80 Russian tons (*79*: 63), corresponding to 31,000–176,000 pounds,[11] for Novaya Zemlya.

Between Hopedale and Hebron as a whole, the local stock of Arctic Charr did not show any signs of depletion during the ten years covered by Andrews and Lear's report;

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[10] On the Arctic coast of Alaska, *malma* is reported from as far East as Point Hope and Cape Lisburne near 166°W (Evermann and Goldsborough, *21*: 264), nominally even from Herschel Island, Arctic Canada (139°W), but without supporting evidence as to identity.

[11] The Russian metric ton equals 2,204.6 pounds.

in fact, the average for the last four-year period (145,000 pounds) was more than twice that for the first four-year period (67,320 pounds). Andrews and Lear have pointed out, however, that the trend of production may not represent a corresponding trend in the numbers of fish, since the intensity of the fishery there depends on whether it is the more profitable to fish for cod or Arctic Charr (*2*: 845).

However this may be, the intensive exploitation of a more or less isolated stock has resulted in unmistakable depletion in two well-documented cases: in Nachvak Bay, northern Labrador, where the catch made by the same schooner decreased from 79,200 pounds during July-August of 1948 to 11,000 in 1950, when the project was abandoned (*2*: 845); and in western Greenland, where the catch at a certain cannery at Godthaab fell from 24,955 pounds in 1915 to 12,540 in 1917, when the cannery was closed (*39*: 72).

Although Arctic Charr may seem almost unbelievably plentiful when crowded together off the mouth of some stream, and while they may in fact be plentiful enough locally to withstand a moderate amount of fishing, it appears that the populations that are more or less isolated geographically cannot long withstand intense exploitation. "Even on the normal Eskimo scale of fishing, streams may become seriously depleted and require a rest for some years before their numbers are restored" (Dunbar and Hildebrand, *16*: 100). Dunbar has reached this same conclusion for those of Frobisher Bay, where, fortunately for the fish, many of the "charr streams were not touched at all by the Eskimo" (*15*: 178–190).

The catch of Arctic Charr is made chiefly in gill nets or in stake nets, close to the land in water only a few feet deep, and during the months when they are in the sea (p. 516). Some are also caught through the ice in winter while they are in fresh water, at least in the Hudson Bay region.

The sea-running Arctic Charr have not yet attracted the attention of anglers in general, nor are they likely to do so unless the Arctic-subarctic regions become more easily accessible; but visitors to the airfield at Frobisher Bay report having great sport with them there (*5*: 33; *73*: 4).

General Range. The *alpinus* species complex (freshwater and sea-running populations combined) is circumpolar and widespread in Arctic-subarctic regions, with isolated (doubtless relict) populations in some cold lakes far south of the boundary of their general range. Their area of more or less continuous occurrence in America embraces Arctic Canada and Arctic Alaska, and the Arctic Archipelago at least as far northward as Discovery Harbor, Grinnell Land, 82°34′N (*30*: 294, 295), which is the northernmost locality whence any salmonid has been reported. *S. alpinus* range southward along the Atlantic coast to the northern side of the Gulf of St. Lawrence, to eastern Newfoundland, and to both coasts of northern Hudson Bay; and along the Pacific coast to northern California. There are isolated populations also in many of the deep, cold lakes of Quebec, northern Maine, northern New Hampshire, and northern Vermont.

Arctic Charr occur around Greenland from the north coast down the west coast and up the northeast coast at least to 77° N. Their range also embraces Iceland, Spitsbergen, Bear Island, and Novaya Zemlya; northern Europe in general, including various alpine lakes southward to the British Isles, Austria, and Switzerland; the Arctic coast of Siberia, with outlying populations as far south as Lake Baikal; and the coastal belt of northeastern Asia southward to Kamchatka, the Sea of Okhotsk, Sakhalin, and northern Japan.

Occurrence of Sea-run Populations in the Western North Atlantic, with its Arctic Tributaries, in Hudson Bay, along Arctic Canada and Alaska, and in the northern North Pacific. The mouth of the Gander River on the coast of eastern Newfoundland is the southernmost point on the Atlantic coast where a sea-run population of *alpinus* is known to be established definitely.[12] In the northern side of the Gulf of St. Lawrence, Arctic Charr have been reported to occur as far west as Trinity River and Bay, tributary to the Saguenay River (*10*: 352–355, as *S. oquassa*; *18*: 185); and by common report, they occur generally off the river mouths thence eastward along the north shore, though they are so overshadowed there in public interest by the Atlantic salmon that precise information as to their local status is lacking. I have found no report of them for the west coast of Newfoundland, though here, as in the case of the east coast, I suspect that *alpinus* as well as *fontinalis* may be represented among the larger "sea trout" taken there.

Arctic Charr are recorded for the St. Mary's River, Hawke Harbor, and Domino Island along the southern part of the Atlantic coast of Labrador. Although the published record does not suggest that they are plentiful anywhere south of the region of Hamilton Inlet, Arctic Charr have been reported (or are represented in museum collections) for every locality farther northward whence saltwater fishes have been listed: along the Labrador coast in the vicinities of Mokovik Bay, Hopedale, Nain, Cape Mugford, the Okkak Islands, Hebron, Ramah, Nachvak and Komaktorvik fjords, and Ryans Bay near Cape Chidley; the recorded localities also include the Ungava Bay region, in general, including Port Burwell; Hudson Strait (reported for Nottingham Island and Wakeham Bay); and Foxe Basin on the coast of western Baffin Island as well as Frobisher Bay and Cumberland Sound on the east coast. Around Greenland, sea-run Arctic Charr are known to range northward to 77° N, at least on the east coast; to Etah (78°20′N) on the west coast (in fresh water to Inglefield Land, 79°); and even to the north coast, where a small specimen was taken by Lange Koch in 1917 (*39*: 68).

Sea-running populations of *alpinus* are similarly widespread around the coast of Hudson Bay southward as far as the vicinity of Great Whale River, in the east, and of Fort Churchill, in the west; Boothia Peninsula, Wallaston Peninsula, Victoria Island, and Herschel Island of Arctic Canada; Camden Bay, Point Barrow, and Collinson Point of Arctic Alaska; and various rivers of Arctic Canada and Arctic Alaska.

Along the northwest coast of America from the region of Cape Barrow southward to northern California, in salt water, *S. alpinus* is represented by a red-spotted

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[12] The color description on pp. 510, 511 is based on Gander River specimens.

charr, the so-called "Dolly Varden," which has commonly been ranked as a separate subspecies, *malma* Walbaum 1792 (pp. 519, 525). They range southward on the Asiatic side to Kamchatka, the Sea of Okhotsk, Sakhalin Island, and northern Japan.

Synonyms, with References for Sea-run Populations of Greenland and America westward to the International Boundary between Canada and Alaska:

Salmo alpinus Linnaeus, Syst. Nat., ed. 10, *1*, 1758: 309 (Lapland, alpine lakes, England); Fabricius, Fauna Groenl., 1780: 173 (descr., range as for *S. carpio* Fabricius, i. e. lakes, rivers, river mouths, Greenland); Johansen, Medd. Grønl., *45* (12), 1912: 668–694 (size, color, migr., season, abund. Denmark Harbor, ne. Greenland).

Salmo carpio Fabricius (not of Linnaeus, 1758), Fauna Groenl., 1780: 170 (detail. descr., diet, lakes, rivers, sea at river mouths, Greenland).

Salmo salar Pennant (not of Linnaeus, 1758), Arctic Zool., Introd., *1*, 1784: cxci (abund. along beaches, w. side Hudson Bay N. of Churchill R.; Arctic charr evidently mistaken for Atlantic salmon).

Salmo rossii Richardson *in* Ross, Narr. Second Voy.... North-west Passage, Append., Nat. Hist., Fish., 1835 (descr., abund., Boothia Penin., Arctic Canada); Fauna Boreal.-Amer., *3*, 1836: 163, pl. 80 (descr., color. ill., abund., Boothia Penin., Arctic Canada).

Salmo immaculatus Weiz (not of Storer, 1850), Proc. Boston Soc. nat. Hist., *10*, 1866: 274 (Hopedale, Labrador); Packard, Labrador Coast, 1891: 400 (Hopedale, Labrador).

Salmo stagnalis Garman (not of Linnaeus, 1780), 19th Rep. Comm. inl. Fish. Mass. (1884), 1885: 80, fig. 19 (descr., color, good ill., Godthaab, Greenland; in MCZ).

Salvelinus stagnalis Dresel, Proc. U.S. nat. Mus., *7*, 1885: 255–258 (descr., color, meas., Disco I., w. Greenland); Kendall, Proc. Portland Soc. nat. Hist., *2* (8), 1909: 228, 230, 231, 232, 234, 236 (early Labrador rec.); Proc. U.S. nat. Mus., *38*, 1911: 503–510 (color, meristic counts, discus. of ident. with Greenland and Ungava Bay populations, util., abund. Komaktorvik Bay, n. Labrador); Henn, Mem. Carnegie Mus., *12* (2 [3]), 1932: 1–2 (meas., Southampton I. specimen, migr., seasons, Greenland); Hildebrand, Medd. Grønl., *125* (1), 1939: 5 (e. Greenland locals.; also Foxe Basin and Melville Penin., Arctic Canada).

Salvelinus alpinus stagnalis Jordan and Evermann, Bull. U.S. nat. Mus., 47 (1), 1896: 510 (descr., refs., Greenland, Boothia Penin.).

Salvelinus umbla stagnalis Dahl, Skr. Svalb. Ishavet, *7*, 1926: 1–12 (age at first sea migr., growth, size at maturity, food, Spitsbergen).

Salvelinus alpinus Halkett, Bull. nat. Mus. Canada, *53* (Biol. Ser., 15), 1928: 117, 118 (abund. s. Baffin I., discus. subsp. *stagnalis*, *alipes*, *naresii*, *arcturus*, *oquassa*); Soper, Bull. nat. Mus. Canada, *53* (Biol. Ser., 15), 1928: 116 (s. Baffin I.); Dymond, Canad. Field Nat., *46*, 1932: 185 (n. shore Gulf of St. Lawrence); Vladykov, Contr. Canad. Biol., N.S. *8* (2), 1933: 19, 20, 39 (spawn. season, sizes, capture, util., Hudson Bay and Strait, consid. distinct from Greenland and Arctic forms); Weed, Copeia, 1934: 131–133 (size, migr., spawn., color, food, cf. *fontinalis*, ne. coast Labrador); Manning, Canad. Field Nat. (1942), *56*, 1943: 128–129 (season, habits, sizes, abund., fishery, Taverner Bay, w. Baffin I., Melville Penin., Arctic Canada, in fresh and salt water); Hinks, Fishes Manitoba, Dept. Mines nat. Resources, 1943: 24 (genl. range, habits, abund., max. size); Jensen, Spolia zool. Mus. Hauniensis, *9*, 1948: 67–78 (abund., local distr., w. and e. Greenland, color, size, secondary sex. chars., migr. schedule, util., fishery, cf. freshw. populations; discus. forms named by Fabricius, 1780; genl. range, growth rate cited from Hansen, Beretn. verdrør. Grønl. Styr., 1940 [1]: 362–363; not seen); Sprules, J. Fish. Res. Bd. Canada, *9* (1), 1952: 1–15 (sizes, growth rate to 22 years, dominant ages, migr., spawn. season, second. sex. chars., abund., fishery, w. coast Hudson Bay); Dunbar and Hildebrand, J. Fish. Res. Bd. Canada, *9* (2), 1952: 97–100 (sizes, fecund., diet at sea, extent and dates of upstream migr., spawn. season, fishery, Ungava Bay region, n. Labrador); Grainger, J. Fish. Res. Bd. Canada, *10* (6), 1953: 326–370 (fishery, descr., ills. of otoliths, age-length relation. based on otoliths, weights, growth rate for other locals., migr., egg sizes, fecund., diet, Frobisher Bay, Baffin I.; also list of sp. and subsp. names for *alpinus* species complex in Greenland, N. America, and n. Asia by ref. to Dymond and Vladykov, Proc. 5th Pacif. Sci. Congr., Canada [1933], Fish., 1934: 3741); Walters, Amer. Mus. Novit., 1643, 1953: 2 (food, color, persist. of parr marks, var. in dentition, Mould Bay, Prince Patrick I., Arctic Canada); Bull. nat. Mus. Canada (1951–1952), 128, 1953: 258, fig. 14, 260 (var. in dentition, Collinson Point, Alaska; Bernard Harbor, Arctic Canada;

locals. in Arctic Canada, Arctic Alaska); Andrews and Lear, J. Fish. Res. Bd. Canada, *13* (6), 1956: 843–860 (fishery, age determ., growth rate, sizes, meristic counts, color of flesh, diet, parasites, ne. Labrador).

Salvelinus rossii Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish. (1928), 2, 1930: 60 (in checklist, Greenland, Boothia Penin., refs.).

Salvelinus alpinus forma *stagnalis* Pfaff, Rep. 5th THULE Exped. (1921–1924), Zool. *2* (7), 1937: 1–3, 5, 6 (abund., Gore Bay, Fury and Hecla Strait, Canada; var. in length — maxillaries, pectorals; dentition).

Arctic Trout, Lowe, Rep. Dominion Exped.... NEPTUNE (1903–1904), 1906: 11 (abund., Cumberland Gulf, Baffin I.).

Synonyms for Freshwater Populations of Greenland and America westward to the International Boundary between Canada and Alaska:

Salmo stagnalis Fabricius, Fauna Groenl., 1780: 175 (detail. descr., remote mountain waters, not descending to sea, Greenland).

Salmo rivalis Fabricius, Fauna Groenl., 1780: 176 (brief descr., small streams, stagnant waters, not descending, Greenland).

Salmo alipes Richardson *in* Ross, Narr. Second Voy.... North-west Passage, Append., Nat. Hist., Fish., 1835: LVII (brief descr., abund., Boothia Penin., Arctic Canada); Fauna Boreal.-Amer., *3*, 1836: 169, pl. 81 (descr., color. ill., streams trib. to Prince Regent Inlet, Boothia Penin., Arctic Canada); Günther, Proc. zool. Soc. London, 1877: 476 (lakes near Discovery Bay, Grinnell Land, Arctic Canada).

Salmo nitidus Richardson *in* Ross, Narr. Second Voy.... North-west Passage, Append., Nat. Hist., Fish., 1835: LVII (brief descr., in lake, Boothia Penin., Arctic Canada); Fauna Boreal.-Amer., *3*, 1836: 171, pl. 82, fig. 1, pl. 86, fig. 2 (descr., color, color. ill., in lake, Boothia Penin., Arctic Canada).

Salmo oquassa Girard, Proc. Boston Soc. nat. Hist., *4*, 1854: 262 (type local., Oquassa or Oquossoc Lake; Rangeley Lakes region, Maine).

Salmo arcturus Günther, Proc. zool. Soc. London, 1877: 294, pl. 32 (descr., color. ill., Discovery Bay, Grinnell Land, Arctic Canada, near 87°30′N in fresh water).

Salmo naresii Günther, Proc. zool. Soc. London, 1877: 476 (descr., color, Discovery Bay, Arctic Canada).

Salvelinus aureolus Bean, Proc. U.S. nat. Mus. (1887), *10*, 1888: 628 (descr., meas., Sunapee Lake, New Hampshire).

Salmo (*Salvelinus*) *marstoni* Garman, Science, July 14, 1893: 23 (descr., color, type local. Lac de Marbré, Ottawa, Quebec; widespread, lakes of n. Quebec).

Salvelinus alpinus Jordan and Evermann, Bull. U.S. nat. Mus., 47 (1), 1896: 508 (descr., cold lakes, mountain streams, n. Europe and ne. Amer.; lists probable synon.).

Salvelinus alpinus alipes Jordan and Evermann, Bull. U.S. nat. Mus., 47 (1), 1896: 509 (descr., refs., lakes, Greenland, Boothia Penin.).

Salvelinus alpinus arcturus Jordan and Evermann, Bull. U.S. nat. Mus., 47 (1), 1896: 510 (descr. by ref. to Günther, 1877, see above; Victoria Lake, Floeberg beach, Discovery Bay, Grinnell Land, Arctic Canada).

Salvelinus alpinus aureolus Jordan and Evermann, Bull. U.S. nat. Mus., 47 (1), 1896: 511 (descr., discus., refs., lakes, n. New Hampshire and Maine).

Salvelinus oquassa Jordan and Evermann, Bull. U.S. nat. Mus., 47 (1), 1896: 514 (descr., refs., Rangeley Lakes, Maine).

Salvelinus oquassa naresii Jordan and Evermann, Bull. U.S. nat. Mus., 47 (1), 1896: 515 (descr., refs., lakes, Arctic Canada).

Salvelinus alpinus marstoni Jordan and Evermann, Bull. U.S. nat. Mus., 47 (1), 1896: 515 (descr., ref., Lac de Marbré, Quebec).

Salvelinus stagnalis Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish. (1928), 2, 1930: 60 (in checklist, refs., Greenland, Boothia and adj. regions).

Salvelinus arcturus Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish. (1928), 2, 1930: 61 (in checklist, ref., Arctic Amer., 82°34′N).

Salvelinus naresii Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish. (1928), 2, 1930: 61 (in checklist, lakes, Discovery Bay, Cumberland Gulf, Arctic Canada, ref.).

Salvelinus alpinus complex, Walters, Bull. Amer. Mus. nat. Hist., *106* (5), 1955: 274–275 (list. freshw. locals., Arctic Alaska).

Synonyms for the *alpinus* species complex of the Pacific Coast of North America westward to Japan:

Salmo malma Walbaum, P. Artedi Genera Pisc., Ichthyol., Emend., 3, 1792: 66 (Kamchatka, based on *malma* of Pennant).
Salmo curilus Pallas, Zoogr. Rosso-Asiat., *3*, 1831: 351 (Kurile Is.).
Salmo callaris Pallas, Zoogr. Rosso-Asiat., *3*, 1831: 353 (Bering Sea).
Salmo laevigatus Pallas, Zoogr. Rosso-Asiat., *3*, 1831: 385 (Kurile Is.).
Salmo nummifer Cuvier and Valenciennes, Hist. Nat. Poiss., *21*, 1848: 365 (Kamchatka).
Salmo erythrorynchos Cuvier and Valenciennes, Hist. Nat. Poiss., *21*, 1848: 366 (Kamchatka).
Salmo spectabilis Girard, Proc. Acad. nat. Sci. Philad. (1856), *8*, 1857: 218 (Fort Dalles, Oregon).
Salmo bairdii Suckley, Ann. N.Y. Lyc., *7*, 1861: 309 (Flat Head R. syst., Montana).
Salmo parkei Suckley, Ann. N.Y. Lyc., *7*, 1861: 309 (Kootenay R., B.C., Canada).
Salmo lordii Günther, Cat. Fish. Brit. Mus., *6*, 1866: 148 (Skagit R., Alaska).
Salmo pluvius Hillgendorf, Mitt. dtsch. Ges. Ostasiens, *11*, 1876: 26 (Japan).
Salvelinus spectabilis Jordan, Proc. U.S. nat. Mus. (1878), *1*, 1879: 79 (refs., in synop.).
Salvelinus bairdii Jordan, Proc. U.S. nat. Mus. (1878), *1*, 1879: 82 (in synop.).
Salvelinus malma Jordan and Gilbert, Bull. U.S. nat. Mus., *16*, 1882: 319 (in synop.); also many subsequent authors.

Salvelinus fontinalis (Mitchill) 1815

Brook Trout, Salter, Squaretail Trout, Sea Trout, Salmon Trout, White Sea Trout

Figure 128

Study Material. I. *Sea Run*: A total of 33 specimens: 11,[13] 46–150 mm TL, from the intertidal zone almost 200 feet below the high-water mark, near White Brook in the vicinity of Jonesport, Maine; 6, about 222–262 mm TL, 209–247 mm SL, from the Wilmot River estuary, south shore of Prince Edward Island;[14] 16, about 156–380 mm TL, from near the mouth of the Little River Codroy estuary, the west coast of Newfoundland.[15]

II. *Fresh Water*: about 300 specimens, large and small, from Labrador, Island of Anticosti, Nova Scotia, New Brunswick, Maine, New Hampshire, Massachusetts, New York, Pennsylvania, North Carolina, Georgia, Lake Superior, Wisconsin, North Dakota (introduced), and California (introduced); MCZ.

Distinctive Characters. The only fish for which sea-run *fontinalis* is likely to be mistaken are young *Salmo salar* (Atlantic salmon, p. 460); *Salmo gairdneri* (rainbow trout, p. 499), an introduced species from the west that seems to have established a sea-run population in the east; *Salmo trutta* (brown trout, p. 498), a second widely introduced species (from Europe) that is known to run down to salt water in Newfoundland;[16] or *Salvelinus alpinus* (Arctic charr, p. 507). And there is not much danger of confusion in any of these cases. Thus, the dark vermiculated markings on the dorsal and caudal fins of *fontinalis* and the conspicuously blunter head and broader pectorals

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[13] Received through the courtesy of Keith A. Havey, Maine Department of Fisheries and Game.

[14] Received through the kindness of the late A. H. Leim, and Marden Smith, Fisheries Research Board of Canada.

[15] Received through the kindness of W. Templeman and A. R. Murray, Fisheries Research Board of Canada.

[16] A few summers ago we saw (and handled) a brown trout that was found on the beach at Cohasset, Massachusetts. And a 6–7 pound fish, caught in Witless Bay, coast of eastern Newfoundland, in 1935, was identified as such by Harold Thompson (Frost, *24*: 13).

(cf. Figs. 128, 125) are enough to set it apart at a glance from *alpinus*. Its minute scales (large and conspicuous in *Salmo salar*) and the total lack of black markings on its sides distinguish it from *S. salar* of any size. Reliable field marks that distinguish it from both *Salmo gairdneri* and *S. trutta* are the minuteness of its scales and the restriction of the teeth on the roof of its mouth to a cluster in front of the vomer; in both *Salmo gairdneri* and *S. trutta* the teeth extend in a row rearward along the shaft of the bone. There should be no danger of confusing *fontinalis* with *Cristivomer namaycush* (lake trout), which has been reported occasionally as taken in brackish water in Hudson Bay, Ungava Bay, and along the coast of northeastern Labrador (*71*: 275; *3*: 295), for the caudal fin of *C. namaycush* is much more deeply forked than that of *fontinalis*, its head is noticeably narrower, and it has many more gastric caeca.

FIGURE 128. *Salvelinus fontinalis*, 236 mm, Little Codroy River, Newfoundland, MCZ 40006.

Description of Sea-run Specimens. Based on six fish, about 223 to about 262 mm TL and 209–247 mm (about 8.25 to about 9.75 in.) SL, from the Wilmot River Estuary, on the south coast of Prince Edward Island (p. 525), and on other available information.

TRUNK fusiform, its maximum thickness about 14–16 % of SL, its maximum depth about 19–23 %; the depth of trunk exclusive of head about 1.2–1.4 times greater than maximum thickness, the precise relationship depending on the relative fatness of a particular specimen; the dorsal profile weakly convex, the ventral profile anterior to anal fin only slightly more so, except in especially well-fed specimens or in sexually ripe individuals in which the sex organs have enlarged. Depth of CAUDAL PEDUNCLE about 10, about twice its thickness. SCALES present on body and tail sectors everywhere; head and fins naked; the scales rounded, entirely enclosed in skin, and so minute that they are likely to be overlooked; about 230 along the LATERAL LINE (reported).

HEAD about 23–25 % of SL, its dorsal profile weakly concave between perpendiculars at upper end of gill opening and posterior edge of eye in some specimens, but not appreciably so in others, thence increasingly convex forward. SNOUT 24–30 % of length of head, bluntly rounded. Tip of LOWER JAW almost even with tip of UPPER JAW, or extending very slightly beyond it; rear end of upper jaw reaching to a perpendicular that varies in position from only slightly behind rear edge of eye to behind eye by a distance about as long as eye or a little longer than eye. EYE 16–19 % of head, but much larger relatively in fingerlings, being 24 % in one 49 mm SL, its rear edge about 24–25 % of distance from the snout rearward to rear edge of gill cover. POSTORBITAL part of head 53–59 % of head. MOUTH moderately oblique. GILL RAKERS 4–8 on lower limb of first arch; 7–9 on upper limb (reported). BRANCHIOSTEGAL rays 9–12 (reported).

TEETH. Upper and lower jaw bones (premaxillaries, maxillaries, palatines, and dentary portion of mandibles) each with a single row of sharp, slightly recurved teeth of moderate size; also a patch on anterior end (head) of vomer on the midroof of mouth (none, however, rearward along shaft of vomer); a single row of smaller teeth around tip of tongue; also a patch of sharp but minute teeth in the pharyngeal region below, and two such patches above, side by side. No teeth on bones at base of tongue.

Rayed DORSAL fin rhomboid and with angular or slightly blunted corners, its base 50–60 % of length of head, its origin about midway (0.47–0.50) from tip of snout to caudal base, its longest ray 0.9–1.0 times as long as the base. ADIPOSE DORSAL fin shaped as in Fig. 128, the midpoint of its base about 60 % of distance from rear end of rayed dorsal base to origin of upper side of caudal. CAUDAL with upper and lower corners abruptly rounded, the rear contour weakly concave, varying from double-sinuous to uniformly arcuate, its breadth when widespread about twice the length of upper and lower margins. ANAL rhomboid, its anterior corner usually bluntly rounded, its posterior corner angular, its outer margin weakly concave, at least in most specimens (Fig. 128), its base 0.7–0.8 as long as dorsal base, its origin about midway between origin of lower side of caudal and a perpendicular at dorsal origin, its longest ray about as long as longest dorsal ray. PELVICS with midpoint of base at a perpendicular about under midpoint of dorsal base, the longest ray about as long as longest dorsal ray; the fleshy appendage beside base of pelvics conspicuous, about as long as eye. PECTORALS with shape, when well spread, as shown in Fig. 128, the origin a little anterior to rear edge of gill cover, the longest ray a little shorter than the longest dorsal ray.

FIN RAYS: dorsal 11–14 reported, anal 9–12 for Moser River Salters (Table XI).

VERTEBRAE 58–62 reported; average 59.5. PYLORIC CAECA, average 38.4 reported.

Color. On *fontinalis* from fresh water, the back and upper part of the sides are some shade of olive, conspicuously marbled with paler and darker markings; the lower part of the sides is marked with many pale yellowish spots interspersed with a smaller number of vermillion dots encircled (typically) with blue. The lower surface varies from grayish blue through shades of pale orange and a fleshy color (reddening at spawning time) with a narrow white midline. The dorsal fin is a paler olive than the back, with coarse blackish vermiculations. The caudal is a darker olive (reddening more or less at spawning time) with darker wavy crossbars, especially on the upper and lower corners. The pectorals, pelvics, and anal are some shade of pink, orange, or crimson, the pectorals and pelvics dusky; the first ray of the pectorals, pelvics, and anal is white or cream-colored, conspicuously edged rearward with black. Fingerlings up to 5 or 6 inches or so are more or less conspicuously marked on the sides with a series of 7–11 (av. 9) dark, vaguely outlined crossbars or blotches, known as "parr marks."

Table XI. Dorsal and Anal Rays of *S. fontinalis**

No. of rays	9	10	11	12	13	14
Dorsal, no. of specimens	—	—	40	120	50	1
Anal, no. of specimens	1	47	123	38	—	—

* After Wilder, *78*: 186, tab. 8.

The young Brook Trout that are destined to move out into salt water cannot be distinguished at first by their color from those that are to remain in fresh water. This continues true in some localities until after they have actually left the stream mouths, for example on the coast of eastern Maine (see *Study Material*, p. 525). In other localities, however, as in the Moser River, Nova Scotia, the sides of the future Salters, now known as "smolts" in conformance with salmon nomenclature, have turned partially silvery, through the deposition of guanin crystals, by the time they are ready to migrate downstream, although they still show their parr marks. It seems that this difference in color between different populations is associated with the age at which they move out into brackish water, for while some of the Maine Salters (p. 525) do this as early as their first summer, and many by their second summer, the smallest sea-run Moser River fish were in their third summer. In any case, the development of the Salter coloration evidently is a reversible process, for Wilder found that Moser River smolts whose sides had already turned partially silvery lost the silver if they were retained in fresh water (*78*: 173).

After the Brook Trout move out into brackish or salt water, their sides tend to become increasingly silvery, the greenish-blue-to-bottle-green marbling of their upper parts becomes obscured, their bellies become paler, and their pectoral, pelvic, and anal fins lose color. In extreme cases, their sides may turn as silvery as those of Atlantic salmon, with the pale yellow spots and crimson dots showing only faintly and the marblings hardly visible. Their pelvic and anal fins are white, perhaps faintly tinged with pink, and show no trace whatsoever of the black edging on the first ray that is so conspicuous on freshwater fish. But the dark wavy markings on the dorsal fin and on the upper part of the caudal continue to be conspicuous.

The published descriptions of the color of sea-run *fontinalis* have in most cases been based on specimens of this sort, but the individual Salters may vary widely in color, even though caught side by side. One of the Prince Edward Island specimens listed above is pale (Fig. 128), although its sides, after preservation in formalin, now show no trace of silver. On another, however, the back and the upper part of the sides are much darker, the marblings, pale spots, and crimson dots are much more evident, as are the dark markings on the dorsal and caudal fins, the lower part of the sides is gray, and the first ray of the pectoral, pelvic, and anal fins is outlined as conspicuously rearward with black as it is in freshwater specimens. The four other Prince Edward Island specimens are intermediate in coloration between these extremes. But none of the Newfoundland specimens (see *Study Material*, p. 525) approaches the extreme sea-run coloration, though they were taken only one mile upstream from where the river empties into the open Gulf of St. Lawrence.[17]

It seems, as Smith remarked a century and a quarter ago (*60*: 354, 355), that the most silvery of the Salters are the ones that pass their marine sojourn in the saltiest water and are taken soon after they leave the stream mouths, whereas the least silvery are those that remain within the estuaries, where the water is more or less brackish.

When the Salters re-enter fresh water, the back and the upper sides soon darken, the silver of the sides fades out, the pale spots on the sides become more intensely orange, the pectoral, pelvic, and anal fins gradually assume the white-black and orange-to-reddish pattern typical of the freshwater fish, the pure white on the lower part of the sides develops a pinkish band in the males, and the belly tends to become gray. Brook Trout fresh-run from the estuary that were contained in pens in the Moser River underwent this alteration between July 15 and September 10, by which date "it was impossible to distinguish sea and fresh water trout by color" (Wilder, *78*: 174). And the Salters of Cape Cod may lose their sea coloring within 10–14 days after they re-enter fresh water (*9*: 8).

Size. Brook Trout are about 14 or 15 mm (0.56 in.) long when hatched, and there is no reason to suppose that *fontinalis* fry destined to run down into salt water differ in size at hatching from those that are destined to spend their life in fresh water. Two or three years later, when they migrate downstream, the Salters average about 175 mm in length (6.9 in.) in Nova Scotian waters, and about 178 mm (7 in.) on the coast of western Newfoundland,[18] a growth rate that agrees closely with 6.5 inches at two years and about 8 inches at three years as reported for hatchery fish (perhaps more abundantly fed) at Caledonia Springs Hatchery, New York (*29*: 312).

The maximum size to which *fontinalis* grow in fresh water varies from one stream to another and from one pond or lake to another, even within short distances. A 1.5-pound fish, generally speaking, is a large one in any small water, and a 5-pound fish is a large one in most of the larger waters. In some northern streams, however, and in northern lakes, many of them grow far larger than that. Goode *et al.*, for example, mention one of 11 pounds that was received by Louis Agassiz from the Androscoggin River in northwestern Maine in 1860, and a Rangeley Lakes fish that weighed 10 pounds after it had been in captivity for three years (*26*: 499, 500). Kendall found records of more than 60 fish heavier than 9 pounds, 15 of 10–11 pounds, and 4 of 12–12.5 pounds, which had been taken at one time or another in the Rangeley Lakes, Maine (*45*: 90–95); he also reported one of 11 pounds for Belgrade Lake, Maine, and one of ten pounds for Square Lake, Maine. The record (weighed) weight is 14 pounds 8 ounces, for one caught July 1916 by J. W. Cook in the Nipigon River, tributary to the north shore of Lake Superior, where Hewitt (*34*: 170) also took one 26 inches

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[17] Information contributed by A. R. Murray, Fisheries Research Board of Canada.

[18] Ibid.

long having a girth of 20 inches; this fish must have weighed close to 13 pounds, as calculated by the accepted formula $W = (L\,G^3)/1000$, where W equals weight in ounces, L the length in inches from eye to base of caudal fin, and G^3 the cube of the girth in inches. Dunbar and Hildebrand's report (*16*: 95, 96) of "speckled trout" weighing up to ten pounds, taken near Fort Chimo, northern Labrador (Ungava Bay), shows furthermore that *fontinalis* may grow equally large right up to the northernmost limit of their geographic range.

Sea-run *fontinalis* in general grow larger than those that remain in fresh water; not very much larger, however, except in situations where the growth rate of the freshwater fish is low. On the south shore of Cape Cod, for example, where few of the native fish that remain in fresh water are heavier than 0.5–0.75 pound, the largest sea-run fish reported by Smith (in 1833) among many hundreds were one of 2.5 pounds, two that weighed close to 3 pounds each, and three that together weighed 8.25 pounds (*60*: 353). The largest, taken at the mouth of a privately owned brook tributary to Buzzards Bay, where a continuous record has been kept since 1870, weighed 3.75 pounds, and the largest recently taken there was 2.75 pounds (information contributed by C. P. Lyman). Rumors of 5-pound Salters on Cape Cod or on Long Island, New York, seem not to have been supported by concrete evidence.

The average for the largest ten Salters from the Moser River, Nova Scotia, measured by Wilder (*78*: 189, tab. 10, 191), was close to 15 inches (381 mm) and 13.4 ounces (381 g), whereas the average for the largest ten freshwater specimens was only 11.12 inches (282 mm) and 12 ounces (340 g); and one Salter of 18.7 inches (about 476 mm), which must have weighed close to three pounds, has been reported for the Moser River (*9*: tab. 1). The heaviest that has been reported to me for the waters of Nova Scotia was eight pounds.[19] On the other hand, no sea-run fish longer than ten inches were seen off the mouth of a small brook in eastern Maine, where a special study of them was carried out by Charles F. Ritzi,[20] though conditions in the marine environment there would seem to be favorable for growth to a large size.

Available evidence suggests that the Salters may average somewhat larger along the southern side of the Gulf of St. Lawrence than in Nova Scotian waters, for Goode *et al.* described them as usually weighing "two and one-half pounds," adding that "they are not seldom caught as heavy as six or eight" (*26*: 499). This accords with Perley's description of catching five-pounders himself on the north shore of Prince Edward Island (*51*: 132) and with W. P. Templeman's report of *Salvelinus* weighing up to eight pounds in the Bay of Chaleur (letter). A Brook Trout weighing six pounds was taken in Grand River Codroy, west coast of Newfoundland, by Sir Bryan Leighton in 1904 (*48*: 81), and fish of seven or eight pounds have been reported for West Brook, some 15 miles north of Bonne Bay, Newfoundland (*50*: 24), if these were not Arctic charr (p. 521). However, catches of 33 fish averaging 3.3 pounds off the mouth of Grandys Brook near the Bureo Islands on the coast of southwestern Newfoundland (*48*: 68)

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[19] Unsigned statement received in reply to an inquiry as to the status of sea-run *fontinalis* in Nova Scotian waters.

[20] Information contributed by Charles F. Ritzi.

Table XII. Average Total Lengths† of Sea-run and Freshwater Brook Trout of the Moser River in Five Seasons, May 18–August 4.* In Parentheses, Number of Fish Examined

Seasons	3rd	4th	5th	6th	7th
Sea-run trout (mm)	213	262	290	354	420
Sea-run trout (in.)	8 3/8	10 5/16	11 7/16	14	16 9/16
	(94)	(103)	(307)	(7)	(1)
Freshwater trout (mm)	164	189	237	296	
Freshwater trout (in.)	6	7 9/16	9 5/6	11 3/16	
	(51)	(123)	(46)	(2)	

† Standard lengths converted to total lengths by the addition of 6 %, a conversion factor determined from the Prince Edward Island Salters listed (p. 525).

* After Wilder, *78*: 191, tab. 11.

and of many of 3–3.5 pounds in Newman's Sound on the eastern coast (*34*: 4) are more nearly representative of the largest Salters that are commonly taken in Newfoundland waters, where the great majority are nearer one pound.

Salters "up to 7 and 10 pounds" are often taken along the Atlantic coast of Labrador (*48*: 68), but some of these "outsize" fish may have been Arctic charr (p. 521). At any rate, it seems that the Labrador Salters do not average any larger than the Nova Scotian fish, for those caught along the southern section of Labrador "usually run from one pound to four pounds in weight."[21] Those reported as being taken near Nain (about 56°30′N) weigh up to only about two pounds (*72*: 130), while Arctic charr there weigh up to 8–10 pounds or more. Even the largest sea-run *fontinalis* that have ever been weighed anywhere, or reliably reported, have fallen far short of the largest of the freshwater *fontinalis* from various Maine and Canadian waters (p. 529).

Rate of Growth. In the Mashpee River, on the south shore of Cape Cod, the Salters average about 7.4 inches (188 mm) TL in their second season, about 8.8 inches (223 mm) in their third season, about 9.9 inches (249 mm) in their fourth season, and about 12.3 inches (312 mm) in their fifth (*9*: tab. 1). The average lengths at corresponding ages for Salters of the Moser River, Nova Scotia, are about the same as these, as appears from Table XII, based on Wilder's observations (*78*: 191, tab. 11); and a yearly increment of 1.4 inches, reported for the fish that sojourned the longest in the sea off the coast of eastern Maine, is of this same order of magnitude. Table XII tends to support the general view that the Salters grow somewhat faster than the freshwater *fontinalis* in the same stream.

Survival Rate. Information about the rate of survival for sea-going *fontinalis* in different localities shows that only 127 (10.4 %) of the 1,220 Salters marked in the Moser River system were retaken in the traps there on their return from the sea, with the percentage greater for those larger than 220 mm (31–35 %) than for smolts of 180–205 mm (8.5 %); and it seems that the yearly mortality for sea-run *fontinalis* is about the same on the coast of eastern Maine, where few survive for more than three

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[21] Information from Newfoundland Ranger S. M. Christian.

growing seasons. Wilder's data show that the survival rate declines abruptly for both Salters and nonmigratory fish of the Moser after they pass their fourth season and that very few of either survive for as long as six years (*78*), though it is known that an occasional *fontinalis* may survive into its eighth year elsewhere (*9*: 14).

Spawning and Reproduction. The migratory populations of *S. fontinalis*, like the nonmigratory fish, spawn exclusively in fresh water in autumn at temperatures ranging from about 49°F (9.4°C) down to about 40°F (4.4°C). In general, spawning by *fontinalis* takes place earlier in the season to the north than to the south, but the precise spawning period at any particular locality is governed by the rapidity with which the water cools with the onset of autumn rather than by the latitude. Brook Trout spawn from mid-October until early December on Cape Cod (probably), from mid-October on into December to the north in New Hampshire (*26*: 499), from mid-October into November in the Rangeley region of Maine (*45*: 84), from late October through December into January (exceptionally into February) on Prince Edward Island (*74*: 356, 357), during October in the Moser River, Nova Scotia (*75*: 185), and from mid-October to middle or late November on the coast of eastern Newfoundland (*24*: 8). In shallow, rocky streams, however, in the Maritime Provinces of Canada, where the water chills very rapidly, they may commence to spawn as soon as late September (*74*: 356, 357). Hence the spawning dates given by Vladykov for the high-lying Laurentide Park lakes, north of Quebec City (*68*: 800), probably are not applicable to the coastal streams along the north shore of the Gulf, where it is more likely that *fontinalis* spawn from mid-October to mid-December, as they do in southern Ontario (*57*: 99). No information is available in this regard for the outer coast of Labrador. Along the southern shoreline of Ungava Bay, however, "it is probable that spawning takes place in September or October," to judge from the state of the gonads (Dunbar and Hildebrand, *16*: 96).

S. fontinalis, like *Salmo salar*, spawn on bottoms of sand or gravel in shallow water, in streams, ponds, or lakes, where either the current or the inflow from some spring keeps the eggs clear of detritus. Here the females smooth out a shallow depression (the so-called redd) into which the eggs settle with the milt from the attendant male, and immediately after the spawning act, the eggs are covered with gravel. The eggs, averaging about $^3/_{16}$ of an inch (about 5 mm) in diameter, do not hatch until the following April or May, the precise date depending on the temperature of the water; 53°F (11.7°C) is about the upper limit for their development (*19*: 281–289); and the eggs develop normally in water as cold as 35°F (1.7°C). The fry, about 0.5 inch (14 or 15 mm) long at hatching, carry a large yolk sac at first, as do species of all the Salmonidae; and they tend to remain close to the redd until they have grown to a length of 1.5–2.0 inches (about 38–50 mm).

Some of the sea-going *fontinalis* of the Moser—probably this is true of the majority—spawn in the autumn of the same year in which they make their first migration to the sea. Others, like young Atlantic salmon (grilse), do not spawn until the second autumn following their original descent to salt water.

Nonmigratory *fontinalis* ordinarily spawn every year once they have reached sexual maturity, but it seems that some of the Salters do not, for the upstream runs, at least in the Moser River, Nova Scotia, include some large fish that show no signs either of approaching sexual maturity or of having spawned during the previous autumn (*75*: 179). It appears, too, that some of the mature Salters may occasionally remain in fresh water throughout an entire twelve-month period (*78*: 195); hence it would not be astonishing if some of them fail to run up into fresh water at all in some years.

It appears that the majority of the Moser River Salters spawn three or four times during their life and that a few may do so five or even six times, assuming that they spawn every year (which some do not) and that they continue fecund throughout their life (which they may not), all of which probably applies to populations of Salters elsewhere.

Habitat and Migrations. In the Moser River, Nova Scotia, about 79 % of the smolt carry out the initial downstream migration in the second spring when they average about 170 mm TL, and the remainder in their third spring (*75*: 179); this applies also to Brook Trout artificially stocked in Cape Cod waters (*49*: 10). On the coast of eastern Maine, however, some move out into salt water in their first spring, when they are only about 46–52 mm or 1.75–2.0 inches long (see *Study Material*, p. 525); Weed has reported similarly that in northern Labrador, in the vicinity of Nain, "many go down to the edge of salt water on the tidal flats during their first or second summer" (*72*: 130).

The migratory schedule of the sea-running *fontinalis*, after their initial descent to brackish or salt water, consists of an upstream migration in late spring or summer by fish destined to spawn that autumn as well as by smaller immature fish, and, after the spawning season, of a downstream migration by smolts, immature larger fish, and kelts (spent fish) to brackish or salt water, where the kelts recover condition during the winter.

The upstream run by the fat fish takes place from late May through June on Cape Cod, with a few entering in September and perhaps even as late as November.[22] On the coast of eastern Maine, the principal run is from May until early August, with some irregular movement to and fro in the autumn;[23] in Nova Scotian waters, as illustrated by the Moser River, the chief run is from about mid-June into August, as in 1939 when 93 % of the run there was in July (*75*: 178, 179).

The Salters appear along the shore during July in the Mira River district of Cape Breton (Breck, *8*: 97), and at about this same time they are running upstream in force in the estuary of the Little River Codroy, Newfoundland.[24] But along the southern sector of the outer Labrador coast (according to Blair, ftn. 26) they are moving upstream in September. Large runs of *fontinalis* are recorded for July and August

[22] Mullan (*49*: 11) has mentioned a probable instance of upstream migration in the Mashpee River in November.
[23] Information contributed by Charles F. Ritzi.
[24] Information contributed by A. R. Murray, Fisheries Research Board of Canada.

for Hamilton Inlet and Sandwich Bay on the outer coast of Labrador (*3*: 294), and the seasonal schedule is about the same as this near Nain (about 56°30′N), where "brook trout weighing up to almost two pounds are found in the sea from the time when the ice goes out early in June" (Weed, *72*: 130).

On Cape Cod, Massachusetts, the return migration downstream takes place soon after the spawning season has ended; i. e. in November and December, perhaps commencing even in October (*7*: 140; *6*: 121; *9*: 26); and seemingly the seasonal schedule is similar to this in the western side of Hudson Bay where Doan has observed that the spent fish apparently winter in the estuaries of the large rivers and then cruise along the coast (*13*: 6).

On the coast of eastern Maine, however, and to the north in general, the great majority of the kelts and smolts, with the immature fish that have run up during the previous summer, spend the winter in fresh water. The principal downstream movement by the Brook Trout takes place the following spring; for example, in the Moser River, Nova Scotia, the smolts move down in April and May and the kelts do so until well into June when the temperature of the water has risen to 64°–65° F or 18° C (*76*). On the coast of western Newfoundland, as represented by the Little River Codroy, the chief downstream run "begins in late April or early May, to cease around mid-June,"[25] although it is preceded by some movement "down the estuary as early as January and February" (Weed, *72*: 130). While they have been reported by P. S. Martin as being in salt water from November on along the north shore of Prince Edward Island (as they are on Cape Cod also), they enter the sea around the middle of May[26] in the southern section of Labrador; and it is not until early June when the river ice opens that they are found in the sea in the vicinity of Nain, northern Labrador (*72*: 130). Thus the annual sojourn in the marine environment (as determined by tagging experiments) is usually 30–60 days on the coast of eastern Maine, with the recorded maximum 106 days and the minimum 1–5 days; the average is 65 days for the larger of the Moser River fish and 71 days for the smolts (*76*: 263). In northern Labrador they are in salt water from early June to late summer, but precise dates have not been given.

Since mature sea-running fish eat very little while they are in fresh water, the feeding period throughout the northern part of their geographic range is thus condensed within only a little more than two months out of the twelve. While they may sojourn in salt water for as much as six months (November to June) in the southernmost part of their range (Cape Cod), the period during which they feed actively probably is no longer there than it is in Nova Scotia—perhaps not so long—for the surface temperature in the bays and estuaries of Cape Cod where they winter usually continues below 40° F from sometime in December until mid-April (*23*: figs. 4, 5 [100]), with the water usually chilling to within a degree or two of the freezing point of salt water during

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[25] Information based on the results of tagging, contributed by A. R. Murray, Fisheries Research Board of Canada.

[26] Information from W. A. Blair, in charge of Salmon investigations for Newfoundland.

January and February and with ice forming in greater or lesser amounts during the coldest part of the winter.

Wanderings in Salt Water. The movements of the Salters after they have dropped downstream to the head of tide vary widely from place to place. At the one extreme, as was formerly illustrated along the southern shore of Cape Cod and is illustrated today by the estuary of the Little River Codroy on the coast of western Newfoundland and by the Wilmot River estuary on the south shore of Prince Edward Island, many Brook Trout (perhaps a majority) may remain with the river influence during the entire interval between their downstream and upstream runs. At the opposite extreme, they may leave the mouths of the rivers, even within the first days after the ice has broken, so that nets set a mile or two offshore will catch more of them than nets set near river mouths; this is the case in the Moser River, Nova Scotia (*75*: 180), and off the southern part of the outer coast of Labrador.[27] We suspect that regional variation in the available food supply rather than the saltiness of the water is the determining factor here, for *fontinalis* in splendid condition are caught in distinctly brackish water as well as in water of salinity characteristic of the open coast nearby.

In any case, sea-run Brook Trout tend to hold very close to the immediate coastline and to water only a few feet deep. Along the south shore of Cape Cod, for example, in the days when Salters were caught there in large numbers, they were taken chiefly in the salt creeks and in the estuaries into which these open, not far out in the bays. Off the Moser River, Nova Scotia, they are seen similarly "in schools in water five to ten feet deep (1.5 to 3 m) around the inner islands and also around some of the small private wharves . . . when lobster pots are brought in and cleaned, or when fish are being dressed," with those of different sizes tending to school separately (White, *77*: 471, 472). They are also found indifferently along sandy beaches, over muddy bottom, and around rocky shores.

The only precise information as to how far offshore they are to be found regularly is that they are taken in drift nets set for Atlantic salmon over the shoals in the Bay of Chaleur,[28] and that they are caught on hook-and-line as much as seven or eight miles offshore, in the western side of Hudson Bay off the Nelson River (*13*: 6). How much farther out to sea they may stray occasionally is anyone's guess.

The most extensive journey along shore that has been reported so far for any of the many Brook Trout marked either in the Moser River, Nova Scotia (*77*: 471), or on the south shore of Cape Cod has been eight miles (*49*: 10); in both cases the fish in question were recaptured in streams other than the ones where they had been marked. For Salters to reach Woods Hole on the southern coast of Massachusetts, as they sometimes do, does not require a swim of more than seven or eight miles from the nearest home stream. On the southern part of the outer coast of Labrador, however, *fontinalis* have been caught in nets set on headlands ten miles away from the nearest river where Salters have been taken.[27] Furthermore, during the period when Salters

[27] Information from Newfoundland Ranger S. M. Christian.

[28] Information contributed by W. P. Templeman.

would ordinarily remain in salt water, or at least in brackish water, they may return temporarily to the stream mouth in pursuit of prey. Thus they re-enter the Fox Island River, Newfoundland, in June and July, apparently to feed on the smelt that spawn there, and return to the sea afterwards with the spent smelt;[29] also, Brook Trout that have wintered in the sea revisit the Dunk River on the north shore of Prince Edward Island in April, or a little afterwards, when the smelt enter the brooks to spawn.[30]

Relation to Temperature. S. fontinalis feed most actively at temperatures of about 45°–65° F (7.2°–18.3° C); they do not thrive in water warmer than 68° F (20° C); and they cannot long survive a temperature higher than about 70° F (21.1° C) unless the water is especially well aerated, when they can withstand 75° F (23.9° C) for a short time. At the other extreme, they become inactive and refuse food if the temperature falls much below about 38° F (2° C), which accords with White's observation that the annual downstream movement of *fontinalis* in the Moser River system is interrupted if the temperature of the water temporarily falls that low (*76*: 260, fig. 2).

Food. The diet of the fingerling Salters is the same while they are in fresh water as that of their nonmigratory relatives; i. e. chiefly the aquatic stages of various insects such as midges (chironomids), caddis flies (Trichoptera), May flies (Ephemeridae), and black flies (Simulidae). They also eat snails and freshwater gammarid crustaceans if these are available, besides terrestrial insects that may fall into the water.

During their sojourn in brackish or salt water they feed chiefly on small fishes, of whatever kinds are the most easily available locally, or on small crustaceans. Evermann, for example, found Brook Trout in the tidal waters of Casco Bay, Maine, "gorged with young eels of the translucent stage" (*20*: 105). The diet list reported for Salters of the Moser River includes young eels, young hake (*Urophycis*), young searavens (*Hemitripterus*), killifishes (*Fundulus*), rock eels (*Pholis*), sticklebacks (*Gasterosteus*), and alewife fry (*Pomolobus*); and smelts (*Osmerus*) as well as silversides (*Menidia*) have been reported as being eaten by them at Prince Edward Island (*75*: 184; *77*: 472). They feed greedily on decapod shrimps, amphipods, and isopods, which, together with *Fundulus*, are their chief food in the Cape Cod region. Weed (*72*: 130) has written that Salters caught in the bays of Labrador had their stomachs crammed with beach fleas (*Gammarus*). Others had been feeding on the tiny swimming larvae of the rock crab (*Cancer*). And they have been found gorged with sea worms (*Nereis*) at Prince Edward Island.

They eat very little, if anything, however, after they re-enter fresh water, probably because of the scarcity there of prey of the sizes to which they have become accustomed in salt water. And it is likely that such of the spent fish as winter in fresh water (p. 534) continue on starvation rations, if they feed at all, until they move down again to the head of tide in the spring.

Predators and Parasites. The smaller Salters are preyed upon, no doubt, by the larger predaceous fishes, such as eels, striped bass (*Roccus saxatilis*), pollock (*Pollachius*

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[29] Information contributed by W. P. Templeman.

[30] Information contributed by P. S. Martin.

virens), silver hake (*Merluccius bilinearis*), and perhaps spiny dogfish (*Squalus acanthias*), and by cormorants and gannets. The larger Salters are so active that they are not likely to suffer seriously from these predators, but seals doubtless take a toll of them. During their sojourn in fresh water they suffer from attacks by herons and eels, as shown by the scars sometimes seen on their sides (*75*: 182); mink and otter are also potential enemies.

N. C. White has contributed the information that when the Salters re-enter the streams they are heavily infested with sea lice (parasitic copepods, genus *Lepeophtheirus*) similar to those that infest fresh-run Atlantic salmon, but these drop off soon after the fish have entered fresh water.

Variations. Anglers have long been aware that the populations of *fontinalis* in different lakes, ponds, and streams differ widely in color, relative size of head, depth of body, size at maturity, and maximum size of growth. Hatchery experience, however, has proven that the rate of growth depends primarily on the supply of food available to each individual fish combined with the yearly duration of the season when the water is neither too cold nor too warm for them to feed actively.

Fat *fontinalis* are clearly deeper-bodied than lean ones, and Ricker has pointed out that the maximum size to which *fontinalis* grow seems correlated with the size of the body of water in which they live, and with the presence of suitable large food, i. e. fish or crayfish (*57*: 73). These generalizations find their expression in the large sizes to which they tend to grow in large streams and lakes in the northern part of their range, contrasted with the stunted but overplentiful populations that inhabit many of the smaller mountain streams of southern North Carolina and northern Georgia, where *fontinalis* "rarely pass the dimensions of fingerlings" (Jordan, *41*: 112) though they are self-sustaining. Also it seems from casual firsthand observation that the heads average larger, relatively, among the slow-growing populations than among fast-growing fish, quite apart from sexual dimorphism.

In general, *fontinalis* average paler when living over a pale sandy bottom in brightly illuminated waters than over a dark bottom in shady situations, but their nuptial coloration usually is more brilliant in the second case than in the first. But this rule is not invariable (for an interesting exception among Labrador fish, see Weed, *72*: 131). Brook Trout that are dark when fresh-caught soon fade after death. In short, it seems unlikely that any of the local populations of *fontinalis* represent recognizable subspecies, except perhaps those in Dublin and Center ponds and Christmas Lake, New Hampshire, which were made the basis of a separate species (*agassizii*) by Garman (*25*: 78).[31]

The *fontinalis* that are taken in salt water in estuaries or at sea differ so widely in their pale coloration and silvery sides from the freshwater Brook Trout that they have been mistaken by various authors (*60*: 141, 142; *51*: 131, 132; *4*: 206; *53*: 2555) for the sea-run form of *Salmo trutta*, the brown trout (p. 498); and those from Hudson Bay, Labrador, and from Newfoundland were described by Suckley (*64*: 310) as a separate species, *Salmo hudsonicus*, which has been accepted as a subspecies by

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[31] For historical account, diagnostic characters, and excellent colored figures of *agassizii*, see Kendall (*45*: 56–68, pl. 6).

Hubbs (*36*: 17; *37*: 258). Anyone, for that matter, who has compared them is likely to have noticed that the adults average thicker but less deep among the sea-run *fontinalis* than among freshwater fish of a corresponding size (*78*: 181, tab. 3, 185, 187). Due to their stoutness, Salters average somewhat heavier than freshwater fish at a given length; Smith, for example, remarked in 1833 that while freshwater *fontinalis* of one pound are about 14 inches long if in good condition, Salters may weigh one pound when only about 11 inches long (*60*: 350). Correspondingly, a Newfoundland Salter of 14 inches TL (see *Study Material*, p. 525) weighs about 2.25 pounds after preservation in formalin. Wilder, however, has shown that these differences are not statistically significant for the females, and that the differences in shape of body and size of head are "less than those between progeny of one pair of trout raised at different temperatures, and much less than the differences found among four widely separated populations of freshwater trout." The readiness, too, with which hatchery fish of strictly freshwater parentage assume the sea-running habit "refutes any claims for a genetic difference between anadromous and freshwater brook trout" (*49*: 8–11). Thus Jordan's dictum[32] of 1905, that the seagoing *fontinalis* are merely sea-run brook trout, has been verified conclusively.

Numerical Abundance. The only precise evidence available as to how many Salters a given stream may harbor nowadays is as follows: 1,220 taken in 1939 in one of the counting traps in the Moser River, Nova Scotia, on their descent to salt water (*75*); between 500 and 1,000 smolts counted on their way downstream from late April through May in the Little River Codroy, coast of western Newfoundland;[33] and 200–400 larger fish taken there from July through August on their return.

The evidence at hand does not suggest that any general alteration has taken place one way or the other in the abundance of Salters in Nova Scotian waters, or to the north. In the Cape Cod region, however, Salters are far less numerous now than they were formerly, if, indeed, any of the undiluted native strain still exists there. A concrete example of their early abundance is that in April 1829 two anglers, in five days, caught 296 (averaging about 0.5 pound) at one of the well-known fishing points in Waquoit Bay (Smith, *60*: 365[34]). In Mullan's opinion this decline has been due primarily to the effects of the Cape Cod Canal, the cranberry industry along the streams, the ditching of marshes for mosquito control, and rural development in general in reducing the area of suitable freshwater habitat (*49*: 21, 22). Catches at the mouth of one privately owned brook tributary to Buzzards Bay suggest furthermore that the disappearance of the eelgrass (*Zostera marina*) in 1932–1933 was an additional calamity for the local Salters; for while the average number of sizeable fish taken there yearly was about 116 for the period 1928–1932, the largest catch for any subsequent year down to 1954 was only 45.[35]

Results of Stocking with Hatchery Fish. The localities of recapture of 92,100 marked

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[32] Information contributed by Charles F. Ritzi.

[33] Information contributed by A. R. Murray, Fisheries Research Board of Canada.

[34] Misprinted as p. 265.

[35] Information from C. P. Lyman.

fish that were released by the Division of Fisheries and Game of Massachusetts in Cape Cod streams in 1949–1956 have shown that hatchery fish of freshwater parentage readily adopt the sea-running habit and wander as far afield as wild Salters are known to do anywhere (*49*: 8–11); tagging experiments have yielded similar evidence for the coast of eastern Maine.[36]

Relation to Man. Sea-run Brook Trout have long been favorites with anglers, for they take a brilliant artificial fly readily, put up a strong resistance, and are excellent fish on the table, firm and pink-meated and of delicious flavor. Waquoit and Poponesset bays, for example, on Cape Cod, with their tributary streams, were famous Brook Trout waters more than a century and a quarter ago (*60*: 349–351); and anglers as early as 1851 resorted "annually during the month of June for sea trout" to the estuary of the Philip River on the Northumberland Strait shore of Nova Scotia (Perley, *51*: 131). Brook Trout fishing, indeed, continues a favorite sport today wherever they are plentiful in localities that are easily accessible and where they are not so overshadowed by the Atlantic salmon that they are looked upon as a nuisance rather than as a sporting asset. They are netted, also, in some numbers for local consumption wherever there are enough of them to make this worthwhile. But they are not plentiful enough anywhere to be of commercial importance.

General Range. Eastern and north-central North America, in cold waters, from northernmost Labrador, the southern part of Hudson Bay, and the tributaries of James Bay, southward coastwise to northern New Jersey, and thence inland along the Allegheny Mountains to North Carolina and northern Georgia; westward about as far as the western slope of the Alleghenies in the southern part of the range; to northeastern Iowa, Wisconsin, southeastern Minnesota, Lake Superior with its northern tributaries, and to eastern Saskatchewan in the northern part; also widely and successfully introduced in high altitude streams and lakes in the Rocky Mountains of the United States, California, British Columbia, and southern Alaska; likewise in various localities in South America, South Africa, and northern Europe.

Occurrence of Sea-run Populations. Migratory populations formerly existed as far southward as Long Island, New York, where Herbert described them as weighing up to five pounds in the salt creeks (*33*: 303) and where Goode again reported them in 1884 (*26*); a century ago they abounded also in suitable places at the head of Buzzards Bay and along the southern shores of Cape Cod in southern Massachusetts.[37] But native Salters have been nearly, if not completely, wiped out on Long Island by overfishing combined with intermixture with hatchery fish; although a few are still taken in the salt creeks and off their mouths along the southern and northern shores of Cape Cod, it is doubtful whether any of the pure native strain still exists there, so widespread and long continued has been the introduction of hatchery stock.

Salters seem never to have been known anywhere between the northern drainage

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[36] Information contributed by Charles A. Ritzi.

[37] For an interesting account of the status of the Brook Trout in the Cape Cod region early in the past century, see Smith (*60*: 348–394).

of Cape Cod, Massachusetts, and Cape Elizabeth, Maine, unless perhaps in one or two small streams tributary to Ipswich Bay, Massachusetts. However, they do populate many of the small tributaries of Casco Bay, Maine (*20*: 105; *45*: 49, table), and there are sea-going populations in the area near Jonesport (see p. 534 and *Study Material*, p. 525); they probably occur elsewhere as well along the eastern part of the Maine coast; but these can hardly be plentiful, otherwise anglers would be familiar with them. Huntsman found no evidence of them in either salt or brackish water along the New Brunswick shore of the Bay of Fundy (*38*: 60), but White has reported them for the river estuaries at the head of the Bay (*75*: 180); according to local information, sea-running *fontinalis* still exist along the Nova Scotian shore of the Bay, notably in Salmon River.

Detailed information is lacking as to their status along the outer Nova Scotian coast west of Halifax, but east of Halifax there are Salters in practically every trout stream that is not blocked by high falls:[38] all around Cape Breton, along the entire southern coastline of the Gulf of St. Lawrence, around Prince Edward Island, the Magdalens, and the Island of Anticosti. Palmer has also reported them as being plentiful enough to be worth the attention of anglers at the mouth of some 26 rivers and small streams along the west coast of Newfoundland, about 39 along the south coast, and about 25 along the east coast (*50*).

Published information about the Salter situation along the north shore in the inner part of the Gulf of St. Lawrence is scanty, doubtless because they are so greatly overshadowed there by Atlantic salmon. But A. A. Blair has contributed the information that all rivers and brooks along this coast are well stocked with them; and Storer noted more than a century ago that Brook Trout were seined by cod fishermen at the brook mouths there (*63*: 264). Blanc Sablon Bay, just within the Strait of Belle Isle on the Labrador side, has been described by Barteau as "filled with sea trout from June through July" (*48*: 90); they are also reported in numbers for Barge, Wreck, Red, Chateau, and Temple bays within the Strait; St. Lewis Bay and Capelin bays northward; and Hawke Bay, for which Barteau has reported a catch of 33 fish that weighed 137 pounds (*48*: 90, 91). Backus has also reported large runs of migrating *fontinalis* for July and August in the Hamilton Inlet-Sandwich Bay region (*3*: 294). The vicinity of Nain (about 56°30′N) is the next region to the north whence they have been reported in scientific literature (*72*: 128), and their presence along the intervening coast was established by my own local inquiry during the summer of 1900.

Nutak Harbor, on the northwesternmost of the four Okkak Islands (57°28′N), is the northernmost station of recent record for sea-run *fontinalis* on the Atlantic coast of Labrador, though Gordon and Backus think it likely that "small populations are more or less continuously distributed around Cape Chidley and into Ungava Bay" (*27*: 17). There are sea-going populations of *fontinalis* in the rivers that drain into the southern part of Ungava Bay (*16*: 95–97) as well as in the southern part of Hudson Bay, especially around the shores of James Bay, where they are widespread in large numbers (*66*: 40).

[38] For regional details, see especially Breck (*8*).

Synonyms and References for Brackish or Salt water:[39]

Salmo fontinalis Mitchill, Trans. Lit. philos. Soc. N.Y., *1*, 1815: 435 (descr., color, Long Island, New York); Perley, Rep. Fish. Bay of Fundy, 1851: 128 (color, abund., New Brunswick and Nova Scotia, descent to sea); Storer, J. Boston Soc. nat. Hist., *6*, 1857: 264 (abund., s. Labrador coast); Garman, 19th Rep. Comm. inl. Fish. Mass. (1884), 1885: 76, figs. 14–15 (early refs., good descr., ills.; not fig. 16—a specimen of *alpinus* species complex, probably subsp. *aureolus*, from New Hampshire).

Salmo alleganiensis Rafinesque, Ichthyol. Ohiensis, 1820: 44 (brooks trib. to Allegheny and Monongahela rivers, Ohio; not seen).

Salmo nigrescens Rafinesque, Ichthyol. Ohiensis, 1820: 45 (Pennsylvania; not seen).

Salmo fario Smith, Nat. Hist. Fish. Mass., 1833: 141 (size, color, in fresh water).

Salmo trutta Smith, Nat. Hist. Fish. Mass., 1833: 140–141 (river mouths, small rivers, Massachusetts); Herbert, H. W., Frank Forester's Fish and Fish. U.S., 1850: 120–125 (Gulf of St. Lawrence, diff. from sea-run *fontinalis* of Long Island and Massachusetts); Perley *in* Herbert, H. W., Frank Forester's Fish and Fish. U.S., 1850: 123–124 (abund., size, capture, Gulf of St. Lawrence); Rep. Fish. Bay of Fundy, 1851: 131 (abund., sea-run, n. shore Nova Scotia, New Brunswick, Prince Edward I., and Magdalens; angling); Bell, Canad. Nat. Geol., *4*, 1859: 206 (abund., Gaspé, Quebec); Reeks, Zoologist, London, 2 (6), 1870: 2555 (abund., sea-run, capture, w. coast Newfoundld.).

Salmo canadensis Smith *in* Cuvier, Anim. Kingd., Pisces, Griffith ed., *10*, 1834: 474, pl. 41 opp. p. 174 (color, color. ills., Canada); Gilpin, Proc. N.S. Inst. Sci., *1* (4), 1866 (descr., Nova Scotia).

Baione fontinalis DeKay, Zool. N.Y., *4*, 1842: 244 (descr., Rockland County, New York).

Salmo hudsonicus Suckley, Ann. N.Y. Lyc., *7*, 1862: 310 (descr., color, cf. *fontinalis*, Hudson Bay and tributaries, Labrador, Newfoundld.); Weiz, Proc. Boston Soc. nat. Hist., *10*, 1866: 275 (brackish water, Square I., Okkak, n. Labrador).

Trutta argentina Scott, G. C., Fishing in Amer. Waters, 1869: 256 (descr., sea-run, Canada, Nova Scotia, Newfoundld.; not seen).

Trutta marina Scott, G. C., Fishing in Amer. Waters, 1869: 256 (see preceding ref.).

Salmo symmetrica Baird, Rep. U.S. Comm. Fish. (1872–1873), 2, 1874: 372 (color, cf. "brook trout," Monadnock Lake, New Hampshire).

Salmo immaculatus Lanman, Rep. U.S. Comm. Fish. (1872–1873), 2, 1874: 221 (descr. after Storer, 1857; name *immaculatus* applied to sea-run *fontinalis* of s. Gulf of St. Lawrence; actually a synon. of *alpinus*).

Salvelinus fontinalis Jordan, Proc. U.S. nat. Mus., *1*, 1878: 80, 82 (*fontinalis* a *Salvelinus*, not a *Salmo*, distinct. chars. in key); Goode, *et al.*, Fish. Fish. Industr. U.S., *1* (3), 1884: 497, 502, pl. 192 (distr., size, habits, spawn., early develop., in salt creeks, Long Island, New York); Jordan and Evermann, Bull. U.S. nat. Mus., 47 (1), 1896: 506 (descr., range, in salt water, synon.); Schmitt, Monogr. Isle d'Anticosti, *4*, Zool., Poiss., 1904: 285 (abund., estuary of Riv. aux Canards); Evermann, Rep. U.S. Bur. Fish. (1904), 1905: 105 (salt water, food, Casco Bay, Maine); Kendall, Proc. Portland Soc. nat. Hist., *2* (8), 1909: 210, 228–242 (saltwater locals., Labrador, for 1891; refs. to other Labrador recs.); Kendall, Mem. Boston Soc. nat. Hist., *8* (1), 1914: 75–103, table p. 99, pl. 7 (genl. acct., color. ill., tidewater, Casco Bay, Maine); Huntsman, Contr. Canad. Biol. (1921), 3, 1922: 60 (no report of sea-run populations, New Brunswick, shore, Bay of Fundy); Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish. (1928), 2, 1930: 60 (range, synon., checklist); White, Trans. Amer. Fish. Soc., *60*, 1930: 101–105 (spawn., freshwater and sea-run populations, Prince Edward I.); Vladykov, Contr. Canad. Biol., N.S. *8* (2), 1933: 18 (sea-run, size, abund., se. Hudson Bay, James Bay); Weed, Copeia, 1934: 131–133 (sea-run, color, food, vic. of Nain, n. Labrador); White, Trans. Amer. Fish. Soc., *64*, 1934: 356–357 (spawn. season rel. to temp.); Vladykov and McKenzie, Proc. N.S. Inst. Sci., *19* (1), 1935: 57 (sea-run, size, Nova Scotia); Frost, Fish. Bull., Dept. nat. Resources Newfoundld., *9*, 1940: 10 (spawn., e. coast Newfoundld.); White, J. Fish. Res. Bd. Canada, *5* (2), 1940: 176–186 (migr., food, sea-run population, Moser R., Nova Scotia, cf. salmon); J. Fish. Res. Bd. Canada, *5* (3), 1941: 258–264 (migr., time in sea, survival rate, Moser R., Nova Scotia); J. Fish. Res. Bd. Canada, *5* (5), 1942: 471–473 (sea life, off Moser R., Nova Scotia); Doan, Bull. Fish. Res. Bd. Canada, *79*, 1948: 1–12 (sea-run, w. coast Hudson Bay); Wilder, J. Fish. Res.

[39] The Brook Trout (really a charr) is so great a favorite with anglers that the literature treating of it has grown to enormous proportions, both in scientific publications and in sportsmen's magazines. As the present account is centered about *fontinalis* in brackish or salt water, the following list includes only those references that touch directly on the sea-going populations, with a few general works included.

Bd. Canada, 9 (4), 1952: 169–203 (sea-run trout, Moser R., Nova Scotia, cf. freshw. trout, color, migr.); Dunbar and Hildebrand, J. Fish. Res. Bd. Canada, 9 (2), 1952: 95–96 (sea-run, Ungava Bay, n. Labrador, size of "spotted trout" in trib.); Vladykov, J. Fish. Res. Bd. Canada, *11* (6), 1954: 904–932 (det. cf. *S. alpinus* species complex and *Cristivomer*); Gordon and Backus, Copeia, 1957: 17 (sea-run, Nutak Harbor, Labrador, 57°28′N); Backus, Bull. Amer. Mus. nat. Hist., *113* (4), 1957: 292–295 (abund. sea-run, Hamilton Inlet-Sandwich Bay area, Labrador, July-Aug., freshw. Labrador locals.); Bridges and Mullan, Fish. Bull. Mass. Fish. Game, 23, 1958: 38 pp. (genl. life hist., ecol., e. *fontinalis*, present sea-run, Massachusetts, refs.); Mullan, Fish. Bull. Mass. Fish. Game, *17*, 1958: 25 pp. (present status sea-run *fontinalis*, Cape Cod, effects of hatchery fish).

Salmo agassizii Garman, 19th Rep. Comm. inl. Fish. Mass. (1884), 1885: 78, fig. 17 (cf. *fontinalis*, good ill., Dublin Pond, New Hampshire, not fig. 18 — a specimen of *alpinus* species complex, probably subspp. *aureolus* or *oquassa*, local. not given).

Salvelinus fontinalis agassizii Jordan and Evermann, Bull. U.S. nat. Mus., 47 (1), 1896: 507 (color, cf. typical *fontinalis*, Lake Monadnock, New Hampshire).

Salvelinus fontinalis hudsonicus Hubbs, Misc. Publ. Mus. Zool., Univ. Mich., *15*, 1926: 19 (cf. typical *fontinalis*, sea-run, Gulf of St. Lawrence); Copeia, 1943: 258 (subsp. of *fontinalis*).

Salvelinus agassizii Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish. (1928), 2, 1930: 60 (listed, Dublin Pond, New Hampshire).

Salvelinus (*Baione*) *fontinalis* Vladykov, J. Fish. Res. Bd. Canada, *11* (6), 1954: 928, 930 (*fontinalis* regarded as sep. subgen. *Baione*).

Sea trout, Smith, Nat. Hist. Fish. Mass., 1833: 348–394 (abund., sea-run populations, angling, catches, Cape Cod, Massachusetts); Millais *et al.*, Newfoundld. Guide Bk., 1905: 65–91 (sizes, abund., sea-run, Newfoundld., Labrador coast N. to Sandwich Bay); Breck, Edw., Sport. Guide to Nova Scotia, Halifax, 1909: 1–101 (Nova Scotia, sea-run, season); Palmer, Salmon Rivers Newfoundld., 1928: 271 pp. (details, sea-run, rivers and streams, Newfoundld.).

Trout, Herbert, H. W., Frank Forester's Field Sports, Append. A, 1849: 303 (abund., size, salt creeks, Long Island, New York).

Sea trout or Canadian trout, Norris, Thad., Amer. Angler's Bk., 1864: 239–247 (sea-run, abund., weights, as game fish, n. and s. shores Gulf of St. Lawrence).

Brook trout, Green, Amer. Angler, 7, 1885: 312 (size at hatching, early growth, size, Long Island, New York, saltwater occur. implied).

Genus *Cristivomer* Gill and Jordan 1878

Lake Trout

By

Henry B. Bigelow
Museum of Comparative Zoology
Harvard University

Cristivomer Gill and Jordan *in* Jordan, Manual Vert. north. U.S., ed. 2, 1878: 356, 359; type species, (*Salmo*) *namaycush* Walbaum; Lakes of Rocky Mountains to Maine and northward.

Generic Synonym:

Salmo, in part, Walbaum, P. Artedi Genera Pisc., Ichthyol., Emend., 3, 1792: 68, for *S. namaycush* Walbaum; and various subsequent authors.

Characters. Essentially as in *Salvelinus* (p. 503), but with: the frontal area of SKULL flat; rear contour of CAUDAL fin deeply forked (Fig. 129); two longitudinal rows of TEETH on tongue parallel and close together (wide apart and forming a triangle in

Salvelinus); and usually more than 120 GASTRIC COECA (av. only 38 or 39 in *Salvelinus*) (*67*: 928).

Size. The Lake Trout is by far the largest of the small-scaled salmonoids of North America. One of 63 pounds was taken on rod and reel by Miss L. L. Hayes in Lake Athapapuskow, Manitoba, in August 1930, and fish even up to 120–125 pounds have been reported by commercial fishermen, but without supporting evidence.

Range. Lakes and some streams of North America, from the northern United States north to the Arctic Circle, sometimes occurring as a stray in salt or brackish water of Arctic Canada.

FIGURE 129. *Cristivomer namaycush*, 290 mm SL, St. Lawrence basin, Canada, MCZ 33163.

Remarks. The Lake Trout of Lake Superior was described by Louis Agassiz in 1850 as a separate species, *Salmo siscowet* (*1*: 336), which was reduced to the rank of subspecies by Jordan and Evermann with the remark "that it is probably a local variety" (*42*: 505). Neither do I find anything in Agassiz' original description to justify any formal recognition of *siscowet* in ichthyological nomenclature.

Species. One species only is known, the common Lake Trout (*C. namaycush*) of northern North America, which perhaps includes one recognizable subspecies, *siscowet* L. Agassiz 1850, in Lake Superior.

Cristivomer namaycush (Walbaum) 1792

Lake Trout, Mackinaw Trout, Togue, Gray Trout

Figures 118, 129

Cristivomer namaycush is typically a freshwater fish; the only reason for mentioning it here is that stray specimens have been reported for Hudson Bay, for Ungava Bay in northern Quebec, and for the northeastern Labrador coast. Should one be taken in salt water, the minuteness of its scales would show at a glance that it is not *Salmo salar* (Atlantic salmon, p. 460) or any other member of the genus *Salmo* for that matter (pp. 459–499); and the rear contour of its caudal fin is much more deeply concave than that of the sea-run *Salvelinus fontinalis* (Fig. 128). The danger might be greater of mistaking a stray for *Salvelinus alpinus* (Arctic charr), for while the head is somewhat longer and the caudal fin more deeply concave in the Lake Trout than in the Arctic charr, the contrasts between the two fish in these respects are not wide (Fig. 118; also cf. Figs. 125, 126, 129). In case of doubt, cut open the body cavity and estimate (even roughly) how many gastric coeca there are, for while the Lake Trout has about 120, the average for the Arctic charr is only about 39 (p. 510).

Synonyms:

Salmo namaycush Walbaum, P. Artedi Genera Pisc., Ichthyol., Emend., 3, 1792: 68 (brief descr. based on *namaycush* of Pennant, Arctic Zool., Introd., *1*, 1784: cxci; lakes far inland from Hudson Bay).

Salmo salar Williams, Nat. Civil. Hist. Vt., 1794: 121, 122 (Lake Champlain, other Vermont locals.).

Salmo symmetrica Prescott, Amer. J. Sci., (2) *11*, 1851: 340 (Lake "Winnipiscogee," New Hampshire, and connecting waters).

Salmo toma Hamlin *in* Holmes, Ezekial, 2nd Rep. nat. Hist. Geol. Maine, 2, 1862: 109 (great lakes, deep mountain tarns, Maine; New Brunswick, Canada).

Cristivomer namaycush Evermann and Kendall, Rep. U.S. Comm. Fish. (1894), 20, 1896: 591 (Lake Champlain, L. Memphremagog, Vermont).

Salvelinus namaycush Walters, Bull. Amer. Mus. nat. Hist., *106* (5), 1955: 275.

Probable Synonym:

Salmo tructa Belknap, J. Hist. N.H., *3*, 1792: 179 ("Winnipisogee" Lake and stream, New Hampshire).

References for Salt Water:

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Family Coregonidae

HENRY B. BIGELOW
Museum of Comparative Zoology
Harvard University

Characters. The same as those in the Salmonidae, but with: Teeth minute, if present at all; Scales relatively large, not more than 13 scales in a transverse series from origin of dorsal fin to lateral line (at least 19 among Salmonidae); and Parietal bones of skull meeting in the midline (not meeting among Salmonidae).

Remarks. The Whitefishes are widespread in middle and high latitudes in lakes and streams throughout Eurasia and North America. They spawn in fresh water and are confined there throughout the greater part of their geographic range, though in many places they run down into brackish water and out into salt water.

Genera. "The taxonomy of this group has been particularly confusing" (*8*: 276) and seems likely to continue so, as to both genera and species. Thus, Jordan, *et al.*, reported five genera: *Stenodus*, *Leucichthys* (with three subgenera), *Coregonus*, *Prosopium*, and *Irillion* for North America (*4*: 61–66). Norman, however, recognized only *Stenodus* and *Coregonus* on a world-wide basis (*7*: 104), an extreme simplification that does not accord with the weight of present-day opinion.

Key to Genera Recognized for North America

1a. Teeth distinct, in bands on jaws and palatines; a patch on vomer and another on tongue.
Stenodus Richardson 1936.
Sheefish or Inconnu.
Fresh and brackish waters of northern Europe and Asia, from White Sea (Mezen R.) eastward to western Bering Sea drainages (Bay of Korf); Kus-

kokwim River, Alaska; western Arctic Canada southward to northern British Columbia (Teslin and Kluane lakes) and to Fort Smith on Slave River between Great Slave Lake and Lake Athabasca (9: 9–10).

1b. Teeth vestigal or wholly lacking.

2a. Base of adipose fin nearly or quite as long as base of anal fin.

Irillion Jordan 1918.
Rivers of Oregon.

2b. Base of adipose fin not more than about half as long as base of anal.

3a. A single fleshy flap on either side on snout between nasal openings; body rounded; gill rakers short, knob-shaped.

Prosopium Milner 1878.
Round Whitefishes.
Northern Siberia; North American Arctic coasts eastward to Bathurst Inlet, Hudson Bay, Ungava Bay, and Labrador Peninsula; southward in the east to the Great Lakes region, Quebec, northern New York, and Connecticut; in the west to Washington, northern Idaho, western Montana, Wyoming, Utah, and Nevada. Not reported in northern or western Ontario, interior Manitoba, Saskatchewan, or Alberta.

3b. Two fleshy flaps on either side on snout between nasal openings; body laterally flattened in most; gill rakers slender, pointed.

4a. Margin of upper jaw noticeably sinuous in contour, the premaxillary bones wider than long; tip of upper jaw extending beyond tip of lower jaw; front of snout bluntly rounded; gill rakers fewer than 28, the longest not more than a third as long as lower limb of arch.

Coregonus Linnaeus 1758, p. 549.

4b. Margin of upper jaw only weakly sinuous in contour, the premaxillary bones longer than wide; tip of lower jaw extending at least as far as tip of upper jaw; front of snout tapering; gill rakers usually more than 31, the longest nearly or quite half as long as lower limb of gill arch.

Leucichthys[1] Dybowski 1870.
Chubs, Ciscoes, and Tullibees.
Alaska in general; Arctic coast of Canada and Hudson Bay; North-Central Canada in general, southward to the Great Lakes region, and to northern and central New York. Not reported for Newfoundland, or for northern or eastern Labrador.

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[1] Walters considers *Leucichthys* a subgenus of *Coregonus* (*8*: 279, 281).

Genus *Coregonus* Linnaeus 1758

Coregoni, Linnaeus, Syst. Nat., ed. 10, *1*, 1758: 310, for *Salmo lavaretus* Linnaeus. Europe.

Generic Synonyms:

Tripteronotus Lacépède, Hist. Nat. Poiss., *5*, 1803: 47; type and only included species, *T. hautin* Lacépède equals *Salmo lavaretus* Linnaeus 1758.

Coregonus Lacépède, Hist. Nat. Poiss., *5*, 1803: 239; type (first mentioned) species, *C. lavaretus* Lacépède equals *Salmo lavaretus* Linnaeus 1758.

Characters. Base of ADIPOSE fin only about half as long as base of anal. BODY laterally flattened, at least in most. SNOUT with two fleshy flaps on either side between nasal openings, bluntly rounded in front. Tip of UPPER JAW projecting a little beyond lower jaw, its margin conspicuously sinuous. PREMAXILLARY BONES wider than long. GILL RAKERS on first arch fewer than 28, the longest not more than a third as long as lower limb of gill arch.

Size. Coregonus often weigh up to five pounds, and occasional specimens are much heavier.

Relation to man. The Lake Whitefishes are highly esteemed market fish wherever they are plentiful enough to support a commercial fishery; in the Great Lakes region they are the most valuable of the foodfishes.

Species. The genus *Coregonus*, as defined above, is represented in North American waters by two rather sharply defined species: *C. nasus* (Pallas) 1776, with the gill rakers shorter than the diameter of the eye (9: 13), occurs in Siberia, Alaska, and Arctic Canada; and *C. clupeaformis*, possibly identical to *C. lavaretus* (Linnaeus) 1758 of Europe, is the common Lake Whitefish of North America. A third form, *nelsoni* Bean 1884, also with fewer gill rakers than *clupeaformis*, has been reported repeatedly for Alaska as a separate species, but it is only doubtfully distinguishable from *C. pidschian* (Gmelin) 1788[2] of northern Asia. Our only direct concern here is with *C. clupeaformis*.

Coregonus clupeaformis Mitchill 1818

Lake Whitefish

Figure 130

Study Material. About 20 specimens, from Lake Superior, Michigan, New York, New Hampshire, Maine, and the Saskatchewan River.

Distinctive Characters. Should a coregonid of this or any other species be taken in brackish or salt water, it is not likely that it would be mistaken for another fish, for while its adipose fin and general make up would evidently relate it to the salmonids and osmerids, its very small mouth with tiny teeth (if it has any) would mark it off at a glance from all of these. There might be more chance of mistaking a Lake Whitefish for an argentinid were it not that the argentinid's pelvic fins are posterior to the rear

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[2] For a recent discussion of this matter, see especially Walters (*8*: 284–288).

end of the base of the rayed dorsal fin rather than under the midpoint of the base of the dorsal, as in the Whitefishes. If a specimen of this family is taken anywhere along the Atlantic coast of eastern North America and if it does not agree in detail with the following illustration of the common Lake Whitefish (Fig. 130), it is probably a Round Whitefish (genus *Prosopium*, p. 548).

Description. As the Lake Whitefish is not a regular member of the saltwater fish fauna anywhere on the Atlantic coast of North America, the accompanying illustration seems sufficient for identification without detailed description.

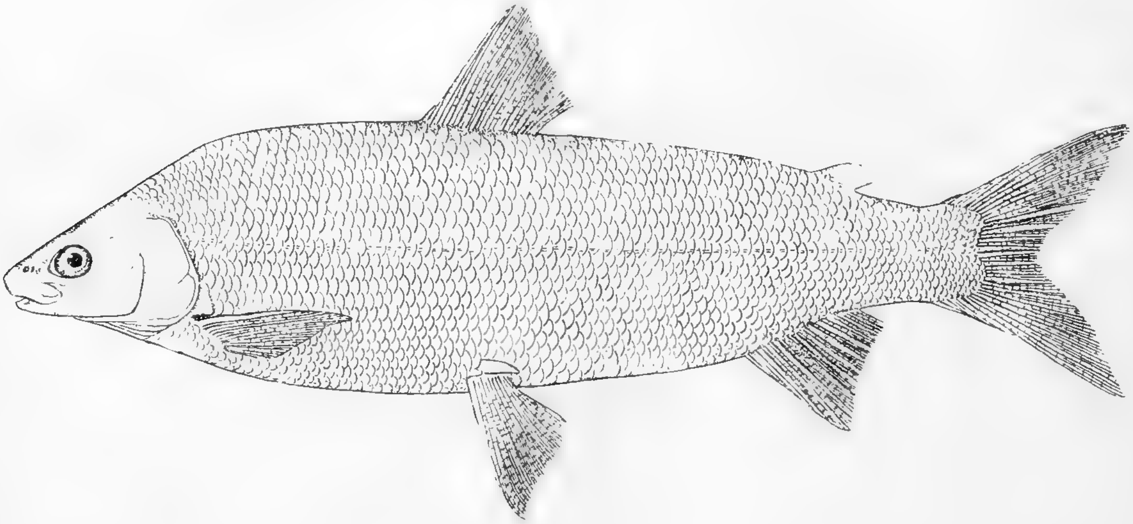

FIGURE 130. *Coregonus clupeaformis*, from Ecorse, Michigan, USNM 10300, after Goode. Drawn by H. L. Todd.

Subspecies. C. clupeaformis, like most of the coregonids, is extremely variable, so much so that Koeltz, in his detailed study (5: 370–381), recognized seven subspecies, four of which, *c. clupeaformis* (Mitchill) 1818, *c. stanleyi* Kendall 1904, *c. neo-hautoniensis* (Prescott) 1851, and *c. gulliveri* Koeltz 1931, are reported for the Atlantic watershed of eastern North America. Discussion of these would be out of place here, for *C. clupeaformis*, so far as is known, occurs only as a stray in salt water in the western North Atlantic, though it does occur more commonly in such situations in Hudson Bay.

Range in North America. Arctic coasts and drainage basins of Alaska and Canada, including the Ungava region of northern Quebec, and southward generally to Nova Scotia (see below), northern New England in general, northern and central New York, south-central Ontario (Peterborough County), the Great Lakes region, northern Manitoba, central and southern British Columbia and Montana, and to the Bristol Bay drainage basin on the Bering Sea coast of Alaska.

Occurrence in the Western North Atlantic. The only published record for a coregonid of any sort in salt water on the Atlantic coast of North America is of two that were taken in "full salt water"[3] in midchannel at the mouth of the Sissibo River, St. Mary Bay, Nova Scotia, in 1919 (*3*: 59). These specimens, no longer in existence, were doubtfully identified as *quadrilateralis*, the Round Whitefish, which is commonly placed in the genus *Prosopium*; but doubtless they were *clupeaformis*, for R. A. McKenzie has written that all of the whitefishes from that general part of the Province received at the St. Andrews Laboratory of late years have been *clupeaformis*.[4] W. B. Scott has also reported that an additional *clupeaformis* was caught off a wharf at Wedgeport, Nova Scotia, in July 1954, and that others were taken or seen there during the ensuing month by W. L. Klawe.[5] But there seems to be no reason to suppose that any regular sea-run populations of whitefish occur anywhere on the Atlantic coast of America or among the Arctic islands to the north.

In Hudson Bay, however, in the vicinity of Churchill on the west coast and in James Bay northward to Great Whale River in the east, both Lake Whitefish (*Coregonus*) and Round Whitefish (*Prosopium*) as well as one of the Ciscoes (*Leucichthys artedi*, subspecies not recorded) appear to run down regularly into salt water (*1*: 12).

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[3] Personal communication from A. G. Huntsman; in Gunter (*2*: 313).

[4] Specimens of *clupeaformis* that were taken in fresh water in the headwaters of the LaHave River, Canada, were inadvertently included among a list of marine records (McKenzie, *6*: 43).

[5] From a letter to J. R. Dymond by W. B. Scott.

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Family Osmeridae

HENRY B. BIGELOW
Museum of Comparative Zoology
Harvard University

and

WILLIAM C. SCHROEDER
Woods Hole Oceanographic Institution[1]

Characters. Essentially as in the Salmonidae (p. 457), but with: sides lacking the FLESHY APPENDAGES above bases of pelvics that characterize Salmonidae; last few VERTEBRAE definitely not upturned; neither an ORBITOSPHENOID bone separating the orbital depressions of the skull nor a POSTOTIC in the auditory region;[2] the BONY PLATE on dorsal side of skull above vomer divided longitudinally by a median suture in some (*Osmerus*, *Allosmerus*, *Thaleichthys*, and *Spirinchus*) but not in others (*Mallotus*),[3] nor among the Salmonidae;[4] only a few PYLORIC CAECA or none (not more than 7 in any western North Atlantic species).

Remarks. In their general appearance the smelt and capelin closely resemble trout and young salmon, but there is no danger of mistaking the one for the other, for the members of the smelt tribe are slimmer-bodied than the salmons, have more deeply forked tails, and their pelvic fins stand farther forward relative to their dorsal fin (see Key, p. 554); they differ further from the salmons in lacking the fleshy appendages above the pelvic bases.

Genera. Six genera seem to deserve recognition within the Osmeridae as defined above, only two of which occur in the western North Atlantic, the others being confined to the northern Pacific. Perhaps we should remark in passing that the "smelt" of New Zealand and of New South Wales, Australia, is not a true smelt, but belongs to the related family Retropinnidae, the dorsal fin of which is far posterior to the pelvics.

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[1] Contribution No. 1149 from the Woods Hole Oceanographic Institution.

[2] For additional details as to skull characters, see Berg (*6*: 240, 428).

[3] For proethmoid bones, see Chapman (*11*: 280–291, figs. 3, 4) and Starks (*106*: 151, fig. 3, 335).

[4] For dorsal view of the skull of the salmons, see especially Parker (*74*: 144, pl. 7, fig. 1) and Gregory (*32*: 154, fig. 48 A, dermethmoid bone).

For a recent account of the occurrence of the New Zealand smelt, with illustrations, see Graham (*32*: 113). The so-called "herring smelt" of the northern North Atlantic belongs to the Argentinidae, a family differing widely from the true smelts in having a very small mouth and a structure in the intestine reminiscent of the spiral valve of elasmobranchs but probably not homologous with it (Part 4).

Key to Genera of Osmeridae[5]

1 a. Scales small, in 170–220 transverse series. *Mallotus* Cuvier 1829, p. 573.
1 b. Scales large, fewer than 80 along lateral line.
  2 a. Teeth on vomerine bone (roof of mouth) and on tip of tongue large, canine-like.
    3 a. Pelvic fins inserted under or posterior to origin of dorsal fin. *Osmerus* Lacépède 1803, below.
    3 b. Pelvic fins inserted definitely in advance of origin of dorsal fin.
      4 a. Head, as seen from above, sharply pointed; gill covers only weakly striated; gill rakers 10 or 11 + 22–26 on first arch; anal fin with only 15–17 rays. *Allosmerus* Hubbs 1925. Coast of northern California.
      4 b. Head, as seen from above, bluntly rounded; gill covers strongly striated; gill rakers only 4–6 + 13–16 on first arch; anal fin with 20–22 rays. *Thaleichthys* Girard 1858. Alaska to Oregon.
  2 b. Teeth on roof of mouth small, not canine-like.
    5 a. Pectoral fins considerably shorter than head; base of anal fin shorter than head, its maximum height less than height of dorsal; upper jaw reaching only a little past anterior edge of eye. *Hypomesus* Gill 1862. Alaska to middle California; also Kamchatka and Japan.
    5 b. Pectoral fins about as long as head; base of anal fin about as long as head, its vertical height considerably greater than height of dorsal; upper jaw reaching back as far as rear margin of eye. *Spirinchus* Jordan and Evermann 1896. Pacific coast of America, Middle California to Alaska.

Genus *Osmerus* Lacépède 1803

Smelts

Osmerus Lacépède, Hist. Nat. Poiss., *5*, 1803: 229; type species, *Salmo eperlanus* Linnaeus, Syst. Nat., ed. 10, *1*, 1758: 310. "Habitat in Europa."

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[5] The so-called "ghost smelt," *Therobromus callorhini* Lucas 1898, which is known only from bones found in the stomachs of fur seals, has been included in the Osmeridae by Jordan, *et al.* (*52*: 68). But Hubbs has suggested that it may not be an osmerid at all (*43*: 49, ftn.), while Chapman has concluded definitely that it is not (*11*: 295). In any case, it cannot be included in this Key for want of information about its external features.

Generic Synonyms:

Salmo, in part, Linnaeus, Syst. Nat., ed. 10, *1*, 1758: 310, for *S. eperlanus* Linnaeus; Pallas, Zoogr. Rosso-Asiat., *3*, 1831: 386, 387, for *S.* (*Osmerus*) *eperlanus* and *S.* (*Osmerus*) *spirinchus*.

Eperlanus Gaimard, Voy. Islande et Groenl., Atlas, Zool., Poiss., 1851: pl. 18, fig. 2; type species *Salmo eperlanus* Linnaeus 1758.

Atherina Mitchill, Trans. Lit. philos. Soc. N.Y., *1*, 1815: 446; type species, *A. mordax* Mitchill 1815. New York.

Not *Atherina* Linnaeus, Syst. Nat., ed. 10, *1*, 1758: 315; type species, *A. hepsetus* Linnaeus; Mediterranean; a member of the Atherinidae (silversides), a family of percoid fishes.

Characters. Body slender, laterally flattened. Head pointed, about 0.2 of length to base of caudal fin. Mouth wide. Upper jaw reaching rearward beyond center of eye. Tip of Lower jaw projecting a little beyond upper. Snout in front of eye about as long as eye. Branchiostegal rays 7–8. Gill rakers about 67 $^0/_0$ as long as eye, about 25–37 on first arch.

Dorsal fin small, its origin at or near midlength of trunk, with 10–11 rays, the first 2 or 3 rays not branched. Adipose fin well developed. Caudal fin deeply forked. Anal with more rays than dorsal, but 17 at most, the first 3 (rarely 2) not branched. Pelvics under or a little posterior to origin of dorsal. Pectorals about as long as upper jaw.

Scales in less than 80 transverse series; thin, transparent, smooth-edged, the exposed surface sculptured with many fine concentric striations, and wholly without pigment; those perforated by the lateral line with a low median ridge, and some weakly indented posteriorly in the midline;[6] scales elsewhere without median ridge and with evenly rounded rear outline. Visible Lateral line not extending beyond origin of dorsal fin.

Teeth. Roof of mouth with a few large canine-like teeth (not shed in spawning season) on lateral tips of U-shaped vomerine bone; teeth also present on tip of tongue; smaller teeth present on the jaws, the palatine bones on roof of mouth, and the pharynx. Bony plate on dorsal side of skull above vomer (Proethmoid of Starks) with a longitudinal median suture.

Vertebrae 55–64. Pyloric caeca 7 at most.[7]

Sexual Dimorphism. At spawning time, large numbers of so-called "nuptial" tubercles develop on the scales of the body and along the rays of the dorsal and pectoral fins of the males, making them so rough to the touch that it is easy to tell the males from the females (*59*: 141; *42*: 86; *89*: 27, 28).

Range. Coastal waters, estuarine situations, and fresh water in lower courses of streams and rivers of the western North Atlantic from the outer coast of Labrador (about 54° N; head of Hamilton Inlet) and the Strait of Belle Isle south regularly to the tidal reaches of the rivers tributary to Delaware Bay (p. 568); the eastern Atlantic from southeastern Norway and the Gulf of Bothnia southward to the Loire River, and

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[6] Smitt has described and pictured the lateral-line scales as being deeply incised posteriorly (*104*: 865, fig. 218). But our own experience with the scales, of both American and European smelts, suggests that this appearance was the result of mutilation.

[7] For other anatomical details, see especially Smitt (*104*: 864, 865) and Chapman (*11*: 280).

reported for Vigo in northern Spain (*5*: 132); the Arctic coasts of Eurasia, Alaska, and Canada eastward as far as the estuary of the Mackenzie River; the western Pacific southward to northern Japan and northern China; and the eastern Pacific to Yakutat Bay, Alaska. They are landlocked in many lakes of Europe, including the Volga River system and the basin of the Caspian Sea (*57*: 241, 308, 315, 323, 346; *49*: 102; *95*: 649), eastern North America, eastern Asia, and the White Sea-Kola Peninsula region. We should perhaps emphasize that, while distributed widely, smelts are unknown along the Arctic coast of Canada east of the Mackenzie, in Hudson Bay, Greenland, Iceland, Spitsbergen, and along the coast of western Norway.

Species. The members of the genus *Osmerus* as limited above were originally described under two names: (1) *Salmo eperlanus* Linnaeus 1758 for the smelts of Europe, with which *spirinchus* Pallas 1811 (*73*: 387), from the lakes and rivers of Russia,[8] and *vulgaris* Gaimard 1838 (*29*: pl. 18, fig. 2), from Iceland, clearly are synonyms; and (2) *Atherina mordax* Mitchill 1815 for western Atlantic smelts. *S. eperlanus* and *A. mordax* (as *viridescens* LeSueur 1818) were retained as separate species, first by Cuvier and Valenciennes, chiefly, it seems, on the assumption that LeSueur would have recognized at first sight a fish with which he had doubtless been familiar since childhood (*19*: 388), and then by Günther (*34*: 166, 167). The list was soon enlarged with *sergeanti*, proposed by Norris in 1868 for the smelts of the Schuylkill River (Delaware), of Brandywine Creek (Pennsylvania), and of the tidal part of the Delaware River (*70*: 93); *dentex*, proposed in 1870 by Steindachner and Kner for those of northern China (*107*: 429); *abbotti* and *spectrum* in 1871 by Cope for those of Wilton Pond and "Cobessicontic" Lake, Maine (*16*: 490); and *dvinensis* in 1882 by Smitt for those of the White Sea (*102*: 34; *104*: 867, ftn. K).

So far as we can learn, Rice's comparison of the number of transverse rows of scales on smelts from various American localities with others from Liverpool, England (*86*: 91), was the earliest comparison of the sort that has been made; he concluded that the American smelts are identical to the European *eperlanus*. The next landmark in smelt taxonomy was Smitt's (*103*: 168–188) very detailed comparison of the proportional dimensions for the smelts of Scandinavia (as *eperlanus*), the White Sea (as *spirinchus*), and the North Pacific (as *dentex*); from this he concluded that the three represented three distinct species. In 1895, however, he followed Rice in uniting the smelts on the two sides of the Atlantic under the older name *eperlanus* (*104*: 869). Since that time opinions have differed widely as to how many recognizably distinct units (species or subspecies) the *eperlanus-dentex-mordax* group actually includes.

One extreme among students concerned primarily with the smelts of North America may be represented by Jordan, *et al.*, who recognized four distinct species (*52*: 67): *eperlanus* (tacitly), *mordax* (with *spectrum* and *abbotti* as subspecies), *dentex*, and *sergeanti*. The other extreme may be illustrated by Fowler's union of *mordax*, including *sergeanti*,

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[8] The Smelt from Kamchatka which Pallas reported as *spirinchus* belong to the form that has subsequently been named *dentex*.

spectrum, and *abbotti*, with the European *eperlanus*, based on his comparison of smelts from France with those from New York and from various localities in New England (*28*: 555). As an example of extreme subdivision of the smelts of the eastern Atlantic, Europe, and the Arctic Ocean, it seems enough to cite the following names applied by Berg (*5*: 132): *Osmerus eperlanus eperlanus*, northern Spain to Scandinavia and the Baltic; *O. eperlanus dentex*, White Sea and Arctic coast; *O. eperlanus eperlanus* natio *ladogensis*, Russian lakes; *O. eperlanus* morpha *spirinchus*, lakes of northern Europe; and *O. eperlanus dentex* natio *dvinensis* morpha *spirinchus*, lakes of the White Sea region and Kola Peninsula.

The differing views in this regard after 1895 seem not to have reflected any extensive contributions to recorded fact until 1934, when Petrow showed (*77*: 179, 182) that smelts of the Arctic coasts of Eurasia and of the northwestern Pacific have a larger number of lateral-line scales (14–30) than smelts of Europe (4–14), that they have somewhat larger teeth, and that on the average they have a longer interspace between the bases of the rayed dorsal fin and adipose fin. Consequently he recognized two subspecies, *eperlanus* and *dentex*, not three, as Berg had done (*4*: 100, 102).

Table I. *Osmerus.* Scales Penetrated by the Lateral Line in: A, 11 specimens, 145–174 mm SL, from Nova Scotia and New England (*mordax*), MCZ; B, 11, 72–206 mm, from Bering Sea (*dentex*), USNM; C, smelts from the White Sea, Arctic coast of Siberia, and eastern Siberia, according to Petrov; D, 6, 67–174 mm, from northern Europe (*eperlanus*), MCZ; and E, smelts from Russia (*eperlanus*), according to Petrow (*77*).

	A	B	C	D	E
Scales	15–26	17–25	14–30	7–11	4–16
Extreme range ...	14–30			4–16	

Unfortunately, Petrow did not extend his comparison in this regard to the smelts of the western North Atlantic. But our own examination of the series listed (Tables I and II) has shown that in this respect *mordax* agrees more closely with *dentex* than with *eperlanus*, a result at which Hubbs had already arrived from his study of the number of gill rakers and the height of the anal fin (*43*: 52). It also appears that the contrast in number of scales is a decidedly consistent one, although we have found nothing to suggest that the western Atlantic, eastern Atlantic, and Bering Sea smelts differ significantly one from another in any of the other features that seem the most likely to be significant from the species standpoint among salmon-like fishes as a whole.

If we can accept the number of lateral-line scales as our criterion, the smelts of the western Atlantic are more closely related to the Arctic-North Pacific smelts than to the European smelts, though the reverse might have been expected on purely geographic grounds. And the separation between the two divisions seems sufficient to warrant the recognition of two corresponding subspecies within the species *eperlanus*, but not of three (*eperlanus*, *mordax*, and *dentex*), as by Wynne-Edwards (*118*: 17). Admittedly the basis for this conclusion is so weak that future examination of more extensive series of specimens from key localities may prove that it is not valid. But our provisional adoption of it here (Key, p. 558) has at least the practical advantage of freeing us from the need to expand the present account of the western Atlantic smelts to cover the eastern Atlantic smelts in corresponding detail.

Table II. *Osmerus.* Proportional Dimensions and Meristic Characters for Three Major Geographic Areas: A, 9 Western Atlantic Specimens from Cape Breton, Halifax, St. John Harbor (Canada); Massachusetts Bay, Nahant, Charles River, Boston Harbor, and Edgartown (Massachusetts); and New York. B, 19 Alaskan and Japanese Specimens from Bristol Bay, St. Michaels, Port Clarence, and Wainwright Inlet, Alaska; Petropaulski Harbor, Kamchatka; and Mororan, Japan. C, 7 European Specimens from the Elbe River; Le Havre, France; and Lake Oppmanna, Sweden.

Averages in Parentheses.

	A	B	C
Standard length	97–198 (167)	104–206 (173)	67–174 (139)
Per cent of standard length:			
Body: depth	13.4–23.4 (17.9)	15.2–20.0 (18.3)	17.2–20.9 (19.3)
Head: length	20.3–24.9 (23.1)	22.2–26.9 (25.0)	23.8–26.6 (25.1)
Distance from:			
snout to dorsal fin	49.2–52.2 (50.9)	48.5–52.5 (50.1)	50.0–54.5 (51.7)
dorsal to adipose fin	21.7–24.2 (23.3)	20.8–27.3 (23.4)	20.4–23.1 (21.8)
adipose to caudal fin	8.7–10.8 (9.7)	7.8–10.7 (9.2)	9.5–10.9 (10.0)
anal to caudal fin	6.0– 8.0 (7.1)	6.5–8.8 (7.5)	6.7– 8.7 (8.0)
Per cent of head length:			
Eye: diameter	18.9–23.3 (21.4)	17.8–23.2 (19.6)	18.2–20.3 (18.8)
Distance from:			
snout to eye	26.3–31.1 (29.2)	25.0–34.5 (29.3)	25.0–31.6 (28.9)
eye to nostril	9.7–12.2 (10.4)	9.3–12.7 (10.3)	7.9– 8.8 (8.5)
Upper jaw: length	44.8–54.2 (49.6)	47.5–59.8 (51.0)	43.8–52.2 (50.1)
Counts:			
Scales: perforated by lateral line	15–26*	17–25	3–10
total longitudinal series	64–69	64–69	59–63
Branchiostegals rays	7–8	7–8	7
Gill rakers: upper, first arch	8–11	9–10	9–11
lower, first arch	17–21	17–22	17–21
Dorsal fin: rays	10–11	10–12	10–11
Anal fin: rays	15–17	15–17	15–17
Ventral fin: rays	8	8	8
Pectoral fin: rays	11–12	11–13	11–12

* Only 4 specimens countable.

Key to Subspecies of *Osmerus eperlanus*

1a. Scales perforated by lateral line, 14–30. *mordax* Mitchill 1815, p. 559.
1b. Scales perforated by lateral line, only 4–16. *eperlanus* Linnaeus 1758.
Northern Europe.

Osmerus eperlanus (Linnaeus) 1758
mordax Mitchill 1815
American Smelt, Icefish

Figures 131, 132

Study Material. Many specimens: 80, 67–230 mm SL, from various coastal and estuarine situations along the coast of eastern North America from Cape Breton (Nova Scotia) southward to New Jersey; numerous specimens from various landlocked situations in New England and New York state; 19, 104–206 mm long, from Bristol Bay, St. Michaels, and Port Clarence in Alaska, Kamchatka, and northern Japan. Also, for comparison, 7 specimens of *O. eperlanus eperlanus* from Le Havre, France; the Elbe River; and Lake Oppmanna, southern Sweden; all in MCZ and USNM.

FIGURE 131. *Osmerus eperlanus mordax,* adult, about 260 mm long (10.4 in.), from Woods Hole, Massachusetts. Drawn by H. L. Todd.

Distinctive Characters. Western North Atlantic fishes with which *O. e. mordax* might be confused are *Mallotus villosus* (capelin, p. 576), a near relative, *Argentina* (argentine, Part 4), or one of the silversides (family Atherinidae), to which it is only remotely related. Its much larger scales, smaller adipose fin, and less projecting lower jaw are enough to mark it off from *M. villosus*; its very much larger mouth and the more forward position of its pelvic fins separate it from *Argentina*; and even the most cursory examination should be enough to separate it from the silverside, for the latter has two dorsal fins with the first supported by spines, no adipose fin, pelvics standing considerably anterior to the first dorsal fin, and a mouth much smaller than that of *O. e. mordax.*

Description. Based on 10 specimens: 9, 150–230 mm SL, and 1, 97 mm SL, from several localities between Cape Breton (Nova Scotia) and southern Massachusetts.

BODY elongated, moderately compressed (Fig. 131), the dorsal and ventral profiles of head and trunk slightly convex, the dorsal profile a little more so than ventral profile;

its depth 4.3–7.5 in SL, its greatest thickness about 1.7–2.4 times caudal peduncle depth or 1.4–2.0 times distance from snout to eye. Least depth of CAUDAL PEDUNCLE 1.0–1.4 times in snout. SCALES everywhere on trunk, extending onto base of caudal but not onto dorsal or anal; 14.5 scales in oblique series from origin of pelvics to midline of back; cycloid, thin, transparent, deciduous, with closely spaced circuli; scales along midsection of sides with vertical axis about 1.5 times the horizontal axis and about equal to diameter of pupil, those toward head and tail somewhat smaller and more roundish; rear margin rounded, most abruptly so at horizontal axis posteriorly; head scaleless. MODIFIED LATERAL-LINE SCALES 14–30 (Table 1, p. 557), beginning at upper margin of gill opening and extending rearward in a nearly straight line, ending somewhere between perpendiculars from rear part of pectorals and a little in front of dorsal; lateral line ending with most posterior modified scale.

HEAD 4.1–4.6 in SL, its dorsal profile straight or nearly so. SNOUT pointed, 3.2–3.8 in head. LOWER JAW projecting. EYE 4.3–5.3 in specimens about 150 mm long or larger, its rear margin about halfway between tip of snout and rear margin of opercle. INTERORBITAL space very gently rounded, 3.5–4.3 (2.6 in 97-mm specimen). POSTORBITAL part of head 1.7–2.0 in head. NOSTRILS situated in line with tip of snout and upper edge of eye, and the two openings close together, the posterior one the larger, its anterior rim bearing a flap, its distance from eye 8.1–12.2 in head. OPERCLE with broadly rounded margin. Margin of PREOPERCLE about halfway between eye and margin of opercle. BRANCHIOSTEGALS 7 or 8. GILL RAKERS very slender, the longest 1.4–1.9 in eye; 8–11 on upper limb of first arch, 17–21 on lower limb, total 25–32.

MOUTH oblique, the gape reaching almost or quite to a perpendicular from anterior edge of eye. MAXILLARY beginning a little in advance of anterior margin of nostril, widening rearward, its posterior margin broadly rounded and reaching from opposite rear edge of pupil to just beyond eye. PREMAXILLARY extending a little past origin of maxillary. MANDIBLE 1.5–1.7 in head.

TEETH. Lower jaw with one or two rows of small canines anteriorly, but one row posteriorly where they are largest; maxillaries and premaxillaries with very small teeth, unevenly spaced; vomer with one to two pairs of canines (sometimes 3 or 5 teeth), these being among the largest in the mouth; palatines and mesopterygoid with a row of low rather blunt teeth; tongue boat-shaped with fleshy lateral margin, with 1 or 2 strong fang-like teeth at the tip, followed by several progressively smaller teeth, and by still smaller teeth behind these.

DORSAL with outer margin straight or nearly so, its base 1.2–1.5 times snout, its origin about midway between tip of snout and caudal base, with 10 or 11 rays, the first 2 unbranched, the longest 1.5–1.8 times length of base. ADIPOSE fin with outer margin rounded, its base 2.2–3.4 times in base of dorsal, its origin over about middle of anal base, it height 1.2–2.0 times in the base. CAUDAL deeply forked, its tips pointed. ANAL with outer margin straight or weakly convex, its base 1.3–1.6 times dorsal base, its origin about equidistant between origin of pelvics and base of caudal, with 15–17 rays, the first 3 unbranched, the longest 0.6–0.7 of length of base. PELVICS with rear margin straight or nearly so, their origin opposite dorsal origin, with 8 rays, the first (outer) unbranched (2 reported), the longest ray 3.3–4.0 times length of base. PECTORALS with rear margin straight or slightly convex, the angles rounded, their origin under rear margin of opercle, with 11 or 12 rays (13 reported), the first (upper) ray unbranched, the longest ray 3.7–4.5 times the base.

VERTEBRAE 62–64 (ten specimens counted, but not the above described specimens).

Color.[9] Back and upper part of sides translucent, yellowish olive or bottle green, sometimes with a brassy sheen; skin of upper parts, including fins, usually more or less speckled with minute purplish black dots that show through the scales. Sides with a broad bright silvery belt enclosing the lateral line, and outlined above by a narrow, vaguely outlined dusky purplish band; lower part of sides less brilliantly silvery. Belly and lower side of head as a whole, white. All the fins transparent, or nearly so; dorsal with a paler shade of same color as back; the caudal similar but more or less dark-edged; anal and pelvics whitish; pectorals colorless or nearly so, except for a greenish margin anteriorly. The lining of body cavity silvery.

Size and Weight. American Smelts from salt water average about 7–9 inches long when full-grown, and about 12–13 inches is the usual maximum. As caught, they ordinarily run between 1 and 4 ounces, depending on size and fatness, and very large ones may weigh as much as 6 ounces. In Great Bay, New Hampshire, the largest of many measured was about 9 inches long. In the Bay of Chaleur, Quebec, 9- to 9.5-inch fish averaged a little more than 0.2 of a pound, while a 10.5-inch fish (270 mm) weighed a little more than 0.25 of a pound (122.5 g).

In some lakes where they are landlocked they commonly run up to 10–15 inches and (by report) up to as much as two-thirds to one pound or so in weight, as in Sebago Lake and North Belgrade Lake in southern Maine and in some of the Nova Scotian lakes, Canada. Other lakes, however, harbor stunted races, e. g. Grand Lake in the St. Croix watershed of eastern Maine (*56*: 277), Lac des Isles in western Quebec, and Lake St. John, tributary to the Saguenay.

Odor. Accounts have repeatedly credited the smelts with a "cucumber" odor, especially smelts of Europe, which have often been described as strong-smelling. But in the American populations this odor is so faint that we have not noticed it, though we have caught and handled many.

Development and Growth. Females weighing no more that two ounces may produce as many as 40,000–50,000 eggs (*85*: 188); one 232 mm (9.12 in.) long, taken in Crystal Lake, Michigan, contained 43,125 eggs (*59*: 142). The eggs, which range in diameter from 0.6 mm to about 1.2 mm in different waters and according to different authorities, sink to the bottom where they stick to each other in clusters or cling to any object on which they settle. In European waters, the eggs hatch in 8–27 days, depending on the temperature of the water. In Massachusetts they have been reported as hatching in 13 days.

The larvae are about 5–6 mm long when they hatch and are perfectly transparent

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[9] From market specimens in excellent condition that we have examined recently.

at first. Once hatched they rise close to the surface and drift downstream. On the average, they grow to 17 or 18 mm during their first month, to 27–34 mm during the second month, and to about 40 mm after 3.5 months, when we have seined several hundred fry of 30–40 mm at Mt. Desert Island, Maine; and the schedule is about the same in European waters, the precise rate of growth depending on temperature.

By the time larvae of the Elbe River in Europe have grown to 8 mm, the yolk sac is mostly absorbed; at 15 mm all the fins are more or less developed, but the caudal is still rounded; and by 45 mm the formation of scales has begun. We see no reason to suppose that development proceeds otherwise in America.[10]

In their second spring, when one year old, the fry average about 86 mm (data for Great Bay, New Hampshire). From scale studies it appears that they average as follows: at two years about 145 mm (5.7 in.) and about 0.6 of an ounce, at three years 171 mm (6.7 in.) and about 1.1 ounces, at four years 220 mm (8.7 in.) and about 2 ounces. The largest measured was 230 mm (about 9 in.). At this locality at least, four or more year-classes are represented in the commercial catches. Those taken in Crystal Lake, Michigan, where they were introduced, grow somewhat faster, reaching 6–8 inches at two years, up to 9 inches at three years, up to 10 inches at four years, and 10.75–12 inches at five years (*17*: 401–424), with a maximum recorded length of 14 inches, probably for a six-year-old. Doubtless they grow much more slowly in other lakes that harbor stunted races.

FIGURE 132. *Osmerus eperlanus mordax*, larva, 26 mm long, from Portland Harbor, Maine, July 31, 1912. Drawn by Mrs. E. B. Decker.

Spawning Habits. The marine fish normally spawn in fresh water, and as a rule they do not travel far upstream; they may go only a few hundred yards above the head of tide. Some spawn in the tidal zone and some even spawn in brackish water behind barrier beaches. But they never spawn in salt water, for flooding with the latter, as sometimes happens, kills the eggs. They spawn on pebbly bottom where there is a current, and often in water only a few inches deep. Most often the spawners are two years old, or older. Spawning takes place in late winter or early spring, depending on the temperature of the water. According to data from hatchery operations, the chief production of eggs takes place in temperatures of 50°–57° F in Massachusetts, and of about 45°–50° F in Grand River, Quebec, representative of the northern part of their range. The spawning period lasts 10–14 days and is completed ordinarily by mid-May in

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[10] For excellent accounts and illustrations of the smelt of the Elbe River, see Ehrenbaum (*25*: append. 3, pl. 1), whose illustrations have been reproduced by Kendall (*56*: fig. 25). For the embryology and early larval development of the American Smelt, see Rice (*86*: 57–76, pls. 1–5).

Massachusetts, not until late May along the coast of Maine, and not until some time in June in the Gulf of St. Lawrence.

The spent fish—except those that die, as many do—drop down again to brackish or salt water immediately after spawning, so that all of them have deserted fresh water by the middle of May in Massachusetts, nearly as early in Maine (where we have seen a bushel of large fish taken as early as May 4 from a weir near Cutler at the mouth of the Grand Manan Channel), and by the end of June at the latest in the Gulf of St. Lawrence.

Habitat and Migrations. Smelt, whether American or European, make their growth in brackish or salt water if they are not landlocked. During the marine phase of their life they are confined to so narrow a coastal belt that none has ever been reported more than six miles or so out from the land and seldom below 2–3 fms.; the deepest record for them is 9–10 fms. at the mouth of Port-au-Port Bay on the west coast of Newfoundland, where 185 specimens were taken in a half-hour haul with an otter trawl. Many of them spend their entire growth period in estuarine situations, including the tidal reaches of rivers.

Their habitat in the summer along any particular section of the coast appears to depend chiefly on the temperature of the water. From Massachusetts southward, most of them (though not all) desert the harbors and similar situations during the warmest season, moving, it seems, only far enough out and deep enough to find slightly cooler water. Along the coasts of Maine and the Maritime Provinces of Canada, however, where water temperatures rule lower, they are found in the harbors, bays, and estuaries all summer.

With the onset of autumn, those that have moved out to sea re-enter the harbors and estuaries, so that by mid-October, or early November at the latest, practically the entire population is concentrated there. In our experience the smaller ones tend to reappear the earliest, but reports are contradictory in this respect. At any rate, by December some have even worked up into stream mouths to the head of tide. But the fish fated to breed that season, most of which are two years old or older, do not actually enter fresh water until late winter or early spring when the water off the mouth of the stream has warmed to at least 39°–42° F (4°–5.5° C), if it has chilled below that figure, and until the ice has gone out of the stream, if any has formed there during the preceding winter.

The movement of the maturing fish into fresh water commences late in February along the southern coast of New England and southward, some time in March along northern Massachusetts, seldom until April along the eastern part of the Maine coast, and not until the latter half of May along the southern shores of the Gulf of St. Lawrence.

This species, though confined to very shoal water, is not a bottom fish but tends to hold position at some intermediate level. The small ones, and probably the large ones also, gather and travel in schools that are composed for the most part of fish of about the same size, i. e. the product of one year's hatch. In the smaller harbors they tend to move in and out with the tide, especially if the tidal flow is strong. But while they may be plentiful close in to the tideline, few of them run up into salt marsh creeks unless these creeks receive some inflow of fresh water; we have never heard of them being trapped on the flats by the outgoing tide, as happens now and then to herring. Although they are not Arctic fish, we have never heard of their being killed by winter chilling, as in the case of some other fishes from time to time.

Their actions, if these are watched from some raft or float, suggest that they travel but little during their inshore sojourn, except as they may be carried to and fro by the tide, as just remarked. Anglers have long known that American Smelt do not dart at bait, but approach it slowly and appear to suck it into the mouth rather than seize it, as most of the predaceous fishes do.

Food. This species is carnivorous and predaceous. In salt and brackish water, shrimps (decapod and mysid) probably are their chief support on the Massachusetts coast; similarly, the stomach contents of those in the Gulf of St. Lawrence have consisted chiefly of copepods, amphipods, and mysids, with algal debris probably taken incidentally. In some localities small fish rank next. We have found them packed full of young Atlantic herring, on the coast of Maine, and a wide variety of fishes has been recorded as occurring in their stomachs, at Woods Hole. They also take small shellfish, small squid, annelid worms, and small crabs as occasion offers. But they cease to feed during the spawning season, as many other fishes do.[11]

Enemies, Disease, and Mass Fatalities. Doubtless the marine population is preyed upon by a wide variety of the larger predaceous fishes, but we have no definite information in this regard for the American coast (see *63*: 236 for the European smelt). In American lakes they are perhaps the favorite prey of landlocked salmon and lake trout and are commonly used as bait for these.

In European harbors, mass destruction of them, from some unknown cause, takes place from time to time (*63*: 39–42).

A mortality of smelt, affecting all sizes and both sexes, occurred in Lake Huron and in Lake Michigan during the fall and winter of 1942–1943 (*72*: 310–337), with the first indication of a recovery being apparent in 1945. It was concluded that this mortality, which all but wiped out the populations in these two lakes, could be explained only as resulting from a communicable disease (bacteria or virus). We have found no record of any happening of this sort in brackish or salt water along the American coast.

Variations. A separate specific name, *sergeanti*, was given years ago to American Smelt of the streams tributary to the head of Delaware Bay because of their smaller size and a slight difference in color (Norris, *69*: 59; *70*: 93). Hubbs recognized *sergeanti* as at least a "race" because of the fewer gill rakers on the first gill arch and because of a slightly higher anal fin than on the more northerly fish (*43*: 52). Similarly, Rice long ago reported small differences in color between those of the Raritan River, New Jersey, and those of more northern localities (*86*: 79), though he did not consider those differences wide enough for recognition in nomenclature.

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[11] For their diet in fresh water, with extensive tables for many different lakes, see Kendall, *56*: 281–287.

It has been found that American Smelts average somewhat larger at maturity in the Bay of Chaleur, Quebec, than in the estuary of the St. Lawrence River (*64*: 71–85), and that those of the Bay of Chaleur have a larger number of vertebrae on the average (62.18–62.9 according to locality) than those from various places between Matane on the southern side of the estuary and Quebec City (60.32–61.92). The first of these differences may be associated with the food supply; the second illustrates the long-known rule that among fish species that occur over a wide range of temperatures, the number of vertebrae average the most numerous among populations that pass their growth stages in colder than in warmer water. Nothing else is known in this regard for any other parts of the American coast. For the American Smelt in fresh water we know only that they run much larger in some lakes than in others.

Racial studies of the subspecies *mordax* of the White Sea region, Arctic Asia, and eastern Siberia by Petrow (as *dentex*) did not reveal any regional differences calling for recognition in nomenclature (*77*: 177–188). For the European subspecies *eperlanus*, Hubbs (*43*: 52) has pointed out that the gill rakers average more numerous in specimens from Scandinavia (32–37) than in those from the English Channel (25–32). And Jensen has reported slight differences, based on extremely detailed comparisons of smelts from different lakes in Denmark, especially in the number of vertebrae (*49*: 73–109).[12]

Abundance. In colonial days, according to Captain John Smith, American Smelt in 1622 were in "such abundance, that the Salvages doe take them up the rivers with baskets, like sives" (*56*: 244). While it seems certain that they were far more plentiful along the coasts of New York and Maine up to the early part of the nineteenth century than they are today, by 1849 a decrease was reported for northern New Jersey, and by 1885 for the streams of Long Island, New York. By the end of the century, at Cold Spring Harbor, the New York State Hatchery, which planted 48 million fry in 1898, produced only a few million in 1899 for lack of ripe females and eggs from nearby waters, and after 1900 its operations were discontinued. Many reports of their depletion in the waters of Massachusetts have been received also; there the number of eggs from the Weir River, tributary to Boston Harbor, fertilized at the Palmer Hatchery, fell from around 100 and 110 million in 1918 and 1919 to 32 million in 1920, after which Smelt hatching was given up.[13] A general decrease seems also to have taken place along the coast of Maine since the end of the last century, and from the same causes that produced the depletion southward, i. e. from contraction of favorable spawning grounds by dams close to the mouth of streams, and perhaps from overfishing. In 1889, for example (*15*: 79), United States waters yielded 1,209,385 pounds of American Smelts in contrast to a yearly average of only 473,550 pounds for the period 1951–1954. But the catch records do not suggest any extensive or

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[12] For a recent survey of variations in the taxonomic features of fishes in general, as associated with regional differences in their environment, see Vladykov (*113*: 122).

[13] For details and for general information as to the smelt, see *84*.

general alteration in their abundance during the past 15 years or so for either Maine or Canada, except locally, as in the Miramichi area, Canada, where their access to fresh water has been hindered by obstructions in the streams. On the contrary, the yearly Canadian catch increased from an average of only 8,000,000 pounds for the 20-year period 1918–1937 (*65*) to 21,295,000 pounds for the later period 1951–1954. This increase doubtless is indicative of an increasing demand for them rather than of any corresponding increase in their abundance.

Artificial Propagation. American Smelt have been a favorable subject for artificial propagation.[14] Many million fry were hatched in past years at the Cold Spring Harbor Hatchery, New York, as well as at the Palmer Hatchery, Massachusetts (p. 565). The results have been widely heralded, for great catch increases were reported for streams where fry were released. The most notable example is that 32 million eggs were collected in 1885 from a New York stream where there had been no Smelts for at least some years previous (*85*: 188). And a similar example, though less spectacular, was reported for Massachusetts.

Relation to Man. The American Smelt is a favorite among the market fish, delicious when fresh-caught or even after being iced properly, and great numbers, especially from the Gulf of St. Lawrence, are marketed. The average landings reported for the four-year period 1951–1954 were 5,323,000 pounds for the Canadian Atlantic coast and 150,700 pounds for the United States coast, or a total of 5,473,700 pounds; that is, 55 million individuals if these ran say, 10 to the pound, all marketed for human consumption. Years ago they served as cod bait in the Gulf of St. Lawrence (*60*: 224), and large quantities were used yearly as manure along the Gulf of St. Lawrence shores of New Brunswick (*76*: 135).

These fish also have great recreational value. As many as 2,336 anglers have been counted "smelting" about Houghs Neck in Boston Harbor at one time, and the same sort of thing is to be seen on a smaller scale throughout their range. On occasion, especially on a rising tide, the fish bite greedily. Sea worms (*Nereis*) are the best bait, especially for larger fish, salt-marsh shrimps (*Crago*) a second best, and small fish a poor third. They have also been reported as taken with a small red artificial fly in the Gulf of St. Lawrence (*60*: 225), and doubtless they might be taken with a fly elsewhere. On the other hand, anglers prefer American Smelt to other bait for landlocked salmon in lakes of northern New England and of the Maritime Provinces, Canada, wherever they are to be had.

Methods of Capture. The commercial catch is made chiefly in nets of various kinds, but partly with hook-and-line. For example, of the 1954 Maine catch, which may serve as a representative year, about 31 % were taken in haul-and-stop seines, about 26 % in gill nets, about 21 % in bag nets operated through the ice, about 4 % in weirs, and about 18 % on hook-and-line. In New Hampshire, however, in that same year, 3 % of the commercial catch was made in bag nets, 23 % in weirs, and 74 % on hook-and-line. Along the New Brunswick shoreline of the Gulf of St. Lawrence, where the

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[14] For methods employed, see especially Rice, *86*: 41–56; also *85*: 188.

catch is much larger than anywhere in United States waters, about 95 % are taken in winter through the ice, in trap nets of one kind or another.

General Range. Western North Atlantic coast, from the outer coast of Labrador at about 54° N, and northern Newfoundland, southward to the head of Delaware Bay; also (as *dentex*) in the White Sea, Arctic coasts of Europe and Asia at scattered localities, northwestern Pacific south to northern Japan and northern China (type locality of *dentex*), Pacific Bering Sea and Arctic coasts of Alaska northward from Yakutat Bay, northern British Columbia (*36*: 55) to Bering Strait, and eastward thence on the Arctic coast of Canada to the delta of the Mackenzie River, where they are reported to be plentiful at the mouth of the Arctic Red River. They are also landlocked in many lakes and rivers.

The European *O. eperlanus eperlanus* range from Vigo in northern Spain northward to southeastern Norway, and up the Baltic to the Gulfs of Finland and Bothnia, chiefly in the watersheds of the Baltic and North seas. They have not yet been reliably reported for Iceland. Like some American Smelts, they are landlocked in many lakes and river systems of foreign places.[15]

Occurrence in the Western North Atlantic. The most northerly locality of positive record for American Smelts in eastern North America is the mouth of Northwest River, tributary to Lake Melville at the head of Hamilton Inlet on the Atlantic coast of Labrador (about 54° N), where Low described them as "abundantly taken" in November and early December (*62*: 329); and they have recently been recorded for various places in the Hamilton Inlet-Lake Melville region (*3*: 295). The next most northerly locality is the Newfoundland side of the Strait of Belle Isle, where, writes Jeffers, "a few were generally observed each summer" (*47*: 207). We have found no proof of their presence anywhere, passing westward, along the north shore of the Gulf of St. Lawrence until nearing the Bersimis River, whence small commercial catches are reported. But they are plentiful near Quebec City, and at least one specimen has been reported to be as far up the St. Lawrence River as Lake St. Pierre (*18*: 20). They are caught all along the south shore of the St. Lawrence estuary. They have been reported for Anticosti Island and are taken regularly in commercial quantities around the Gaspé Peninsula and Magdalen Islands. In the shallow, semi-enclosed bays of Prince Edward Island and on the north shore of New Brunswick Harbor there occur what are probably the greatest concentrations of American Smelt in the western side of the Atlantic. Many years ago they were described as ascending the smaller streams of Newfoundland "in thousands as soon as the ice disappears" (Reeks, *82*: 2556), and they have recently been reported by the Newfoundland Fishery and Research Commission as plentiful there in the shallow bays and river mouths on both the west coast at the mouth of the Humber River and Port-au-Port Bay and the east coast in the rivers of Notre Dame Bay. They were also described long ago as common around the wharves at Cape Breton, Nova Scotia.

American Smelt are familiar thence southward along the coasts of outer Nova

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[15] For recent summary, see Jensen, *49*: 102.

Scotia and northern New England wherever local surroundings are favorable, and they are widespread along the shores of southern New England, as well as New York, where the stream mouths of Long Island formerly were centers of abundance (p. 565). Their range also includes northern New Jersey—the Raritan River in particular; and there is a reliable old record of them in the lower reaches of streams and rivers of Delaware and Pennsylvania, at the head of Delaware Bay (Schuylkill River and Brandywine Creek in particular), and as far up the Delaware River as the swift water at Trenton, New Jersey (*70*: 94); but it is questionable whether there are any survivors today of this southernmost population. We have found no reliable basis for the repeated statements that they range southward to Virginia.[16]

They differ widely in numbers from place to place, even within short distances, depending on how well the local surroundings meet their rather exacting requirements. Thus Great Bay, New Hampshire, is a center of abundance, perhaps second only—considering its size—to the much more extensive shoal bays on the north shore of New Brunswick. But the inner part of the Bay of Fundy on the New Brunswick side is a region of great scarcity.[17]

There are progressively fewer American Smelts southward along the coast as a whole. This gradation may be illustrated for recent years by average landings that were about 25–40 times greater for the Gulf of St. Lawrence shore of New Brunswick than for the longer Maine shoreline. For 1899, when the status of American Smelts represented natural conditions more nearly than their present status, the catch for Maine was 1,055,000 pounds, but only 154,000 pounds thence southward along the coast of New England. Westward and southward from Connecticut the commercial catches are negligible, and seemingly always have been.

Occurrence in Fresh Water. It has long been a matter of common knowledge that some American Smelts are also landlocked. In eastern North America there were indigenous populations in Long Lake, near Plymouth, Massachusetts (whence the Museum of Comparative Zoology received 10 specimens in 1875).[18] They occur in some lakes in New Hampshire (Squam, Winnisquam, and Winnipesaukee) and in many of the coastal lakes and ponds of all the principal river basins in Maine.[19] There are native Smelt in: many of the Nova Scotian (*61*: 29) and New Brunswick lakes; Lake Memphremagog (partly in Vermont and partly in Quebec); Lake Champlain (in abundance); Lake St. John, eastern Quebec; Lac des Isles, Green Lake, and Lac Brulé in western Quebec northwest of Montreal; and in Muskrat and Doré lakes of Ontario, which are tributary to the upper Ottawa River, at an altitude of about 3,000 feet above sea level (doubtless as a "relic of the time following the retreat of the last ice sheet, when an arm of the sea extended up the Ottawa Valley to the head of Lake Timiskaming"; Dymond, *23*: 59). No doubt there are native Smelts in various

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[16] Based seemingly on Jordan and Gilbert (*53*: 293).

[17] For discussion, see Jeffers, *46* (1932): 27.

[18] Perhaps elsewhere on Cape Cod (locality not specified), to judge from an article in *Forest and Stream* for April 18, 1889.

[19] For the Smelt lakes of Maine, see Kendall, *56*: 273–278.

other Canadian lakes, but we have not chanced to hear of them. We have not found any report of landlocked Smelt for Newfoundland.

There are smelts of the subspecies *mordax* in lakes of the White Sea region, the Kola Peninsula (*5*: 132, as *eperlanus dentex* natio *dvinensis* morpha *spirinchus*), and eastern Siberia. In Europe the subspecies *eperlanus* is widespread in lakes of Germany, Denmark, southern Norway, Sweden, Finland, and Russia; even in the Volga River and the Caspian Sea there are smelts, as has long been known (*57*: 241).

Artificial Introductions. It has been a matter of scientific record for more than a century and a half that the introduction of smelts from one lake to another is possible if the new situation is favorable for them (*8*: 182), and on various occasions they have been introduced successfully from salt to fresh water. The literature on this species includes repeated references to such introductions on both sides of the Atlantic, either by the transfer of fertilized eggs or by the transport and release of adult fish. In America, the earliest recorded case was near the close of the 18th century, when they were successfully introduced into Jamaica Pond near Boston (*83*: 20), whence the Museum of Comparative Zoology received a series in 1875. As our concern here is primarily with the marine form, it is enough to add that introductions[20] account for their presence today in certain lakes of New Jersey, the Rangeley Lakes, Moosehead Lake, the upper Penobscot River, and Eagle Lake in Maine, and the Great Lakes region. They are now (1957) so plentiful in Lake Erie that catches taken there are regularly on sale in Boston markets.

Synonyms and Selected References:

Salmo eperlanus Pennant, Arctic Zool., *1*, Introd., 1784: 127 (name, Kamchatka); Mitchill, Rep., in part, on Fishes of New York, 1814: 12 (New York; earliest rep. in e. N.Amer.); Trans. Lit. philos. Soc. N.Y., *1*, 1815: 435 (color, anal rays, Passaic R., New Jersey); Gmelin, Naturg., Fische, 1818: 298 (freshw. lakes, Prussia).

Salmo (*Osmerus*) *eperlanus* (in part) Pallas, Zoogr. Rosso-Asiat., *3*, 1831:[21] 386 (descr., Baltic and White seas, Kamchatka, Sea of Okhotsk; includ. subspp. *eperlanus* and *mordax*).

Salmo (*Osmerus*) *spirinchus* (in part) Pallas, Zoogr. Rosso-Asiat., *3*, 1831:[21a] 387 (descr. includ. smelts of Europ. Russia and e. Siberia, subspp. *eperlanus* and *mordax*).

Atherina mordax Mitchill, Trans. Lit. philos. Soc. N.Y., *1*, 1815: 446 (descr., adipose fin noted).

Salmo eperlano marinus Gmelin, Naturg., Fische, 1818: 299 (North Sea, Baltic).

Osmerus viridescens LeSueur, J. Acad. nat. Sci. Philad., 1818: 230 (descr., Boston, Massachusetts, to Newport, Rhode Island); DeKay, Zool. N.Y., *3*, 1842: 243; *4*, 1842: pl. 39, fig. 124 (descr., New York); Storer, Mem. Amer. Acad. Arts Sci., N.S. *2*, 1846: 449, 450; also separate, Cambridge, 1846: 197, 198 (brief descr., cf. Europ. smelt; Maine, Massachusetts, New York); Cuvier and Valenciennes, Hist. Nat. Poiss., *21*, 1848: 388–389 (diagn., New York, cf. Europ. *eperlanus*); Perley, Cat. [in part] Fish. N. Brunsw., Nova Scotia *in* Rep. Fisher. Bay of Fundy, ed. 1, 1851: 135; Descr. Cat. [in part] . . ., ed. 2, 1852: 202; Descr. Cat. [in part] . . ., as separate, ed. 2, 1852: 24 (size, abund., odor, cod bait and manure, feed., capture); Rep. Fisher. Gulf of St. Lawrence, ed. 2, 1852: 22, 23 (rivers, abund., capture, spawn., 2 spp.); Bell, Canad. Nat. Geol., *4*, 1859: 206 (Gulf of St. Lawrence); Fortin, Rep. Magistr., Exped. Protect. Fisher., Gulf of St. Lawrence (1861, 1862), 1863: 120 (Quebec City; not seen); Norris, Proc. Acad. nat. Sci. Philad. (1861), 1862: 58–59 (diffs. between smelt of Schuylkill R. and north. *viridescens*); Günther, Cat. Fish. Brit. Mus., *6*, 1866: 167 (Boston and New York; scarcely distinct from *eperlanus*); Storer, Fish. Mass., 1867: 149, pl. 25, fig. 4 (descr., size, abund., Massachusetts); Reeks, Zoologist,

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[20] For details, see Kendall (*56*: 351), Dymond (*24*: 12, 13), and Van Oosten (*71*: 64, 65).

[21] Date of publication probably was 1814, according to Sherborn (*99*: 164–167).

London, (2) *6*, 1871: 2556 (abund., Newfoundld.); Adams, A. L., Field Forest Rambles, London, 1873: 243 (spawn., distr., abund., New Brunswick coast, streams, food for pigs); Cox, Bull. nat. Hist. Soc. New Brunsw., *3* (13), 1895: 66 (abund. New Brunswick, landlocked in lakes); Montpetit, Poiss. d'eau douce Canada, 1897: 6, 477 (Quebec City, Trois Rivières, Quebec; not seen).

Osmerus eperlanus (in part) Smith, Nat. Hist. Fish. Mass., 1833: 147 (habitat, abund.); Richardson, Fauna Boreal.-Amer., *3*, 1836: 185 (Halifax, N.S., New England; like Europ. smelt, but origin of pelvics farther rearward, under 6th D. ray; descr. Europ. smelt); Storer, J. Boston Soc. nat. Hist., *2*, 1838: 432 (descr., abund. Massachusetts); Rep. Fish., Reptiles, Birds, Mass., 1839: 108 (descr., local abund., refs.); Liljeborg, Svenska VetenskAkad. Handl. (1850), 1851: 304 (Archangel); Perley, Rep. Fisher. G. of St. Lawrence, ed. 2, 1852: 23 (see under *O. viridescens* above) Rice, Rep. Comm. Fish. Md., 1878: 41–94 (hatchery methods, develop., Raritan R., New Jersey, variations, scales show Amer. smelt same as Europ. smelt, refs.); Smitt, Hist. Scand. Fish., ed. 2, *2*, 1895: 869, 872 (*mordax* synon. of *eperlanus*); Knipowitsch, Ann. Mus. Zool., Acad. imp. Sci. St. Petersb., *2*, 1897: 153 (White Sea region); Fowler, Proc. Acad. nat. Sci. Philad., *63*, 1912: 555 (*mordax* united with *eperlanus*, cf. French and Amer. specimens).

Osmerus spirinchus Liljeborg, Svenska VetenskAkad. Handl. (1850), 1851: 304 (White Sea); Smitt, Svenska VetenskAkad. Handl. (1885), N.F., *21* [8], 1886: 168, 189 (White Sea; cf. proport. dimens. for *spirinchus*, *dentex*, *eperlanus*); Hist. Scand. Fish., ed. 2, *2*, 1895: 867 (name for Arctic smelts), 868 (distinct from *eperlanus* and *dentex*).

Osmerus mordax Gill, Proc. Acad. nat. Sci. Philad. (1861), Append., 1862: 53 (in synop., fishes e. coast N. Amer.); Adams, Field Forest Rambles, London, 1873: 306 (freshw., New Brunswick); Baird, Rep. U.S. Comm. Fish. (1871–1872), 1873: 826 (Woods Hole, Massachusetts); Gill, Rep. U.S. Comm. Fish. (1871–1872), 1873: 810 (e. coast U.S.); Lanman, Rep. U.S. Comm. Fish. (1872–1873), 2, 1874: 224, 225 (season, abund., Bay of Chaleur, n. New Brunswick, cod bait, capture with artif. fly); Jordan, Manual Vert. north. U.S., ed. 1, 1876: 261; and later edits. (descr., range); Goode and Bean, Bull. Essex Inst. Salem (1879), *11*, 1880: 23 (abund., season, Essex Co., Massachusetts; cf. Europ. *eperlanus*); Bean, Proc. U.S. nat. Mus. (1880), *3*, 1881: 105 (Maine, Massachusetts, Connecticut); Jordan and Gilbert, Bull. U.S. nat. Mus., *16*, 1882: 293 (descr., Virginia northward); Goode, *et al.*, Fish. Fish. Industr. U.S., 1 (3), 1884: 543, pl. 199 (range, habits, early abund., fishery); Stearns, Proc. U.S. nat. Mus. (1883), *6*, 1884: 124 (abund., C. Breton, Nova Scotia); Bean, Fish. Penn., 1893: 64 (Pennsylvania); Jordan and Evermann, Rep. U.S. Comm. Fish (1895), 1896: 294 (Virginia to Gulf of St. Lawrence; also Lake Champlain and L. Memphremagog); Bull. U.S. nat. Mus., 47 (1), 1896: 523 (descr., range); Low, Ann. Rep. geol. Surv. Canada, App. III to Rept. L, N.S. *8*, 1896: 329 (Northwest R., Lake Melville, head of Hamilton Inlet, Labrador); Anon., Rep. U.S. Comm. Fish. (1897), Append., 1898: 188 (no. and descr. of eggs, culturing procedure, artif. propag., Cold Spring Harbor, Long Island, New York); Bean, 7th Rep. Forest Comm. N.Y. (1901), 1902: 256, 351 (New York locals., spawn., eggs, food); Bull. N.Y. St. Mus., *60*, Zool. 9, 1903: 282 (descr., size, distr., bait and food for larger salmonoids, habits, season in N.Y., artif. propag. New York, New Jersey, Pennsylvania; lakes); Schmitt, Monogr. Isle d'Anticosti, 4, Zool., Poiss., 1904; 285 (common, Anticosti; plent. n. coast, Esquimaux Pt.); Fowler, Rep. N. J. St. Mus. (1905), 1906: 115 (descr., ill., New Jersey, Delaware; *sergeanti* Norris 1868 a synon.); Tracy, 36th Rep. R.I. Comm. inl. Fish., 1906: 57 (season, abund., food, max. size, Rhode Island); Evermann and Goldsborough, Proc. biol. Soc. Wash., *20*, 1907: 105 (St. Lawrence R. to Quebec City, Trois Rivières; landlocked, New Brunswick and Quebec); Fowler, Amer. Nat., *41*, 1907: 7 (Schuylkill R. and Delaware R.); Kendall, Occ. Pap. Boston Soc. nat. Hist., 7 (8), 1908: 48 (New England locals.); Proc. Portland nat. Hist. Soc., *2* (8), 1909: 221 (C. Breton, Nova Scotia, by ref. to Stearns, 1883); Tracy, 40th Rep. R.I. Comm. inl. Fish., 1910: 84 (descr., Rhode Island); Sumner, Osburn, and Cole, Bull. U.S. Bur. Fish., *31* (2), 1913: 743 (Woods Hole region, parasites); Halkett, Check List Fish. Canada, 1913: 55 (genl. range, Lac des Isles, Gatineau R. system, Quebec); Cockerell, Bull. U.S. Bur. Fish. (1912), *32*, 1914: 136 (scales descr.); Fowler, Proc. Boston Soc. nat. Hist., *35*, 1917: 112 (Maine, Massachusetts locals.); Latham, Copeia, 1917: 18 (season, Orient, New York); Wilson, Proc. U.S. nat. Mus., *53*, 1917: 59 (copepod parasite, Woods Hole, Massachusetts); Huntsman, Trans. roy. Soc. Canada, (3) *12* (4), 1918: 63 (Gulf of St. Lawrence, warm surface water layer); Fowler, Proc. biol. Soc. Wash., *32*, 1919: 56 (tidal streams, head of Delaware Bay); Proc. biol. Soc. Wash., *33*, 1920: 149 (New Jersey locals., lakes where introduced); Huntsman, Contr. Canad. Biol. (1921), 3, 1922: 60 (Bay of Fundy locals., landlocked, Chamcook and Utopea lakes, New Brunswick); Linton, Proc. U.S. nat. Mus., *64*, 1925: 71, 102 (cestode parasites); Bigelow and Welsh, Bull. U.S. Bur. Fish. (1924), *40* (1), 1925: 143 (descr., ill., habits, abund., develop., commerc. import., Gulf of Maine);

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Osmerus dentex Steindachner and Kner, S.B. Akad. Wiss. Wien, Math. Nat. *61*, 1870: 429 (descr., n. China, lat.-line scales, *dentex* and *eperlanus*); Jordan and Gilbert, Bull. U.S. nat. Mus., *16*, 1882: 294 (diagn., Port Clarence, Alaska); Goode, *et al.*, Fish. Fish. Industr. U.S., 1 (3), 1884: 544, pl. 199 (Kamchatka, Port Clarence, Alaska); Murdoch, Rep. intern. Polar Exped. Pt. Barrow, Alaska, 1885: 131 (abund., Wainwright Inlet, Alaska); Smitt, Svenska VetenskAkad. Handl. (1885), N.F. 21 (8), 1886: 166–188 (cf. *eperlanus* and *spirinchus* [name used for White Sea smelt]); Turner, L. M., Contr. nat. Hist. Alaska, 1886: 102, pl. 10 (ill., abund. St. Michaels, Alaska, use by Eskimos); Jordan, Rep. U.S. Comm. Fish. (1885), 13, 1887: 830 (Alaska); Nelson, Rep. nat. Hist. Collect. Alaska, 3 (Fish.), 1887: 313 (color, abund., Kotzebue Sd., St. Michaels, Alaska); Smitt, Hist. Scand. Fish., ed. 2, *2*, 1895: 868 (fewer gill rakers than in *eperlanus*); Jordan and Evermann, Bull. U.S. nat. Mus., 47 (1), 1896: 524 (descr., Bering Sea coast, Alaska; w. coast N. Pacific S. to n. China); Jordan and Gilbert *in* Jordan, *et al.*, Fur Seals . . . Islands N. Pacif. (1896–1897), 3, 1899: 439 (Kamchatka, Alaska); Scofield *in* Jordan, *et al.*, Fur Seals . . . Islands N. Pacif. (1896–1897), 3, 1899: 497 (Port Clarence, n. Alaska, cf. Kamchatkan specimens); Jordan and Snyder, Proc. U.S. nat. Mus., *23*, 1901: 349 (Jap. specimens "not evidently different from Alaskan"); Jordan and Snyder, Proc. U.S. nat. Mus., *24*, 1902: 587 (descr., color, Kushiro, n. Japan); Schmidt, P. IU., Pisces Mar. Orient. imp. Rossici, 1904: 278–281, 335, 356, 396 (cf. other named species, distr., e. Siberia; Russ.); Smith and Pope, Proc. U.S. nat. Mus., *31*, 1907: 463 (Shiogama, Japan); Evermann and Goldsborough, Bull. U.S. Bur. Fish., *26*, 1907: 269 (ill., Alaskan locals., refs.); Preble, Biol. Surv., U.S. Dept. Agric., N. Amer. Fauna, *27*, 1908: 513 (Arctic Red R., Mackenzie R. Delta); Pavlenko, Trud. Obshch. estest., Kazan Univ., *42* (2), 1910: 15 (Peter the Great Bay, e. Siberia; Russ.); Snyder, Proc. U.S. nat. Mus., *42*, 1912: 403 (n. Japan, in markets); Jordan and Metz, Mem. Carneg. Mus., *6* (1), 1913: 10 (ill., Korea); Halkett, Check List Fish. Canada, 1913: 55 (Naas R., Brit. Columbia, Red R. of North, Mackenzie Delta, Arctic Canada); Hubbs, Proc. biol. Soc. Wash., *38*, 1925: 52 (N. Pacific, Arctic coast of Alaska, cf. Atlantic smelt); Jordan and Hubbs, Mem. Carneg. Mus., *10* (2), 1925: 149 (Hokkaido, Japan); Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish (1928), 2, 1930: 67 (in checklist, Alaska and nw. Pacific, S. to n. China); Tanaka, Fish. Japan, *48*, 1930: 947, pl. 188, fig. 515 (descr., ill., refs., Hokkaido, Japan); Schrenkeisen, Field Bk. Fresh-w. Fish. N. Amer., 1938: 72 (possible occur. landlocked, Pacific coast); Gunter, Amer. Midl. Nat., *28* (2), 1942: 308 (fresh and salt water, w. coast, N. Amer.); Nakamura, Contr. Centr. Fisher. Sta. Japan, 1 (43), 1946–1948: 259 (factors affect. hatch. of eggs).

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Osmerus spectrum Cope, Proc. Amer. philos. Soc., *11*, 1871: 490 (Wilton Pond, Maine); Kendall, Occ. Pap. Boston Soc. nat. Hist., 7 (8), 1908: 48 (Wilton Pond, Maine).

Osmerus mordax var. *spectrum* Jordan, Manual Vert. north. U.S., ed. 1, 1876: 262 (proport. dimens., Wilton Pond, Maine); Jordan and Gilbert, Bull. U.S. nat. Mus., *16*, 1882: 294 (diagn., Wilton Pond, Maine).

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Osmerus eperlanus dvinensis Smitt, Öfvers. VetenskAkad. Forh., Stockh. (1882), *39* (8), 1883: 34 (name applied to White Sea smelts); Berg, Freshw. Fish. Russia, 1923: 102 (refs., Russ.).

Osmerus dvinensis Smitt, Hist. Scand. Fish., ed. 2, *2*, 1895: 867, ftn. K, 868, table (name applied to White Sea smelts, by ref. to Smitt, 1882; sep. from *O. e. eperlanus* by length of longest anal ray and gill-raker counts).

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Osmerus mordax spectrum Jordan and Evermann, Bull. U.S. nat. Mus., 47 (1), 1896: 523 (descr., Wilton Pond, Maine); Jordan, Manual Vert. Anim. NE. U.S., 1929: 54 (size of eye and mouth, Wilton Pond, Maine); Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish. (1928), 2, 1930: 67 (Wilton Pond, Maine).

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Osmerus sergeanti Jordan, Manual Vert. Anim. NE. U.S., 1929: 54 (species or subsp., S. of New York).

Osmerus eperlanus dentex natio *dvinensis* morpha *spirinchus* Berg, Zoogeographica, Jena, *1*, 1933: 132 (lakes, White Sea region and Kola Penin.).

Osmerus sergeanti Hubbs, Proc. biol. Soc. Wash., *38*, 1925: 52 (species, possibly race).

Osmerus eperlanus mordax Wynne-Edwards, Bull. Fish. Res. Bd. Canada, 94, 1952: 17 (*mordax* subsp. of *eperlanus*).

Smelt, Perley, Rep. Sea River Fisher. N. Brunsw., ed. 2, 1852: 37, 62, 81, 82 (cod bait, abund., taken with fly); Chambers, E.T.D., Forest and Stream, *61* (20), 1903: 380 (Lakes Memphremagog and St. John, Quebec; stunted race in St. John); Stevenson, Canad. Field Nat., *58*, 1944: 128 (status in Lake Huron in 1943); McKenzie, Progr. Rep. Fish. Res. Bd. Canada, Atl. Sta., 35, 1944: 24 (decrease in nos., Miramichi region; favorable results of stream clearance); McKenzie, Bull. Fish. Res. Bd. Canada, 70, 1946: 3–20 (hist., fishery methods, catches, ne. New Brunswick).

March 1964

MUSEUM OF COMPARATIVE ZOÖLOGY
AT HARVARD COLLEGE
CAMBRIDGE 38, MASSACHUSETTS
"THE AGASSIZ MUSEUM"

To: Dr. Columbus O'D. Iselin
Woods Hole Oceanographic Institution
Woods Hole, Massachusetts;

with the compliments of the Fish Department

Henry B. Bigelow, Professor of Zoology, Emeritus
William C. Schroeder, Honorary Associate in Ichthyology

Giles W. Mead, Curator of Fishes
Myvanwy M. Dick, Research Assistant in Fishes

Associates in Ichthyology

Richard H. Backus (Woods Hole Oceanographic Institution)
Robert H. Gibbs, Jr. (United States National Museum)
N. B. Marshall (British Museum, Natural History)

Genus *Mallotus* Cuvier 1829

Capelin

Mallotus Cuvier, Règne Anim., nouv. ed., *2,* 1829: 305, 306; type species, *Clupea villosa* Müller, O.F., Zool. Danicae Prod., 1777: 245. Greenland.

Generic synonyms:

Clupea Müller, Zool. Danicae Prod., 1777: 245; for *C. villosa* Müller.

Salmo Fabricius, Fauna Groenl., 1780: 177, for *S. arcticus* Fabricius, Greenland; Bloch, Naturg. ausländ. Fische, *8,* 1794: 99, pl. 381, fig. 1 for *S. groenlandicus* Bloch, Greenland; Pallas, Zoogr. Rosso-Asiat., *3,* 1831: 389, for *S. socialis* Pallas, islands between Asia and America.[22]

Osmerus Nilsson, Prod. Ichthyol. Scand., 1832: 11, for *O. arcticus* Nilsson, Arctic Ocean and northern Norway; Cuvier and Valenciennes, Hist. Nat. Poiss., *21,* 1848: 385, pl. 621, for *O. microdon* Cuvier and Valenciennes, Norway.

Not *Salmo* Linnaeus 1758; type species, *S. salar* Linnaeus 1758.

Not *Clupea* Linnaeus 1758; type species, *C. harengus* Linnaeus 1758.

Not *Osmerus* Lacépède 1803; type species, *Salmo eperlanus* Linnaeus 1758.

Characters. Essentially as in *Osmerus* (p. 555), except as follows: SCALES much smaller and much more numerous, 170–220 transverse rows along lateral line,[23] each scale with only about 5–6 concentric striae posterior to the so-called nucleus and 3 anterior to it, the visible lateral line extending to base of caudal fin; all TEETH so small as to be easily overlooked, there being no conspicuous fangs either on roof of mouth or on tongue; the ADIPOSE fin about half as long at its base as the anal, and shaped as in Figs. 133, 134; the PECTORAL fins broadly rounded (rhomboid in smelts; cf. Figs. 131, 134); rays of the pectorals (15–20) and ANAL (20–21) more numerous (*Osmerus* with 13 at most in pectorals, 17 in anal; Table II); and the plate on dorsal side of skull above vomer (PROETHMOID of Starks) not divided by a longitudinal median suture (p. 555).[24]

Sexual Dimorphism. The two sexes differ so conspicuously, one from the other, that male and female capelin are separable at a glance. The base of the anal fin is strongly convex in males but nearly straight in females. The least depth of the caudal peduncle is greater in males (about 80–85 % of distance from tip of snout to eye) than in females (about 60–75 %). The scales on the males are lanceolate along a band close above the lateral line from the gill opening to the base of the tail, and along a second similar band low down on the side extending from the pectorals to the pelvics and thence to the anal, but on females they are rounded. The dorsal fin usually originates a little farther forward in males (about 52–54 % of SL from snout to dorsal) than in females (about 55–60 %). The 5th–12th anal rays are thicker in males than in females. The margin of the anal is weakly convex, indented opposite the 9th and 10th segmented rays in mature males but about straight in females. The pectoral fins are longer in males (about 80–85 % as long as head) than in females (about 60–65 %) and much wider (Figs. 133, 134).

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[22] For date of publication, see Sherborn (*99*: 167).

[23] A total of 150 according to Jordan and Evermann (*51*), followed by Hubbs (*43*: 51) and Chapman (*11*: 299).

[24] For additional skeletal characters, see Chapman *11*: 291–293, figs. 2, 5, 6, 13, 14.

The difference in appearance between the sexes becomes greatly accentuated with the approach of spawning time, when the skin on maturing males thickens along the bands of modified scales, each of which develops a finger-like extension clothed with epidermis (Fig. 135 G–I), so that the nuptial bands then appear as two furry or plush-like ridges (Figs. 133, 135 F). Templeman has reported (*110*: 146) that "while maturing males showed only faint traces of these ridges on May 20th all the males near the beaches have well developed spawning ridges a month later"; this illustrates the rapidity with which this nuptial development may take place. Small roundish so-called nuptial tubercles also develop along the rays of the pectoral, pelvic, dorsal, and anal fins (Fig. 135 C); these are most prominent and the most numerous on the paired fins, less so on the dorsal, and usually sparsest and smallest (or lacking) on the anal. Scattered tubercles also develop on the lower side of the head (*39*: 417–420). In maturing males the outer ends of the terminal branches of the rays along the midsection of the anal fin fuse together at their tips to form a plate-like structure (Fig. 135 D; *114*: 200).

Finally, in Pacific specimens the vertebrae are reported to be more numerous on the average in males (av. 65.65) than in females (av. 65.13) (*39*: 419), but in Atlantic specimens as more numerous in females (av. 65.65) than in males (av. 65.52) (*110*: 148), a puzzling situation that we are not in a position to clarify.

Remarks. Capelin are small, slender, silvery, smelt-like fishes, growing to a maximum length of about 7.5–8 inches (p. 579). Though marine in habit, they run up into very shallow water to spawn, and occasionally into the mouth of rivers. They are North Boreal to Arctic in nature and are present in countless multitudes in their centers of abundance. They are distinguishable from *Osmerus* by the differences given on p. 554.

Range. North Atlantic and tributary parts of the Arctic; in the eastern Atlantic, from Spitsbergen and Jan Mayen (*48*: 90), southeastern Greenland, Iceland, White Sea, and northern Norway southward to Trondheim Fjord in abundance, occasionally to Oslo Fjord and the Faeroes;[25] in the western Atlantic, from southwestern Greenland, Hudson Bay, and northern Labrador, southward to Newfoundland (including the islands of St. Pierre and Miquelon), the Gulf of St. Lawrence, northern Nova Scotia, and occasionally to the eastern part of the Gulf of Maine; Arctic coasts of Alaska and Canada (Bathurst Inlet, Coronation Gulf, and Welcome Gulf) (*87*: 710; *88*: 187, 188; Bean *in 58*: 135); in the North Pacific southward to the Strait of Juan de Fuca in the east and to Korea (*66*: 1) and northern Japan (*43*: 55) in the west.

Species and Subspecies. The capelins of the North Atlantic and North Pacific were originally described as two separate species, the former as *villosus* Müller 1777 (*67*: 245), the latter first as *catervarius* Pennant 1784[26] (*75*: cxxvii) and later as *socialis*

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[25] Jensen (*48*: 90, ftn.) has reported four specimens (in the Museum in Copenhagen) for the Faeroes, taken in 1870, and A. Vedel Tåning informs us that 50 were trawled among the Faeroes in 1938.

[26] This account was evidently taken from Steller (*108*: 149), as pointed out by Schultz (*98*: 15). For the nomenclatural validity of this name, see Hubbs and Chapman (*44*: 296).

Pallas 1814 (*73*: 389). These early names for the Pacific capelin seem then to have been overlooked; at least all the subsequent references to them seem to have been under the name *villosus* down to 1937 (Soldatov and Lindberg, *105*: 57; Hart, *39*: 417–420); and this same course was followed by Saemundsson as recently as 1949 (*93*: 93). In 1937, however, Schultz (*98*: 13–20) reported that the capelin of the Bering Sea region differ statistically from those of the Murman coast and of Newfoundland in the number of scales and pectoral fin rays, in the distance from the tip of the snout to the insertion of the pectoral fins, and in what he termed the "character index," i. e. the number of dorsal rays, plus the number of anal rays, plus the number of pectoral rays, plus the number of scales below the lateral line, minus the total number of gill rakers on the first arch (see Key, below). He also reported that Pacific capelin average smaller at maturity than the Atlantic fish.

Accordingly, Schultz revived *catervarius* as a distinct species, in which he has been followed by Clemens and Wilby (*13*: 23, 97) as well as by Hubbs and Chapman (*44*: 296); and Vladykov (*114*: 201) has contributed the additional information that the number of fused rays in the anal fin tend to be greater in Pacific capelin than in Atlantic specimens (Table III). On the other hand, Vladykov, while adding support to the impression generally held that Pacific capelin average smaller than Atlantic fish, has pointed out that the greatest length credited to a capelin anywhere was 10 inches or less for the Arctic coast of Alaska (*26*: 105), where *catervarius* rather than *villosus* is to be expected on geographic grounds, if the two are separable.

Table III. Relative Frequency in the Number of Fused Rays in the Anal Fin (in per cent) for Pacific and Atlantic Capelin.

Number of Fused Rays	Relative Frequency *Pacific*	Relative Frequency *Atlantic*
4...........	11.5	38
5...........	66	54
6...........	13.5	5

All in all, our present state of knowledge seems best expressed by rating *catervarius* as a subspecies of *villosus*, as Rumjanev has done (*91*), at least until someone has an opportunity to study adequate series of capelin from the Arctic coast of Canada; for example, from Bathurst Inlet, or from Coronation Gulf, where they were reported many years ago (p. 574), or even from Hudson Bay—localities that are intermediate between those of record for *villosus* on the one hand and for *catervarius* on the other.

Key to Subspecies of *Mallotus villosus*

1a. Character index (see above) 30 or more (30–38 recorded).
villosus Müller 1777, p. 576.
1b. Character index (see above) not more than 29 (22–28 recorded).
catervarius Pennant 1784.
Both sides of the North Pacific, southward to northern Japan and Korea in the west; to the Strait of Juan de Fuca in the east.

Mallotus villosus (Müller) 1777, subspecies *villosus*

Capelin

Figures 133–136

Study Material. Over 100 specimens, 115–165 mm SL, from Newfoundland (including Labrador), St. Pierre and Miquelon, Halifax, Nova Scotia, Grand Manan, New Brunswick, and northern Norway, MCZ; also many handled both alive and freshly caught on the Atlantic coast of Labrador many years ago.

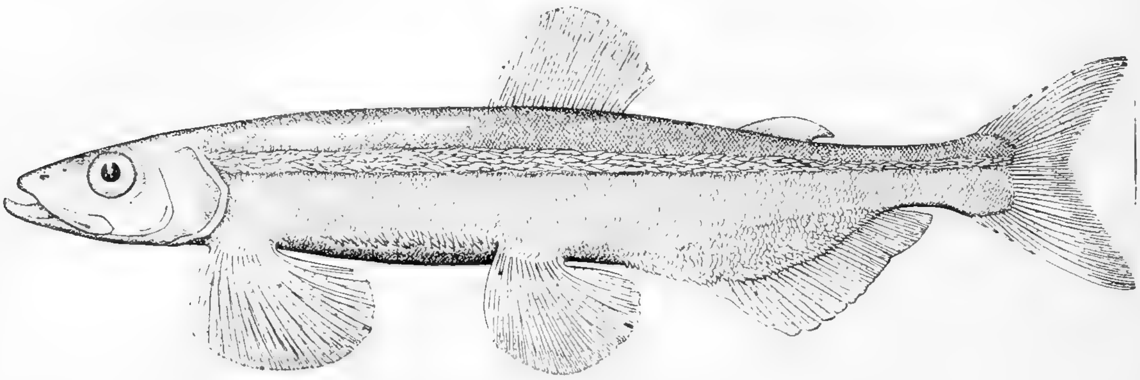

FIGURE 133. *Mallotus villosus villosus*, sexually mature male, from comparison with specimens 150–160 mm SL, from St. Pierre and Miquelon, south of Newfoundland. After Cuvier and Valenciennes as emended by Jessie H. Sawyer.

Distinctive Characters. The only fishes of the North Atlantic with which the adult of this species is at all likely to be confused are *Osmerus eperlanus* (American smelt, p. 559), *Argentina* (argentine, Part 4), or, in the southernmost part of the capelin's range, the silverside (*Menidia*). It takes little more than a glance to separate it from all of these, for its scales are very much smaller than those of *O. eperlanus* and its adipose fin is of a different shape (cf. Figs. 131, 134); its mouth is much larger but its scales much smaller than in *Argentina*; and it is only in its slender form and silvery color that it resembles the silverside, which has a much smaller mouth and a rayed (not adipose) second dorsal fin. For differences between the larvae of *M. v. villosus* and those of other fishes with which they are likely to be taken, see p. 581.

Description. Based on five males, 129–160 mm, and five females, 129–153 mm SL, from Newfoundland (including Labrador), St. Pierre and Miquelon, and Grand Manan.

BODY elongated, moderately compressed, its depth 5.8–6.2 in SL, its greatest thickness about 1.2–1.7 times distance from snout to eye; the dorsal and ventral profiles of head and trunk slightly convex, but males with contour more abruptly rounded along base of anal fin. Least depth of CAUDAL PEDUNCLE in males 15.2–16.7 times in SL, in females 19.0–21.8 times, thus noticeably deeper in males. SCALES present everywhere on trunk as well as on base of caudal, but not on dorsal or anal; 177–205 (170–220 reported); 32–37 in oblique series from origin of pelvics to midline of back—16–20 above lateral line (18–23 reported) and 16–19 below (18–23 reported); scales very small, cycloid, thin, not as deciduous as in *Osmerus*; the largest scales below lateral line, those of the females mostly ovoid with vertical axis about 1.5 times horizontal axis; the scales above lateral line smaller and more nearly round; mature males with a prominent band of lanceolate scales, about 5 or 6 scales wide, immediately above lateral line from gill openings to base of caudal; the scales narrow and very elongated posteriorly (Fig. 135 G–I); other differentiated scales extending along lower sides from near tip of pectorals to near anal base, of various shapes, some lanceolate (between pectorals and pelvics) and others more or less as shown in Fig. 135 (opposite anal), the apexes of some pointing obliquely downward. Scales along upper sides and back in males ranging in shape from roundish, but with longest axis horizontal, to pointed or flap-like rearward. A row of MODIFIED LATERAL-LINE SCALES in both sexes, from gill opening to base of caudal, with a median horizontal channel that is connected here and there from scale to scale. Most of the scales, particularly above the lateral line, with some of the circuli complete, but others, chiefly below the lateral line, with all of the circuli interrupted dorsoventrally; the scales above lateral line with fewer circuli than those below.

FIGURE 134. *Mallotus villosus villosus*, female, about 175 mm TL (7.75 in.), from Grosswater Bay, southeastern Labrador. After Goode; drawn by H. L. Todd.

HEAD with dorsal profile straight or very gently convex, 4.3–4.7 in SL. SNOUT pointed, 2.9–3.5 in head. EYE 3.9–4.7, its rear margin midway between tip of snout and rear margin of opercle, or a little closer to opercle. INTERORBITAL space straight or slightly concave, 3.5–4.6. POSTORBITAL part of head 2.0–2.3 in head. NOSTRILS in line with end of snout and upper edge of eye, the two openings on each side close together, oval-shaped, the posterior one with a flap, the distance from eye 7.0–8.5 in head. OPERCLE with broadly rounded margin. Margin of PREOPERCLE about 0.33 of distance between perpendiculars from rear margin of eye and margin of opercle. BRANCHIOSTEGALS 8. GILL RAKERS very slender, the longest 1.2–1.6 in eye; 8–10 rakers on upper limb of first arch (11 reported), 24–27 on lower limb (31 reported), total 32–37 (42 reported).

MOUTH oblique, the gape reaching to a perpendicular from nostrils. LOWER JAW

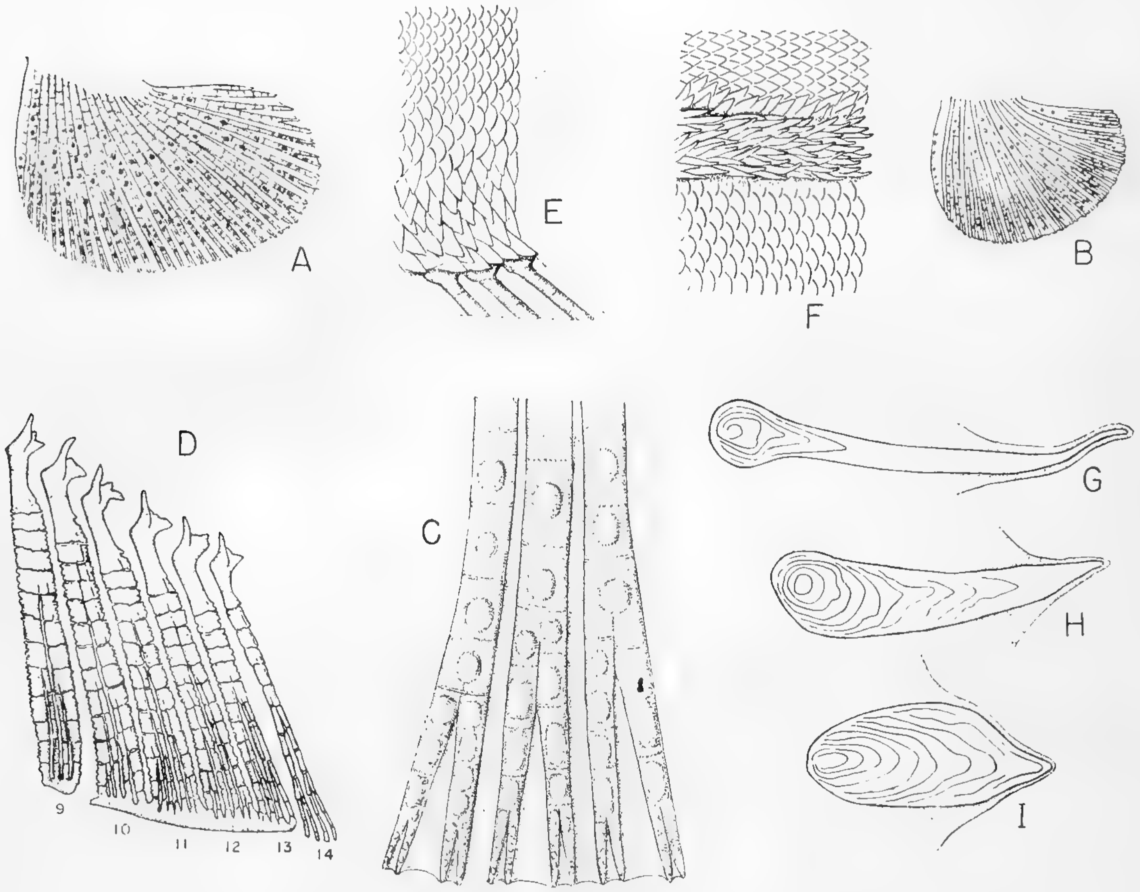

FIGURE 135. *Mallotus villosus villosus.* A, pectoral fin of sexually mature male, about 175 mm TL, from St. Pierre and Miquelon Island; fin widely spread to show distribution of nuptial tubercles on rays; about ×1.3. B, pelvic fin of same specimen; about ×1. C, distal portion of pelvic rays of same specimen as seen by reflected light; drawn to larger scale to show nuptial tubercles. D, middle sector of anal fin (from 9th–14th rays) showing bony distal plate developed in breeding males; from Vladykov. E, scales along side above first three split anal rays; about ×3. F, scales on side below dorsal fin, from close above to close below upper nuptial ridge; about ×3. G, scale from midbelt of upper nuptial band. H, scale from close beside upper nuptial band. I, scale from close above middle of base of anal fin. G–I from camera lucida drawings; about ×13. Drawn by Jessie H. Sawyer.

projecting. MAXILLARY beginning about halfway between anterior nostril opening and tip of snout, widening rearward, its posterior margin rounded and reaching to about opposite center of pupil. PREMAXILLARY extending a little past origin of maxillary, its length about equal to distance between tip of snout and nostril. MANDIBLE 1.6–2.0 in head.

TEETH. Lower jaw, maxillaries, and premaxillaries with a row of minute teeth, close-set, unevenly spaced. Vomer with a row of about 3 very small teeth on each side of a very short, toothless, median space. Palatines with one or two rows of very small teeth. Tongue boat-shaped, with numerous small retrorse teeth, but with no fangs as in *Osmerus.*

Dorsal with outer margin straight or slightly convex, its base 1.5–2.0 times snout, its origin a little closer to base of caudal than to tip of snout, its distance from latter about 52–54% of SL in males and 55–60% in females, with 12–14 rays,[27] the first 2 or 3 unbranched, the longest ray 0.9–1.3 times length of base. Dorsal adipose fin with outer margin straight or slightly convex anteriorly and straight or slightly concave posteriorly, situated behind dorsal, its base 1.7–1.8 times in dorsal base, its origin ranging from about over origin of anal fin to about over middle of anal base, its height 3.0–5.8 times in its base. Caudal deeply forked, its tips pointed in some but rounded in others. Anal with outer margin weakly convex in mature males and indented opposite 9th and 10th segmented rays but about straight in females, its base 1.5–1.7 times dorsal base in males but 1.2–1.4 times in females, its origin from tip of snout a distance of 70–73% of SL in males but 75–79% in females, and its origin from origin of pelvics a distance of 1.5–1.7 times in distance between anal origin and caudal base in males but 1.2–1.4 times in females, with 19–21 rays (17–22 reported),[27] the first 3 or 4 unbranched, the longest ray 2.3–3.1 times in anal base. Pelvics with rear margin weakly convex, their origin varying from slightly in advance of, to slightly behind, dorsal origin, with 8 rays, the first (outer) ray unbranched, the longest ray 1.4–1.8 times in head. Pectorals with rear margin broadly rounded, their area, when spread, larger in males than in females of about the same size, their origin under rear margin of opercle, with 18–20 rays, the first (upper) unbranched, the longest ray 1.5–1.7 times in head in males but 1.8–2.1 times in females.

Vertebrae 64–70 reported.

Sexual Dimorphism. See p. 573.

Color. In life, translucent, olive to bottle green above, with metallic reflections like the American smelt (p. 561) but with the back and head darker at spawning time. Sides a uniform silvery color below lateral line. Scales dotted with very small to minute dusky specks. Belly white. Lining of body cavity a dusky silvery color.

Size. The largest standard lengths (snout to base of caudal fin) that we have found to be definitely recorded for any Atlantic Capelin are 215 mm for males and 230 mm for one female, from the east coast of Newfoundland, where spawning males range from 130 to 215 mm and spawning females from 110 to 210 mm TL.[28] An average of 146.7 mm SL or 164.4 mm TL reported by Vladykov for 63 specimens (sex not specified) from the inner part of the Gulf of St. Lawrence and Cape Breton, Nova Scotia (*114*: tab. 2, 202), suggests that Capelin may tend to mature at a somewhat smaller size in higher than in lower temperatures. The weights of Newfoundland Capelin at different total lengths are given in Table IV.

Development and Growth. Newfoundland Capelin produce about 15,000–52,000 eggs, according to size.[29] And it is not likely that they are either much more productive or much less so in other parts of the Atlantic. The eggs of Newfoundland fish (Fig.

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[27] Last two rays of dorsal and anal, branching from a common base, were counted as one.

[28] Totals of 59,042 males and 23,567 females measured by Templeman (*110*: 145).

[29] Counts by W. P. Templeman.

Table IV. Average Weights of Newfoundland Capelin at Different Total Lengths.†

Length (mm)	Weight (oz.)		Length (mm)	Weight (oz.)		Length (mm)	Weight (oz.)	
	♀♀	♂♂		♀♀	♂♂		♀♀	♂♂
140 ...	0.48	—	170 ...	0.91	0.96	195 ...	1.40	1.57
150 ...	0.63	—	180 ...	1.03	1.13	200 ...	—	1.61
160 ...	0.71	0.78	190 ...	1.29	1.47	205 ...	—	1.75*

† After Templeman, *110*: 125.

* Four fish.

136 A–D) average 0.96–0.97 mm in diameter, are spherical, transparent, and of a reddish or reddish yellow hue, and have a moderately broad perivitelline space. They have no oil globule, though the yolk contains many minute globules that tend to unite as development proceeds. The eggs sink and are so sticky that they cling to each other or to anything on which they chance to come to rest.

Jeffers has observed that incubation occupies 55 days at a temperature of 0° C, 30 days at 5° C, and 15 days at 10° C, with about 12° the upper maximum, though the eggs may hatch in water as warm as 15° and in salinity as low as 7 ‰ (*46* [1931]: 17, 18).

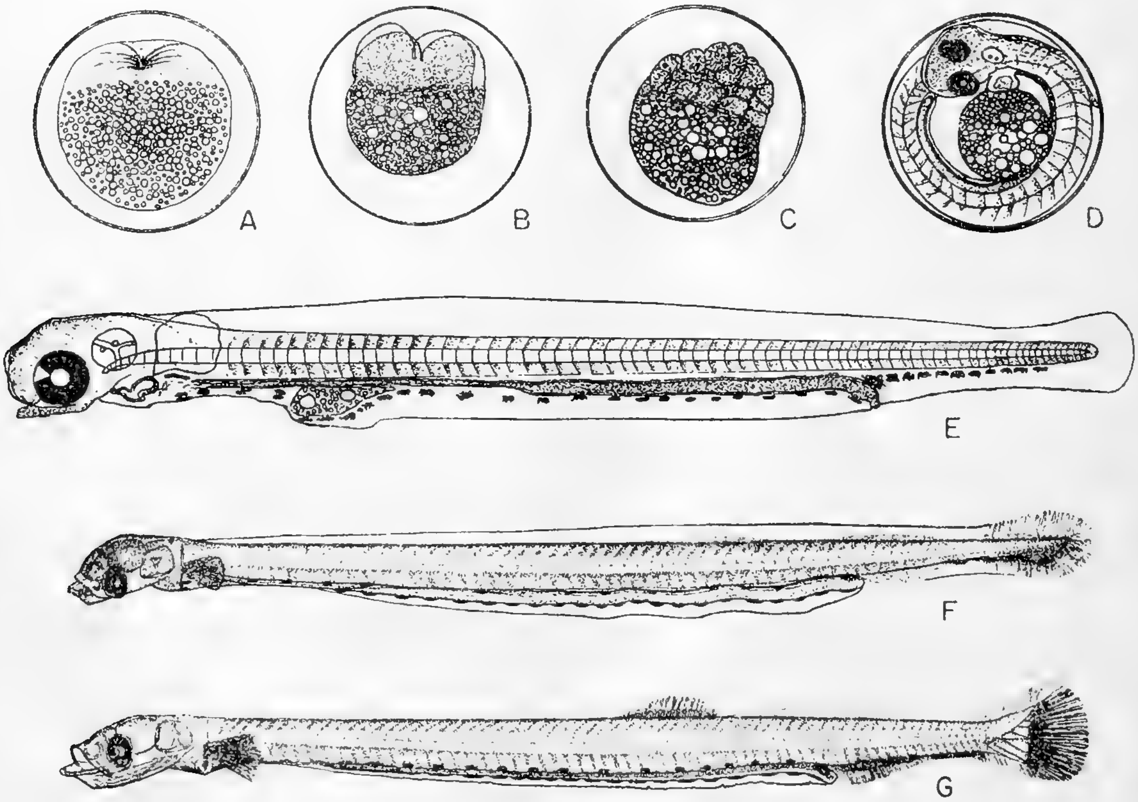

FIGURE 136. *Mallotus villosus villosus.* A–C, egg in segmentation stages. D, larva before hatching. E, newly hatched larva, 6 mm long. F, larva 9 mm long. G, larva 16 mm long. A–E, after Sleggs (*106*); F–G, after Templeman (*110*).

The larvae at hatching are 6–7 mm long (Fig. 136 E),[30] very slender, and wholly transparent except for a double ventral row of black pigment spots between the heart and the yolk sac, thence rearward a single row to the base of the future caudal fin, and a larger spot above the anus; and soon an additional row develops a little farther up along each side. The pectoral fins are already formed at hatching; the yolk sac has been absorbed at a length of about 7 mm; at 9 mm (Fig. 136 F) the first indications of the dorsal and adipose fins are apparent; at 20–30 mm all of the fins are clearly outlined; and at 30–40 mm the young fry begin to assume the outlines of the adult. It seems that most of the larvae are 20–40 mm long by their first winter, 40–65 mm early in the following spring, and 60–80 mm by midsummer, when they are about one year of age. Table v gives the subsequent relation between age and total length for Newfoundland fish taken inshore in late June and July, according to Templeman's detailed studies of the scales and otoliths of extensive samples (*110*). These values correspond closely to lengths of 60–80 mm at one year, 135–150 mm for males and 105–125 mm for females at two years, and 155–205 mm for males and 130–195 mm for females at three years, as reported in 1933 for Newfoundland Capelin by Sleggs from length-frequencies combined with scale studies (*100*: 37). Pitt found much the same rate of growth for Grand Bank Capelin (*79*: 295–311).

Table V. Total Lengths (mm) of Newfoundland Capelin at Two through Five Years of Age, Taken Inshore in Late June and July.*

	Males		Females	
Ages	Range	Av.	Range	Av.
2 years...	140–180	159.7	115–165	141.8
3 years...	130–200	174.9	130–195	158.8
4 years...	155–210	189.6	150–205	176.7
5 years...	—	—	165–200	185.6

* After Templeman, *110*.

Comparison of Capelin Larvae With Other Larvae. Larvae of *Clupea harengus* (Atlantic herring) might be mistaken for those of *v. villosus* if taken together. But the position of the yolk sac, with its anterior end at least as far forward as the origin of the pectorals in *C. harengus* and definitely posterior thereto in *v. villosus*, will serve to distinguish them from each other until the yolk has been absorbed. During the earlier stages also, the anus is about 83% of the way back along the body in *C. harengus* but only about 75% of the way back in *v. villosus*. At lengths greater than 15–20 mm the presence of the adipose fin marks *v. villosus* as such.

Should larvae of *Osmerus eperlanus* (American smelt) be taken with those of *v. villosus*, an event not reported as yet, the two can be separated up to a length of about 15 mm by the presence in *O. eperlanus* of a ventral pair of black spots anterior to the pectoral fins. At larger sizes the very evident air bladder of *O. eperlanus* sets it apart from *v. villosus*.

Other northern fish larvae that parallel the larvae of *v. villosus* in their slenderness are those of *Pholis gunnellus* (rock gunnel) and *Ammodytes* (launce). But there should be no danger of confusion here, for the anus in these is near the middle of the body, as compared with about 75% of the way back in *v. villosus* (*110*: 68, 69).

[30] For excellent illustrations of Newfoundland larvae, see Dannevig (*20*: pl. 3, figs. 26, 27); for descriptions and illustrations, see Templeman (*110*: 70–75, figs. 18–20); for Icelandic larvae, see Schmidt (*96*: 16–18, pl. 1, figs. 24–28).

Age at Spawning. Sleggs (*100*: 21–30) and Templeman (*110*: 87–106) have shown from length-frequencies, scales, and otoliths that a great majority of the Newfoundland Capelin spawn when they are three years old, and this is also believed to be the case around Iceland as well as off northern Norway. But a few Newfoundland females do not spawn until they are four or even five years old, and Hansen has recently reported, from a study of otoliths combined with length-frequencies, that in western Greenland waters 48–69 % (according to locality) do not spawn until the fourth or fifth year (*37*: 121–124). On the other hand, Rachmanowa (*80*: 120) concluded that most of the spring-spawning fish on the Murman coast are only two years old (zweijährigen), and most of the summer spawners only one year old (einjährigen). But we are not in a position to judge the validity of these results, for no illustrations of the scales on which the observations were based are included in the account.

In either case, most of them die shortly after they have spawned once, though some females may spawn twice or even three times during their life.[31]

Spawning Season. In the western Atlantic the Capelin are spring-summer spawners, with the season opening some weeks later in the northern part of the breeding range than in the southern part. In Hudson Bay they have been reported as spawning from late July into early August (*112*: 21). For the years 1941 and 1942, when detailed information was obtained for many localities in Canada (*110*: 56, 57, figs. 14, 15), they were spawning from July 25 to August 20 along Labrador north of Hamilton Inlet, from June 18 to August 25 on the outer Labrador coast south of that point, from June 1 to August 25 along the coast of eastern Newfoundland, from June 1 to August 4 along the western part of the coast of southern Newfoundland, from June 6 to July 2 along the northern part of the coast of western Newfoundland, and from June 1 to August 12 in the Strait of Belle Isle. The chief production took place during the last three weeks of June and first three weeks of July in eastern and southeastern Newfoundland, and some weeks later in outer Labrador. In 1931 and 1932 the season seems to have been earlier, at least in Newfoundland waters, for the latest dates reported by Sleggs were June 28 to July 3. But year-to-year variations of this sort seemingly are not wide, for Anspach, writing in 1819, described the Capelin as coming into Conception Bay about the 20th of June, to continue "on this coast for about six weeks" (*2*: 400, 401). Templeman has also reported that on rare occasions Capelin "may return again to the beaches to spawn" some weeks after the main spawning period has ended. And it seems that Capelin larvae taken around Newfoundland in April and May are more likely to be the product of late spawning inshore than of spawning that may commence as early as February offshore, as has been suggested (*101*: 35).

Along the coast of western Greenland the Capelin spawn from May through June and less commonly into July (*27*: 177, 178; *90*: 135), from early March into June around southwestern and southern Iceland, and until August around the northwestern, northern, and eastern coasts (*92*: 413). The spawning season lasts from late April or

[31] See Templeman (*110*: 62–64) for the evidence upon which this statement rests.

early May through June in northern Norwegian waters (*14*: 152); but on the Murman coast the fish are inshore from March to July; and Rachmanowa's observations (1928) suggest that there may be two reproduction peaks, an early one in March and April and a late one in June and July.

Spawning Grounds. Capelin spawn on the bottom close inshore and on the offshore banks as well (see below). It has been a matter of common knowledge for generations that most of the hordes of Capelin of Newfoundland (including Labrador) spawn right up on the beaches, even in the wash of the waves;[32] and multitudes spawn similarly along the intertidal zone in Greenland waters. But considerable spawning also takes place near shore, from 2 or 3 fms. down to 20 fms. or so; occasionally even at 40–50 fms.;[33] and at 25–35 fms. on the Grand Bank, where Pitt has recently reported the widespread presence of spawning populations (*79*: 279–281). In Icelandic waters they "most frequently breed in rather deep water."[34] Around northern Norway also, they have been reported as spawning mostly at depths of 4–20 fms. (*94*: 172); if beach spawning takes place at all there, this is not in an amount sufficient to have attracted the attention of either local fishermen or scientists. In the Barents Sea "eggs are most often caught . . . above depths from 50–100 meters" (Rass, *81*: 31).

Type of Bottom for Spawning. When Capelin spawn on the beach, they usually select stretches of gravel for the purpose rather than sandy stretches where the eggs are more apt to be buried by the action of the waves. The chief production of eggs on the Newfoundland beaches occurs where the grains of gravel run about 5–15 mm in diameter (*110*: 41), and on the Grand Bank where the sand grains are almost 0.5–2.2 mm (*79*: 280). Pacific Capelin, which are supposed to average smaller than those of the Atlantic, are reported as spawning chiefly where the gravel size is 1–5 mm (*40*: 24). But the fish do sometimes deposit their eggs on rocks, on sand, and even on algae, more commonly so, it seems, on the western Greenland coast than on the Newfoundland coast (*48*: 82). And when they spawn regularly below the intertidal zone, as seems the general rule in Norwegian waters, they may do so on sand, or without regard for the nature of the bottom.

Spawning Activities. The schools that come in on the beach consist solely of mature males and mature or maturing females; the juvenile fish remain somewhat farther out, where quantities of them are often seen, most of them deeper down. On the whole the larger fish spawn earlier than the smaller ones.

"The spawning act," writes Templeman, "has been observed by a few scientists, and by tens of thousands of Newfoundlanders," for Capelin spawning on the beach are in such dense schools that they are in plain view from the strand (*110*: 33). So spectacular are their spawning activities that these have been described in vivid terms,[35] the earliest, it seems, for the Pacific subspecies *catervarius* Pennant, in 1784 (*75*: CXXVII; *73*: 389), and time and again for the Atlantic *villosus*.

[32] Anspach, for example, wrote in 1819 (*2*: 401) of Capelin depositing their eggs "on the sand" in Conception Bay.

[33] For details, see especially Templeman (*110*: 59–61).

[34] Information contributed by A. Vedel Tåning, from observations by H. Einarsson.

[35] The accounts by Perley (*76*: 135) and Lanman (*60*: 225), often quoted, evidently were taken (partly verbatim)

As the fish run in on the beach, either two males may squeeze a female between them or a single male may keep in close contact with a female. The spawning trios or pairs, having run up the beach as far as they can, deposit their sperm and eggs and then separate to regain deeper water again if they be fortunate; so many of them are not that the beaches where Capelin are spawning usually are lined with windrows of dead fish. Thus Anthonie Parkhurst described them as early as 1600 as "driven drie by the surge of the Sea . . . you can take up with a shove-net as plentifully as you do wheate in a shovell" (*in 35*: 133). The mass strandings of Capelin have been described repeatedly since then, as by Anspach in 1819 for Conception Bay (*2*: 400). Even if the Capelin do escape in the wash of the waves, they are so exhausted and the fins of the males so battered that multitudes of the dead and dying are to be seen floating close inshore. It appears that nearly all of those remaining must perish soon thereafter, so unusual is it for a Capelin to spawn more than once during its lifetime.

Spawning is said to take place chiefly in cloudy weather or at night, without regard for the stage of the tide, and it is likely that the course of events is similar for Capelin that spawn in deeper water where they do not come under direct observation.

The eggs spawned on the beach are soon mixed with gravel by the waves, resulting in "a quivering mass of gravel and attached eggs" (Templeman, *110*: 41). But multitudes of those that have failed to adhere there drift offshore to sink to the bottom, where they too stick to anything with which they come in contact, often massing on nets and anchor lines.

Relation of Spawning to Temperature. In Newfoundland coastal waters, the Capelin spawn chiefly when and where the temperature is between 6° and about 8 or 9° C, but never in water warmer than about 10.5°; on the Grand Bank they spawn at 2.8–4.7° C (*100*; *110*; *83*), along western Greenland in water as cold as 3–5° C,[36] and in the Barents Sea at 2° (*81*: 29–33).

Habits and Migrations. The migratory pattern of the Capelin consists essentially of a passive dispersal of the larvae followed by the wanderings of the juveniles in search of food; this tends to bring them inshore and near the surface in early summer but offshore and into deeper water in autumn, leading finally to the inshore migration of the mature or maturing fish toward their spawning grounds in spring and summer.

There is no direct evidence from actual captures that Capelin as a whole spread very far during their period of growth, at least in the western side of the Atlantic. The greatest distance from land where immature fish have actually been taken, off Labrador or Newfoundland, is only about 75 miles for fry small enough to have been picked up in tow nets, and 150 miles for larger (hence older) juveniles trawled at or near the bottom (p. 585, Fig. 137). Around Iceland, where young fry abound close inshore, Jespersen has recorded captures of fry 60–70 miles offshore to the west, with a few taken at distances up to 200 miles or so toward the southeast (*50*: 12,

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from the earlier accounts by Chappell (*12*: 131–134), as Kendall (*55*: 29) and Hardy (*38*: 4–8) have pointed out. For recent accounts, see Sleggs (*100*: 38–40) and Templeman (*110*: 32–39).

[36] Information contributed by A. Vedel Tåning.

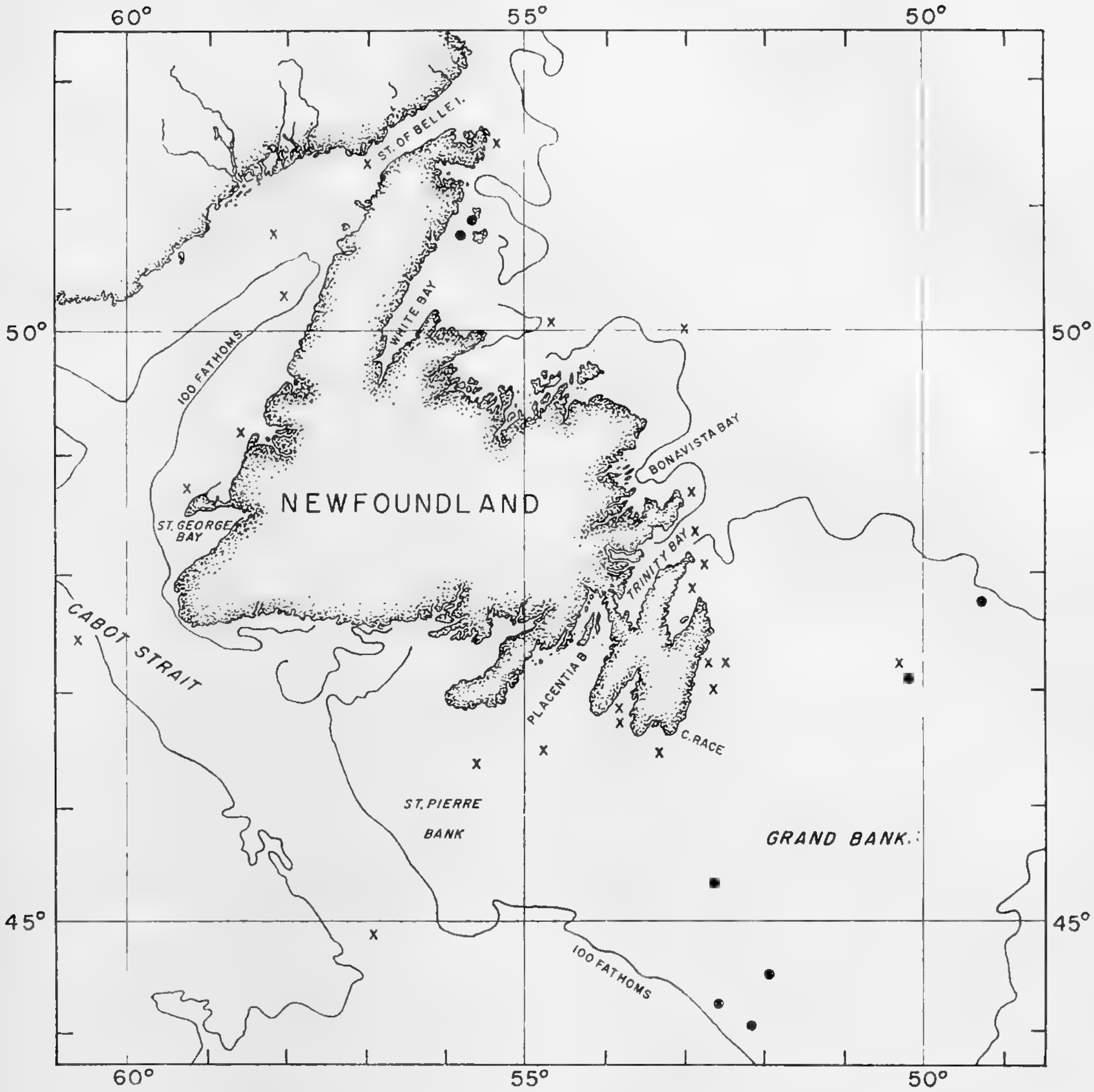

FIGURE 137. Recorded localities off Newfoundland where Capelin have been small enough to be taken in tow nets (x) or large enough to be trawled on or near the bottom (●). From Rep. Newfoundland Fish. Res. Comm.

fig. 8, and 15, fig. 10). A. Vedel Tåning has informed us that young fry from the Icelandic area are sometimes carried as far southward as the Faeroes, or even farther. While the fish of northern Norway and the White Sea region may disperse more generally in the Barents Sea, recent studies have not supported an older view that the center of population for the Capelin of the North Atlantic lies in the northern part of the Norwegian Sea, whence Capelin fan out, as it were, to northern Scandinavia, Spitsbergen, Jan Mayen, Iceland, Greenland, and the coast of North America.

Some, perhaps a majority, of the Capelin that are hatched well up in the ex-

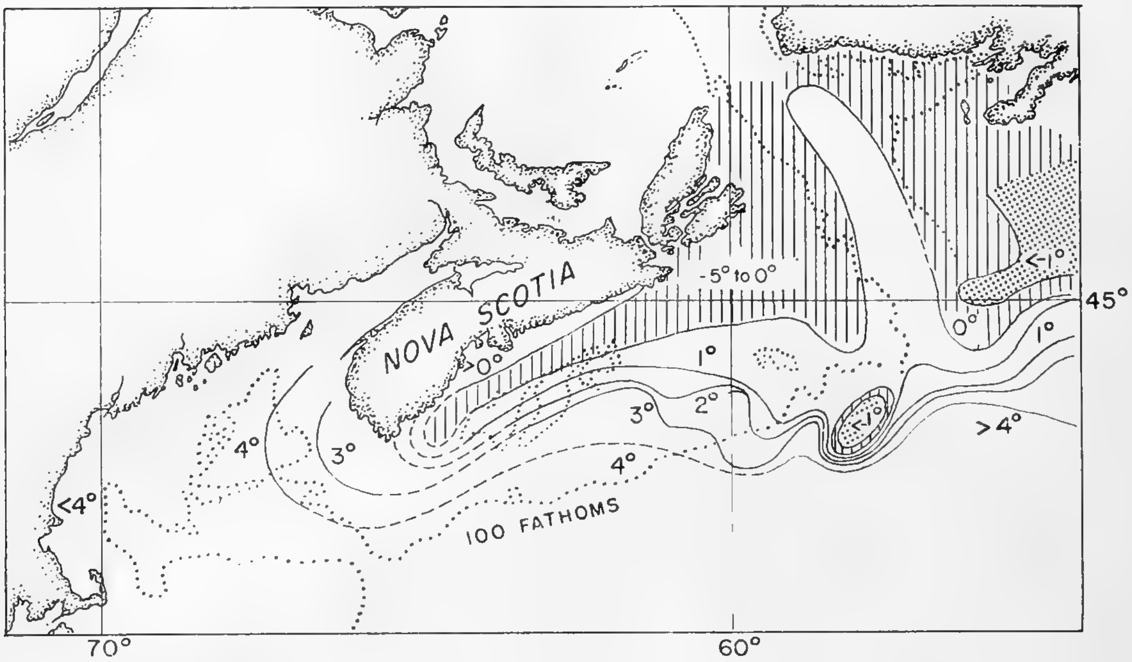

FIGURE 138. Distribution of the coldest water, irrespective of depth, from southern Newfoundland to the Gulf of Maine, for May 1915. After Bigelow, somewhat emended.

tensive bays of Newfoundland and Labrador pass the winter there, near bottom; they have been found repeatedly in the stomachs of winter-caught cod, and recently in the stomachs of seals taken in winter from Lake Melville above the head of Hamilton Inlet, Labrador (*3*: 295).

Those that are produced along the outer coasts, and some of the Bay Capelin as well, come under the influence of the general pattern of coastal circulation that is characteristic off western Greenland and Newfoundland (including Labrador) during the part of the year when Capelin are near the surface. On this basis the hosts of Capelin on the southern part of the west coast of Greenland (with some recruits from the southeast coast) may be expected to tend northward, perhaps as far as Disko.

There is nothing in the published record to suggest that Capelin are ever carried across the northern part of the Labrador Sea from Greenland to America, or that they survive the journey if they are. But those hatched on the outer coast of Labrador may be expected to come under the influence of the inner edge of the ice-laden Labrador Current until the latter slackens, in autumn (Fig. 138). Also, "a smaller branch of the Arctic current enters the Gulf of St. Lawrence (but not as a steady stream) through the Strait of Belle Isle on its north side" (Huntsman, *45*: 277, 278; Fig. 139); this doubtless brings some Capelin with it besides the icebergs that it sometimes carries as far as the Island of Anticosti. But there is no knowing how important a role this current may play in maintaining the stock of Capelin in the inner part of the Gulf of St. Lawrence.

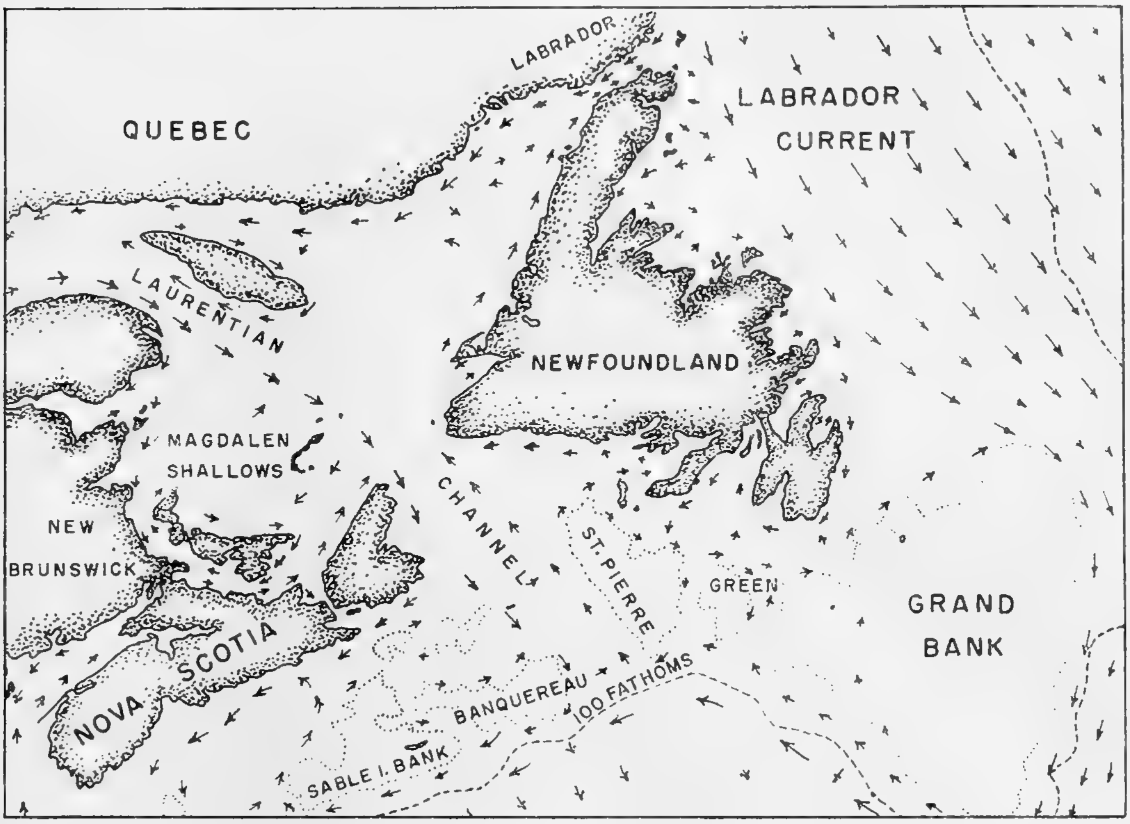

FIGURE 139. Prevailing circulation, spring and summer, around Newfoundland, in the Gulf of St. Lawrence and along the Atlantic Coast of Nova Scotia. After Huntsman.

Capelin hatched along the northern part of the coast of western Newfoundland, together with the older juvenile fish, may similarly be expected to drift at first northward and then outward along the southern side of the Strait of Belle Isle, if they travel that far. Off the coast of eastern Newfoundland, however, where the main drift of the Labrador Current lies well out from the coast (usually skirting the eastern edge of the Grand Bank rather than flooding the latter), the Capelin might be expected to either pass their juvenile years nearby or disperse over the Bank. This expectation is borne out by the localities where the larvae and older juveniles have been taken (Fig. 137).

Presumably the waves of Capelin that occasionally invade the Bay of Fundy are carried thither by the ice-chilled Nova Scotian Current which brings water colder than 3° C (37°–38° F) along the Nova Scotian coast and into the eastern side of the Gulf of Maine at some time in the spring in most years (Fig. 138).[37] It is not likely that any Capelin or their offspring ever find their way north again, if any succeed in reproducing that far south.

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[37] For additional details, see Bigelow, *7*: 831, 832; Taylor, *et al.*, *109*: 311, fig. 14.

Food. Capelin feed chiefly on euphausiid shrimps as well as various isopod-, gammarid-, and copepod-crustaceans. The stomachs of Capelin taken from among the spawning schools have been found full of Capelin eggs—evidence that they may not fast as rigorously at spawning time as various other fishes do.

Enemies. "A list of the animals that prey on the Capelin would include the names of almost all fish, sea birds and sea mammals that inhabit the parts of the world where capelin are to be found" (Templeman, *110*: 132). Seals, for example, subsist largely on them; finback whales have often been found full of them; during their periods of abundance they are one of the chief items in the diet of the white whale (*Delphinapterus*) in the estuary of the St. Lawrence River and no doubt elsewhere; they are also eaten by the common porpoise of the north (*Phocaena*) (*33*: 47). The nesting colonies of puffins, murres, guillemots, gulls, terns, and shearwaters all take heavy toll of them. And the list of fishes known to prey regularly on them includes spiny dogfish (*Squalus acanthias*), Greenland shark (*Somniosus microcephalus*), Atlantic salmon (*Salmo salar*), Arctic charr (*Salvelinus alpinus*), Atlantic herring (*Clupea harengus*) which often gorge on Capelin larvae, sculpin (*Myoxocephalus*), eelpout (*Macrozoarces americanus*, in American waters), wolffish (*Anarrhichas*), flounders (*Pseudopleuronectes*), Greenland halibut (*Reinhardtius hippoglossoides*), and Greenland cod (*Gadus ogac*). But their worst enemy by far on both sides of the Atlantic is the Atlantic cod (*Gadus morrhua*), which not only devour immense numbers of Capelin when the latter come in to spawn, but also harry the young in deeper water offshore, seemingly without letup.

Other serious losses to the potential population of the Capelin result from the drying out of great numbers of eggs spawned on the beaches, and from "immense destruction of the exposed spawn [that] is wrought by maggots or small beach flies of the genus *Fucellaria*" (Sleggs, *100*: 44).

Variations. Neither the average numbers of vertebrae that have been reported for various localities (*37*: 121–124; *110*: 109–115; *79*: 285–290) nor other numerical and proportional characters (*68*: 64) have suggested any consistent racial differences between the Capelin of different regions.

Numerical Abundance. Attention has been called time and again to the multitudes in which Capelin gather when they come inshore. Perhaps it will suffice here to refer to Anspach's description of them in 1819 in Conception Bay, Newfoundland, as being present in schools so immense as to color the surface of the sea and to enable two persons to fill a common-sized boat with them in less than two hours (*2*: 400), and to Hardy's description of the water surface as appearing like "a living mass as far as the eye can reach" (*38*: 8, 9).

However, the only precise available information as to their actual numbers is Slegg's calculation based on the counts of measured samples of beach material (*100*: 42, 43): The number of eggs per cubic foot was between six and seven million, at which rate "it would require about a third of a million females to furnish the spawn on a hundred yards of beach and a like number of males. When we take into account the spawn below the tidal zone, it seems safe to say that a million capelin spawned upon each hundred yards of beach" on this particular occasion. Templeman has written similarly of "possibly hundreds of millions" spawning at Grand Beach on the east coast of Newfoundland (*110*: 52). With this same sort of thing taking place here and there from Saglek Bay in northern Labrador to southeastern Newfoundland and St. Pierre Island, along western Greenland, and along at least the coast of southern Iceland, (where Jespersen has recorded a catch of 5,900 larvae in one 20-minute haul with a "young fish" trawl [*50*: 11]), the total number of Capelin involved must surpass human reckoning.

Periodic Fluctuations in Abundance. It has long been known that Capelin may be decidedly erratic from year to year in their appearances at particular localities within short distances; for example, around the southwestern angle of Newfoundland, where they may even fail to spawn at all, as seems to have happened locally in 1941 and 1942 (*110*: 55–58, figs. 14, 15), and around Ungava Bay near the northern boundary of their range, where they were reported as far more plentiful in 1884 than in 1947–1949 (*22*: 104). Capelin also appear from time to time in schools far to the south of their regular range, as in the Gulf of Maine in the west and off Norway in the east (*119*: 15). The fish also range much farther eastward along the Murman coast in some years than in others (*80*: 119). Catches of 4,800,000 pounds of Capelin in the Gulf of St. Lawrence in 1919, 1,990,000 in 1951, 677,000 in 1952, 147,000 in 1954, and 497,000 in 1956 suggest that the numbers of Capelin declined greatly there during recent years. But the decline suggested by these figures seems as likely to have resulted from a decrease in the demand for Capelin as from any general reduction in their numbers. We question also whether the poundage credited to Newfoundland for 1952[38] is realistic, for we have been informed by letter from John D. Kaylor of the General Foods Corporation, a fisheries expert of long experience, that "on the spot inquiries in many places, plus personal observation during the height of the capelin run [of 1958] show a total catch for *all* uses at less than 5 million pounds for all Newfoundland."

It is said that Capelin have not visited the coast of western Greenland in such hordes of late years as they did during the colder-water period from about 1885 down to the 1920's, but they may have continued equally abundant in deeper water, farther out from the immediate tideline.

Relation to Man. The Capelin, a delicious morsel as we can bear witness, is an important fish, not only in the natural economy of northern seas but in that of the native inhabitants of Greenland, where great quantities are dried in good Capelin years during the spawning run, to be used for human food during the winter. So vital an item is the Capelin in the winter diet of the Greenland Eskimos that they suffer great hardship in any particular district in a year when the run fails. The Capelin are used there for dog food as well.

In Newfoundland, great quantities were netted for human consumption during

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[38] We are greatly indebted to the late A. H. Leim and W. P. Templeman of the Fisheries Research Board of Canada, and to F. B. Clark, Canadian Consul (commercial) at Boston, for information regarding the commercial landings of Capelin in Newfoundland for recent years.

the first quarter of the 19th century, to be dried for shipment to London, to be exported "by the thousands of barrels to the eager French fishermen on the Bank" as bait (Hardy, *38*: 8), and to be used locally as manure. Then there followed a period lasting down through the first quarter of the present century when Capelin were in so little demand in Newfoundland that Sleggs, writing in 1933, estimated the local consumption of them to be not "more than a few pounds per head, annually" and the exports for some time past as "insignificant" (*100*: 57). Capelin were in greater demand, however, along the Quebec shore of the Gulf of St. Lawrence than in Newfoundland (see *Periodic Fluctuations in Abundance*, p. 589); 130,268 pounds of dried Capelin plus 29,117 pounds of fresh and salted fish were exported from the Island of St. Pierre to France in 1924; and 116,855 pounds (frozen) were shipped to the United States in 1925 (*10*: 151).

Of late years Capelin have been taken in much larger quantities in Newfoundland than had been the case for many years previous to the Second World War, sure evidence of an increase in the demand (for catches 1952, 1954, see p. 589). We owe to F. B. Clark, of the Canadian Consulate General, the information that 634,000 pounds (2 %) of the Newfoundland catch for 1954 were used for human consumption (fresh, dried, or smoked), and the remainder (98 %) for other purposes, such as fresh and frozen bait for cod fishermen, fertilizer, etc. In addition, it has been reported that Capelin are utilized as fish meal, as food (lightly salted and dried) for dog teams, as canned cat food, and as a source for a high quality marine oil (*111*: 7, 8, 18).[39]

Methods of Capture. Wherever Capelin are caught they are taken chiefly in cast nets or dip nets, but sometimes in beach seines and even in tubs, buckets, and hand scoops, as has been described in vivid terms by Hardy for Conception Bay, Newfoundland (*38*: 8). We have never heard of one being caught on hook-and-line.

General Range and Occurrence in the Western North Atlantic. The general range of the Capelin is outlined on p. 574. In Greenland, Capelin are known on the east coast northward to Scoresby Sound (about 70° N) and on the west coast northward to Thule (76°30′ N); on the west coast they did not occur of old with any regularity north of Vaigat (about 70° N), but by the 1930's they were abundant in Northeast Bay, and by 1935 they had spread to the northern part of the Upernavik district (about 74°25′ N); one was even taken at Thule that year, and a second was taken in 1936 (*48*: 87, 88).

On the American side of the Labrador Sea, the most northerly point where we find them reliably reported on the Atlantic coast of northern Labrador is Saglek Bay between 57 and 58° N (*41*: 5). Capelin have not been recorded for Baffin Island, but for Ungava Bay a few have been reported recently though larger numbers were recorded for 1884 (*22*: 104). They have also been recorded for many localities in the northern part of Hudson Bay southward to James Bay, sometimes in great abundance (*112*: 20), for Melville Peninsula in the Arctic (*78*: 7), for Bathurst Inlet (*87*: 710), and for

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[39] We are indebted to Leslie W. Scattergood, U.S. Fish and Wildlife Service, for bringing this reference to our attention, and to W. P. Templeman, St. Johns, Newfoundland, and John D. Kaylor, General Foods Corporation, for personal communications regarding the utilization of Capelin.

the mouth of the Great Fish River, tributary to Bathurst Inlet, where Richardson found them present "in multitudes" (*88*: 187). For records of the Capelin farther westward along the Arctic coast of America, see Walters (*116*).

Southward from Saglek, Labrador, Capelin have been reported by fishermen for so many points as to show that they visit every suitable spawning beach in greater or lesser numbers all along the outer coast; they have been taken even as far inland as Lake Melville above the head of Hamilton Inlet.[40] They are reported to be widespread along the coast of eastern Newfoundland and along the eastern part of the south coast; and it was known that Capelin swarm about the islands of St. Pierre and Miquelon long before Duhamel, writing in 1769, called their abundance on the Grand Bank to scientific attention. It seems that the waters along the western part of the southern coast of Newfoundland and along the southern part of the western coast have become too warm for regular spawning by the time the Capelin are sexually ready to spawn (*110*: 54–57). But they do spawn yearly along the northern part of Newfoundland's west coast as well as in the Strait of Belle Isle, though perhaps not as abundantly in the Strait as on the east coast of Newfoundland; this, it seems, applies also to the north shore of the Gulf of St. Lawrence in general.

In good Capelin years, considerable numbers of them appear on the south shore of the St. Lawrence River estuary and at the entrance to the St. Lawrence River; for instance, the reported catch for the Gaspé region (Gaspé and Bonaventure counties) and for Rimouski County, Quebec, in 1919 was 3,635 barrels whereas in 1929 it was only 240 barrels; Capelin have been reported to occur as far up the St. Lawrence River estuary as Trois Pistoles, about opposite the Saguenay River (*115*: 79). They are well known around Anticosti Island (*97*: 285; see also *Study Material*, p. 576). But we find no definite evidence that Capelin visit the southern part of the Gulf in any numbers, or with any regularity, if they occur there at all.[41]

To the south of Cabot Strait, Capelin occur only sporadically[42] and in limited areas. "The southeastern corner of Cape Breton is the center of such an area, where large quantities were taken in 1917. Halifax is the center of another area" where Capelin were reported for about 1853 (Hardy, *38*: 5, ftn.) and were abundant in 1919. On rare occasions they appear for a year or two in the Bay of Fundy in great numbers; Perley, for example, writing in 1852, reported them for a number of localities near St. John, New Brunswick; they were next reported in the Bay in 1903; a few were taken in 1915; in the autumn of 1916 they were so plentiful that a catch of 3,000 pounds of fish in the Passamaquoddy region included 2,000 pounds of Capelin. They have also been reported for various other Fundian localities. In the spring of 1917 they reappeared on the Nova Scotian side of the Bay, and in 1919 they were taken

[40] Backus (*3*: 295) has reported Capelin found in the stomachs of cod taken there in winter. And one has been reported for Northwest River, at the head of Lake Melville (*54*: 210).

[41] The late A. H. Leim informed us, from his personal observations, that the fish reported in the commercial statistics for 1930 and preceding years as Capelin from Prince Edward Island "doubtless were silversides (*Menidia*) which are known there as 'capelin.'"

[42] Letter from A. G. Huntsman.

not only in the deep water off Passamaquoddy Bay through the late winter and early spring but to the west as well, far up the Penobscot River. There is even one specimen labeled Woods "Holl," Massachusetts, in the collection of the Academy of Natural Sciences of Philadelphia (*28*: 555), whether correctly so or not. None seems to have been seen since 1919 in the Gulf of Maine, nor have Capelin ever been reported as spawning south of the Gulf of St. Lawrence, so far as we can learn.

A final item, remarked on first by Cuvier and Valenciennes in 1848 (*19*: 408), is that on the shores of the White Sea, spawned-out Capelin that are washed up on the shore often become enveloped in nodules of beach material, within which their skeletons persist, perfectly preserved, until the nodules fall apart. This type of subfossilization, commented on in greater detail by Collett (*14*: 161), has also been reported for Iceland (*1*: 42), and for Greenland, where Quaternary "clay plates are not rarely found which . . . contain a skeleton or impression of capelin. . . ." Such clay balls containing remains of Capelin are well known from the Quaternary deposits in Norway also (*48*: 92), and from Bosnia at an elevation of 580 m above the sea (*9*).

Synonyms and Selected References:

Clupea villosa Müller, Zool. Danicae Prod., 1777: 50 (Greenland; not seen); Gmelin *in* Linnaeus, Syst. Nat., ed. 13, *1* (3), 1793: 1409 (north. seas; for publ. date, see Hopkinson, Proc. zool. Soc. Lond., 1907: 1035–1037).

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Salmo groenlandicus Bloch, Naturg. ausländ. Fische, 8, 1794: 99, pl. 381, fig. 1 (refs., descr., ill., spawn., food, use in Greenland, vernac. names); Shaw, George, Genl. Zool., *5*, 1804: 70 (descr., abund., spawn. migr., food, use, Greenland, Iceland, Newfoundland); Richardson, John, *in* Franklin, Narr. . . . Journey to Polar Sea, Append. 6, Fishes, 1823: 710 (abund., spawn., Bathurst Inlet, Arctic Canada).

Clupea lodna Hermann, Observ. Zool., posth. ed., F. L. Hammer, Paris, *4*, Pisces, 1804: 290–328 (316) (see Hubbs, Copeia, 1936: 124–125; "the capelin, *Mallotus villosus*, is called *Clupea lodna* [from Iceland, described from plate by Olafsen and Povelsen]," Reise Island, 2, 1774–1775: pl. 28).

Salmo villosus Müller, Zool. Danica, 4, 1806: 45, pl. 160 (descr., ill., Greenland).

Mallotus villosus Cuvier, Règne Anim., nouv. ed., *2*, 1829: 306 (diagn., cod bait); Storer, Mem. Amer. Acad. Arts Sci., N. S. *2*, 1846: 454; also separate, Cambridge, Mass., 1846: 229 (descr., refs., Greenland, Newfoundland); Cuvier and Valenciennes, Hist. Nat. Poiss., *21*, 1848: 392 (sp. *Malottus*), pls. 622, 623 (descr., ills. male and female, habits, food, abund., season, St. Pierre and Miquelon, use, early refs.,); Gaimard, Voy. Islande et Groenl., Atlas, Zool., Poiss., 1851: pl. 18, fig. 1 (ill., male, Iceland); Agassiz, L., Proc. Boston Soc. nat. Hist., *3*, 1851: 42 (modern subfossil., Iceland); Perley, Cat. [in part] Fish. N. Brunsw., Nova Scotia *in* Rep. Fisher. Bay of Fundy, ed. 1, 1851: 135; descr. Cat. [in part] . . ., ed. 2, 1852: 203; (descr. Cat. [in part] . . ., as separate, ed. 2, 1852: 25 (never farther S. than N. Brunswick, spawn., odor, export, cod bait, import. food in Greenland, never enters freshw. streams); Rep. Fisher. G. of St. Lawrence, ed. 2, 1852: 7–9 (cod bait and manure, rel. to cod fishery); Storer, J. Boston Soc. nat. Hist. (1850–1857, *6*, 1857: 265 (N. shore, Gulf of St. Lawrence); Bell, Canad. Nat. Geol., *4*, 1859: 207 (Gulf of St. Lawrence); Gill, Proc. Acad. nat. Sci. Philad. (1861), Append., 1862: 53 (catalog., e. coast N. Amer.); Canad. Nat. Geol., N.S. *2*, 1865: 259 (in synop., Gulf of St. Lawrence, Bay of Fundy); Weiz, Proc. Boston Soc. nat. Hist. (1864–1866), *10*, 1866: 275 (spawn., season, abund. of fry, Square I., near Okkak, n. Labrador); Hardy, Proc. N.S. Inst. Sci., *1* (2), 1867: 4–13 (n. Nova Scotia and Halifax, abund., spawn., enemies, use, Newfoundland); Jones *in* Hardy, Proc. N.S. Inst. Sci., *1* (2), 1867: 5–6 (descr.); Reeks, Zoologist, London, (2) *6*, 1871: 2556 (abund., spawn., Newfoundland); Lanman, Rep. U.S. Comm. Fish. (1872–1873), 2, 1874: 225 (spawn. activ., after Chappell, 1818: 132–133); Bean *in* Kumlien, Bull. U.S. nat. Mus., 15, 1879: 135 (Bathurst Inlet, Arctic Canada); Jones, Proc. N.S. Inst. Sci. (1879–1882), *5*, 1882: 93 (S. to Halifax, Nova Scotia, in cold years); Stearns, Proc. U.S. nat. Mus. (1883), *6*, 1884: 124 (n. Gulf of St. Lawrence, no def. locals.); Goode *et al.*, Fish. Fish. Industr.

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Fishes of the
Western North Atlantic

Part 3

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