Fishes of the Western North Atlantic

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MEMOIR I

FISHES OF THE WESTERN NORTH ATLANTIC

Part One
Lancelets, Cyclostomes, Sharks

Part Two
Sawfishes, Guitarfishes, Skates and Rays, Chimaeroids

Part Three
Soft-rayed Bony Fishes: Orders Acipenseroidei, Lepisostei, and Isospondyli
Sturgeons, Gars, Tarpon, Ladyfish, Bonefish, Salmon, Charrs,
Anchovies, Herring, Shads, Smelt, Capelin, et al.

Part Four
Soft-rayed Bony Fishes: Orders Isospondyli and Giganturoidei
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Part Five
Orders Iniomi and Lyomeri
Lizardfishes, Other Iniomi, Deepsea Gulpers

Part Six
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Xenoberyces (Stephanoberyciformes), Anacanthini (Gadiformes)
Halosauriforms, Killifishes, Squirrelfishes and Other Beryciforms,
Stephanoberyciforms, Grenadiers

Part Seven
Order Iniomi (Myctophiformes)
Neoscopelids, Lanternfishes, and Atlantic Mesopelagic Zoogeography

Part Eight
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Part Nine, Volume One
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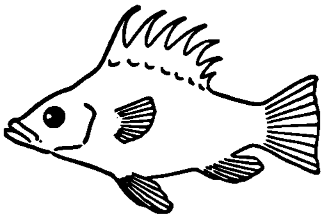
Order Beloniformes
Needlefishes, Sauries, Halfbeaks, and Flyingfishes

MEMOIR II

THE ELEMENTARY CHEMICAL COMPOSITION OF MARINE ORGANISMS
by A. P. Vinogradov

MEMOIR
SEARS FOUNDATION FOR MARINE RESEARCH
Number I

Fishes of the Western North Atlantic



PART SIX

Order Heteromi (Notacanthiformes)
HALOSAURIDAE, NOTACANTHIDAE, LIPOGENYIDAE

Suborder Cyprinodontoidei

Order Berycomorphi (Beryciformes)
POLYMIXIIDAE, BERYCIDAE, DIRETMIDAE, TRACHICHTHYIDAE,
ANOMALOPIDAE, HOLOCENTRIDAE, ANOPLOGASTERIDAE

Order Xenoberyces (Stephanoberyciformes)
GIBBERICHTHYIDAE, STEPHANOBERYCIDAE, MELAMPHAIDAE

Order Anacanthini (Gadiformes)
in part
MACROURIDAE

NEW HAVEN

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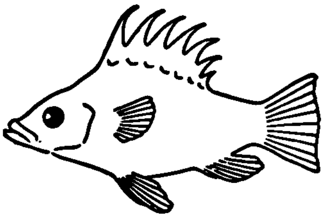

Authors

DANIEL M. COHEN
U.S. National Marine Fisheries Service

N. B. MARSHALL
British Museum (Natural History)

ALFRED W. EBELING
University of California, Santa Barbara

DONN E. ROSEN
American Museum of Natural History

TOMIO IWAMOTO
University of Miami

PEARL SONODA
California Academy of Sciences

SAMUEL B. McDOWELL
Rutgers University, Newark

WALTER H. WEED, III
Yale University

LOREN P. WOODS
Field Museum of Natural History

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BILL SCHROEDER

on board the CAP'N. BILL II, 1953, with *Harriotta raleighana*.
(Courtesy of the late Jan Hahn, W.H.O.I.)

WILLIAM CHARLES SCHROEDER was born on Staten Island, New York, 10 January 1895, the son of William and Emma (Caffrey). He married Adah Jensen in 1916, and there are two children, William Herbert Earl Schroeder (Lt. Comdr., U.S. Coast Guard, ret.) and Gloria M. (Mrs. William F. Gallagher).

He has followed a career in science devoted to studying the ichthyofauna of the western North Atlantic. He became a Scientific Assistant in the United States Bureau of Fisheries at the age of 22, a post he held for the next 15 years and which, for a time, placed him in charge of the Department of Scientific Inquiry. His first papers (1920 and 1924) dealt with the clam industry of southern Florida; his first publication on fishes, co-authored with H. B. Bigelow in 1927, was concerned with the sharks and skates of the northwest Atlantic [*Bull. Harvard Mus. Comp. Zool.*, *68* (5), 239–251]. The classic Hildebrand and Schroeder "Fishes of Chesapeake Bay" followed in 1928.

Over the next 20 years he published individually or co-authored with Bigelow a series of 30 ichthyological notes and papers, the most substantial of which were his studies on the cod (*Bull. U.S. Bur. Fish.*, *46*, 1–136, 1930) and his guide to Caribbean commercial shark fishing in 1945. Then, in 1948, he and Bigelow produced the sections on the Cyclostomes and Sharks for Part One of this Memoir series, and in 1953 those on the Sawfishes, Guitarfishes, Skates, Rays, and Chimaeroids for Part Two. The year 1953 also marks the appearance of the indispensible Bigelow and Schroeder "Fishes of the Gulf of Maine".

Nearly all this while (1932–1952) he was Business Manager of the Woods Hole Oceanographic Institution; he became its Ichthyologist in 1952, and was a Senior Scientist from 1964–1968. He was also Associate Curator of Fishes at Harvard, 1936–1961. An additional 23 papers between 1950 and 1968 bear his stamp, bringing the grand total to well over 3,000 pages and 1,000 illustrations. With Bigelow he described one new family, seven genera, and 42 new species from amongst the Cyclostomes, Elasmobranchs, and Chimaeroids. He has served as a member of the Board of Editors of "Fishes of the Western North Atlantic" since the inception of the series.

It has been said of Bill Schroeder that he neither looks nor acts as if he were important. Cape Cod fishermen accept him as an equal. And scientists name new species after him: a mollusk (Clench and Aguayo, 1938), a crustacean (Chase, 1939), an anchovy (Hildebrand, 1943), a carp (H. M. Smith, 1945), a freshwater ray (Fernandez-Yepez, 1960), a sawshark (Springer and Bullis, 1960), a bathyclupeid (Dick, 1962), and a new genus of cat sharks, *Schroederichthys* (Springer, 1966).

"Honest men esteem and value nothing so much in this world as a real friend". In that spirit, and with rare appreciation, this sixth Part of Memoir 1, "Fishes of the Western North Atlantic", is dedicated to Schroeder, William C.

D.M. – 26 March 1972.

Introduction

WITH the publication of this sixth part of FISHES OF THE WESTERN NORTH ATLANTIC it seems desirable to reaffirm the objectives of the series. In this respect, two statements in the PREFACE to Part One, published in 1948, are particularly pertinent.

"The reason for the present series of volumes is to correlate the contents of the rich storehouse of knowledge relating to the fishes that live in the waters of the western North Atlantic."

"It has been written on the premise that it should be useful to those in many walks of life—to those casually or vitally interested in the general phenomena of life in our waters, to the sportsman whose interests are closely associated with pleasure and relaxation, to the fisherman whose livelihood depends upon knowledge of where fishes are gathered together, as well as to the amateur ichthyologist and the professional scientist."

Secure in the wisdom of hindsight we must also call attention to a statement in the INTRODUCTION to Part One, which notes that a widely accepted general outline of classification will be followed. Although such may have existed in 1948, a decade of research by a number of ichthyologists studying both recent and fossil fishes has demonstrated that there does not presently exist any easy way to chart the family tree of fishes. Although the overall study of fish phylogeny is now an active field, the end point, an adequately documented and widely accepted classification, is not yet available. For this reason, and because of the great difficulty in bringing to completion at approximately the same time, sections by many authors studying groups requiring varying amounts of basic research, this series no longer will adhere strictly to a particular sequence of presentation. Instead, accounts of coherent groups, will be published as they become available. Authors are free to treat major group relationships, but phylogeny will not necessarily be reflected by order of appearance.

One other policy change should be noted. In hopes of lessening the proliferation of preliminary literature which has preceded the appearance of previous Parts, in this volume, for the first time, original descriptions are presented; included herein are the original accounts of a previously unrecognized family and several genera, species, and subspecies.

Included in this Part is a comprehensive treatment of the benthic, deep-sea, eel-like fishes of the Order Heteromi, including many extralimital forms.

The Cyprinodontoidei, or killifishes and their relatives, are treated in a fashion that departs widely from previous format. Although many species are significant constituents of the brackish-water fauna, these fishes are headquartered in fresh-waters, and to treat the genera and species in standard fashion would be neither possible nor desirable. Instead, a general discussion of the group is presented along with an illustrated key to salt and brackish-water forms that are known to occur within our area. Cyprinodontoids are one of the groups whose phylogenetic placement is presently under debate. The present account treats a coherent taxonomic unit, whatever its ultimate placement in a phyletic scheme.

The order Berycomorphi includes fishes from tropical shores, the continental slopes, and the bathypelagic realm. At the inception of this series a complete account of this group would have been impossible; however, exploratory fishing, deep-water oceanographic cruises, and extensive tropical shore collecting has provided a wealth of new material for study.

Xenoberyces, included by some ichthyologists with the previous order, contains deep-water pelagic fishes. Again, a modern treatment of these would not have been possible a quarter of a century ago.

The account of the Anacanthini, or cod-like fishes, is commenced in this Part with the treatment of the largest family, the Macrouridae or rattails, abundant fishes of the continental slopes and abyss. As with the Heteromi, exploratory fishing and oceanographic expeditions have recently provided the bulk of material upon which the present account is based. Other anacanthine families will be treated in a subsequent volume.

The following abbreviations have been used throughout in order to avoid repetition of the names of natural history collections housing the preserved specimens upon which the accounts have been based.

AMNH — American Museum of Natural History, New York
ANSP — Academy of Natural Sciences, Philadelphia
BLBG — Biological Laboratory, National Marine Fisheries Service, Brunswick, Georgia; collections now at USNM, UF, UMML
BMNH — British Museum (Natural History), London
BNM — Zoologisk Museum, Bergen
BOC — Bingham Oceanographic Collection, Yale University
CAS — California Academy of Sciences, San Francisco
CNHM — Field Museum of Natural History, Chicago
FMNH — Field Museum of Natural History, Chicago
IFAN — L'Institut Fondamental d'Afrique Noire, Dakar
KU — Department of Biology, Kochi University
MCZ — Museum of Comparative Zoology, Harvard University
MOM — Musée Océanographique, Monaco

MMF — Museu Municipal do Funchal, Madeira
MNHN — Muséum National d'Histoire Naturelle, Paris
MRAC — Musée Royal de l'Afrique Centrale, Tervuren
MSNG — Museo Civico di Storia Naturale, Genoa
SAM — South African Museum, Cape Town
SU — Stanford University Collections, now in the California Academy of Sciences
TABL — Tropical Atlantic Biology Laboratory, National Marine Fisheries Service, Miami; collections now at USNM, UF, UMML
TU — Tulane University, New Orleans
UF — University of Florida, Gainesville
UH — University of Hawaii, Honolulu
UMML — University of Miami Marine Laboratory
USNM — National Museum of Natural History, Washington, D. C.
ZMUC — Universitetets Zoologiske Museum, Copenhagen

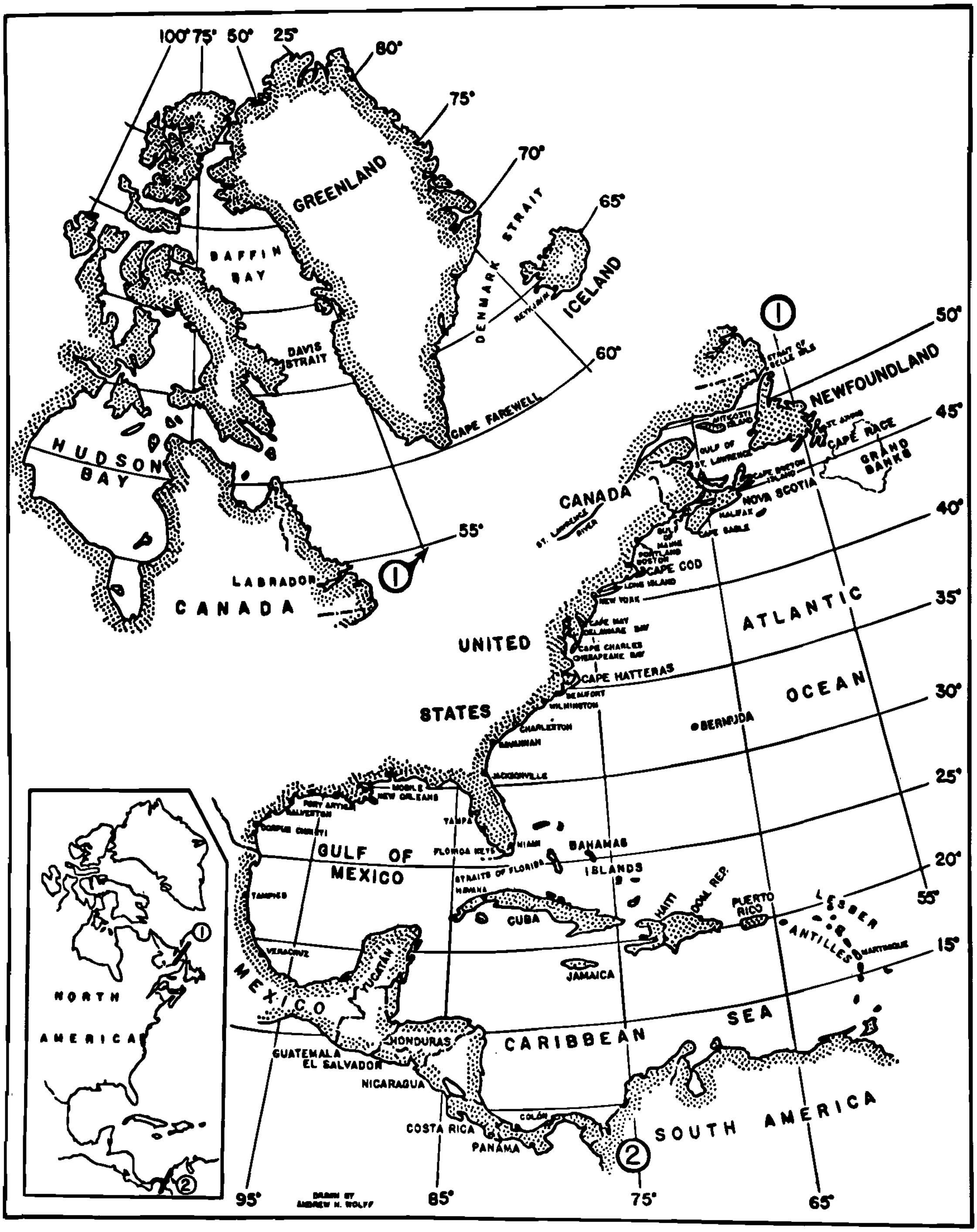
Other often used abbreviations are:

TL — total length
SL — standard length
hl — head length
m.w. or m.w.o. — meters of wire out

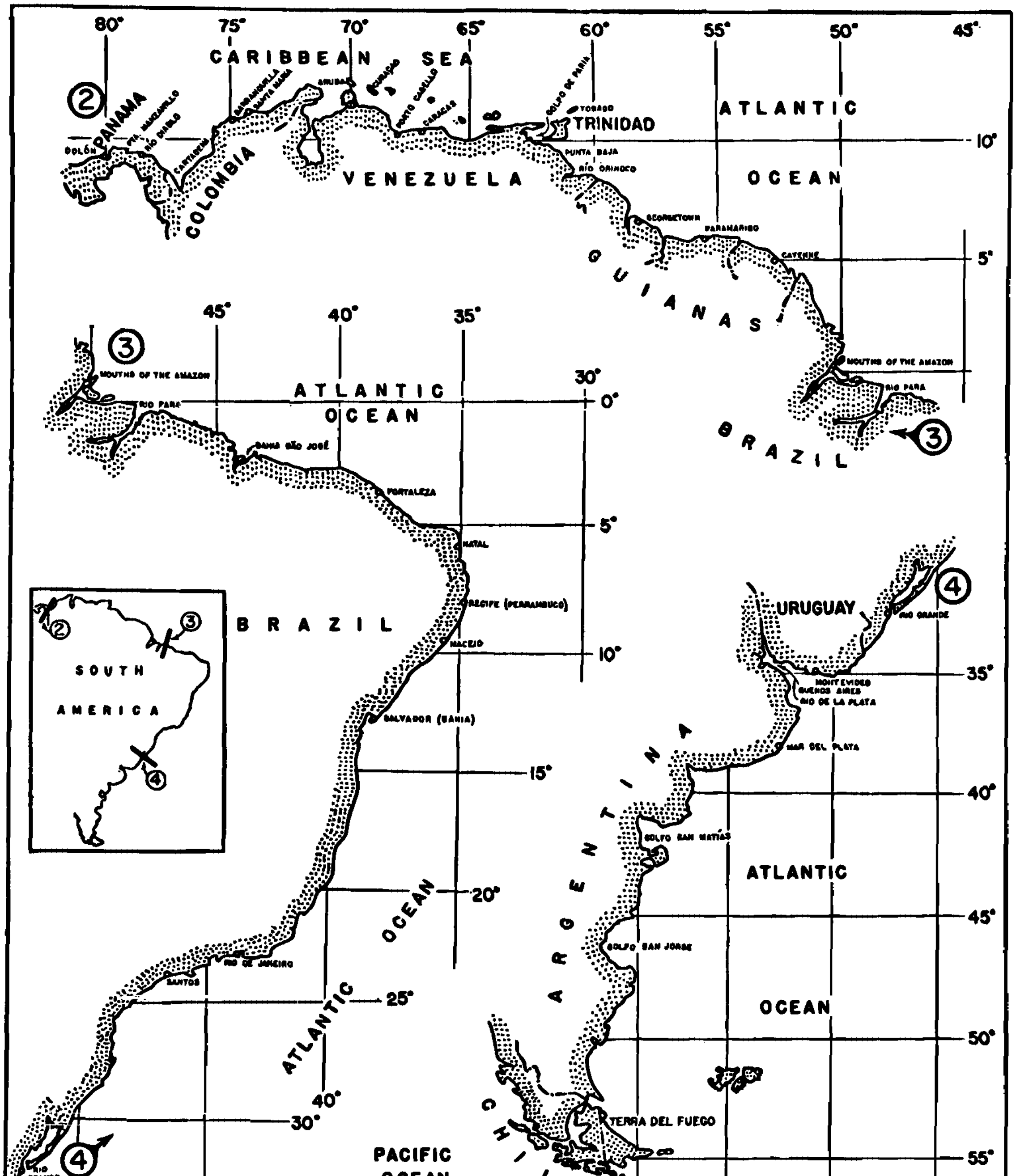
The editors are grateful to all of the authors for their cooperation, but particularly to those whose patience was sorely strained over the years while their manuscripts awaited publication; we also thank the home institutions of the authors for supporting their work. We are indebted to the Sears Foundation for publication, to the National Science Foundation for funds (through NSF grant G 7123) with which to assist in defraying research costs, and to the many individuals who have contributed specimens and data and who have helped in many other ways. The Editor-in-Chief acknowledges his particular gratitude to the National Marine Fisheries Service for its continued support of this series; he also thanks Mrs. Jane Shaw for her painstaking efforts in preparing the manuscript for the printer and in compiling the index.

January, 1972
Washington, D. C.

Daniel M. Cohen
Editor-in-Chief



North America



South America

Order Heteromi (Notacanthiformes)

SAMUEL B. McDOWELL

Rutgers University, Newark

Acknowledgments. The accounts of the Order Heteromi and of the families Halosauridae, Notacanthidae, and Lipogenyidae were made possible by the kind assistance of a number of institutions and many individuals, who not only made specimens available, but gave me the use of their special knowledge, much unpublished. I am particularly grateful to Denys Tucker; to C. M. H. Harrisson; to the staff of the British Museum (Natural History) and in particular to P. H. Greenwood, N. B. Marshall, G. Palmer, and A. Wheeler; to Enrico Tortonese of the Natural History Museum, Genoa; to Jean Guibé of the Muséum National d'Histoire Naturelle, Paris; to M. Penrith of the South African Museum, Capetown; to the late Kiyomatsu Matsubara, of Kyoto University; to G. E. Maul, Museu Municipal do Funchal; to the ichthyology department of the National Museum of Natural History (United States National Museum), and in particular to R. H. Gibbs, E. A. Lachner, and L. P. Schultz; to the U.S. Fish and Wildlife Service, and particularly to H. Bullis, Jr. and D. M. Cohen; to Carl Hubbs of the University of California; to the Field Museum of Natural History (Chicago Museum of Natural History) and particularly to the late Mrs. M. Grey and to L. P. Woods; to the Stanford University Museum and to G. S. Myers; to W. A. Gosline, University of Hawaii, to J. E. Morrow, formerly of the Bingham Oceanographic Laboratory, Yale University; to C. R. Robins of the University of Miami; to J. C. Tyler of the Academy of Natural Sciences, Philadelphia; to the Museum of Comparative Zoology at Harvard College, and particularly to the late H. B. Bigelow, to Mrs. Myvanwy Dick, to G. W. Mead, and to W. C. Schroeder;

and to the American Museum of Natural History, particularly to J. W. Atz, Miss F. La Monte, D. E. Rosen, and V. Walters.

Part of the expenses of foreign travel were borne by the Rutgers University Research Council, to whom I give thanks.

Characters and Synopsis of the Suborders

Characters. This order is recognizable by combining: a backwardly directed bony spine (small in Halosaurospinae of Halosauridae, but very prominent in the others) on dorsal edge of rear of maxilla; abdominal pelvic fins that are connected with each other by membrane, at least at extreme base; eye covered by a transparent window continuous with the skin of the head; tail, when unregenerated, long and tapering and without distinct caudal fin (although a branched terminal filament may represent that fin); snout projecting strongly in advance of mouth; pectoral fin high on side of body, behind upper end of gill cleft.

The internal features that both distinguish it and show the close mutual affinities of its members are the following: premaxilla attached directly to ethmoid region without the intervention of a rostral cartilage; premaxillo-ethmoid ligaments not crossed; maxilla making at least a small contribution to the border of the mouth; maxilla with an inflected ethmoidal process, the blade in direct contact with premaxilla; no autopalatine bone, the anterior end of the palatoquadrate unossified and not in direct contact with ethmoid cartilage (if latter is present); dermal palatines connected across midline by fibrous connective tissue to exclude the reduced or vestigial vomer from the roof of the mouth; epihyal and hyomandibular closely bound, the interhyal short and cartilaginous or absent; hyomandibular with a single facet for cranial attachment; hyomandibular and symplectic forming a hinge; lateral ethmoid absent (Notacanthoidei) or greatly reduced (Halosauroidei) to a slender bar of cartilage ventral to the olfactory nerve; vertebral facet of skull formed entirely by basioccipital (the facet representing a centrum fused to the skull); no posterior temporal fossa, the posterior ascending semicircular canal (imbedded in cartilage representing the epiotic) lying directly beneath the transverse series of extrascapulars bearing the supratemporal commissure, so that no epaxial muscle fibers extend between dermal roof and otic capsule onto the dorsal surface of the otic capsule; lateral temporal fossa completely roofed by intertemporal (dermal) component of pterotic, the intertemporal overlapping the sphenotic to conceal it (at least in large part) from above and replacing the dermosphenotic functionally (the true dermosphenotic is either absent or, perhaps, fused indistinguishably into the pterotic); true subtemporal fossa (for the origin of the pharyngeal levator muscles, such as seen in *Elops*, ichthyodectids, and osteoglossids) absent, but a shallow concavity, bordered by the origins of pharyngeal levators and containing an enlarged segment of the lateral head vein, present on the side of the cranium medial to the hyomandibular (much as in albuloid fishes); lateral wall of braincase, anterior to the ear capsule, formed entirely by the lateral wall of the trigemino-facial recess, the lateral wing of the parasphenoid, and the portion of the pterosphenoid ("alisphenoid") associated with the sphenotic process; the true lateral wall of the braincase anterior to the ear neither ossified nor chondrified, so that there is no trace, even in cartilage, of an orbitosphenoid or basisphenoid, and in consequence, the cranial cavity is broadly continuous with the orbital cavity, without distinct posterior myodome for the rectus muscles of the eyes; parasphenoid with a high lateral wing that extends up to meet the pterosphenoid and form a false sidewall of the braincase (as in a number of fishes), this lateral wing passing between the nerve of the supraorbital canal and the nerve of the infraorbital canal (highly peculiar); a distinct venous foramen in the prootic well posterior to the exit of the hyomandibular nerve.

Supraorbital sensory canal connected or intermediated with infraorbital sensory canal anterior to nostrils by an arc-shaped canal ("Allis's loop", see discussion below) that is innervated by the nerve (buccal) of the infraorbital canal; the Allis's loops of the two sides connected, in turn, by a sac-like rostral commissure that lies upon the anterior surface of the premaxillae (in Halosauridae, there may be an anastomosis of the supraorbital canals on the dorsal surface of the snout, in addition to the true rostral commissure, and in Notocanthoidei the Allis's loop-rostral commissure system may be isolated from both the supraorbital and the infraorbital canals); infraorbital canal with a blind backward-and-upward spur (the alinasal canal) behind nostrils; no supraorbital bone; supraorbital canal with a lateral snag, originating behind the eye, that runs across frontal to form an anastomosis with the supratemporal portion of the infraorbital canal upon the pterotic; supraorbital canal continued behind the level of this anastomosis to run upon the parietal (but without any bony tube or groove upon the parietal); parietals large, in contact on midline, and completely separating frontals from supraoccipital, both superficially and as seen from within the cranium; supratemporal portion of infraorbital canal running along lateral border of pterotic; preopercular canal unconnected to supratemporal canal, the lateral extrascapular not overlapping the levator operculi muscle or making contact (even as a membranous flap) with the preopercular; no extension of sensory canals onto opercular bone; no suturally-distinct angular bone; intergular bone absent; opercular bone contributing extensively to margin of opercular flap, but subopercular very narrow and with only very short posterior edge in contact with opercular margin; branchiostegals slender and curved.

Post-temporal represented only by its superficial canal-bearing portion, without deep cranial process (Halosauroidei) or absent (Notacanthoidei); postcleithrum absent; cleithrum and supracleithrum present (except in *Lipogenys*) but slender, the cleithrum separated from the skin by the rectus cervicis musculature; endochondral shoulder girdle reduced to the small pterygials, hypercoracoid, and hypocoracoids, the mesocoracoid being absent; first pectoral "ray" articulating directly with hypercoracoid, neither segmented nor divided into two halves, one on the extensor side and the other on the flexor side of the fin, as are the other rays (this first "ray" seems rather to be a fulcral spine and differs from the true pectoral rays in its musculature); pelvis distant from shoulder girdle, without posterior processes extending behind fin articulation; pelvic fin flanked laterally by a fulcral spine without direct pelvic or pelvic-muscular connections; true pelvic rays articulating with radial elements that are unfused to either the pelvis or the fin rays.

Ribs born on ovoid parapophyses that are sunken in pits on the side of the centrum, but remain unfused to the centrum even in large adults; epineurals ossified; no hypural elements differentiated.

Oviducts completely absent, the eggs falling into the abdominal cavity to be passed out through a pair of abdominal pores; testicular ducts present; kidneys fused posteriorly and extending well posterior to anus into the tail; urinary ducts entering a median urinary bladder; swim bladder present, with undivided interior, its duct unconnected to gut except by ligament; no extension of swim bladder into head region, but bladder extended (without constriction or any other demarcation) anterior to pneumatic duct; end (posterior) of pneumatic duct connecting with bladder enlarged and bearing two unipolar retia mirabilia; swim bladder supplied by a branch of the coeliac artery; pseudobranch absent; cerebellum strongly overlapping optic lobes.

General Discussion. This order of fishes contains two well-marked groups, the halosaurs (Halosauroidei) and the notacanths (Notacanthoidei) that have often been considered as separate orders. Gill (*10*) proposed the name Heteromi for the notacanths and placed the halosaurs in an order Lyopomi, but Boulenger (*4*) placed both halosaurs and notacanths together under the name Heteromi, and also included (mistakenly) the fossil Dercetidae and the living Carapidae in this order.

Marshall (*21*) has presented strong anatomical evidence of the relationship between halosaurs and notacanths and has shown that the supposed peculiarities of the preopercular of halosaurs, pointed out by Günther (*16*), are erroneous. Greenwood *et al.* (*14*) have accepted the close relationship of halosaurs and notacanths.

Although one can compile a long list of osteological differences between halosaurs and notacanths, most of these differences can be attributed to the difference in structure of the lateral line. In halosaurs the lateral-line canals are enormously enlarged, with ossified supporting bones on the head; on the flank behind the level of the pectoral fin the canal is much displaced ventrally to run near the ventral profile. In notacanths, on the other hand, the lateral-line canals are of the usual small caliber and the canal of flanks run level with the vertebral column, again as in most fishes; but the bones supporting the canals of the head are largely unossified (although formed of a tough and flexible material). Thus, the posttemporal is absent as a bone in notacanths, but present as a tubular placque bearing the connection between the main (body) canal and the supratemporal commissure in halosaurs. Again, it appears that in both halosaurs and notacanths the epiotic is nearly unossified, but while this is quite obvious in notacanths, in halosaurs the dermal extrascapular bone (carrying the lateral portion of the supratemporal commissure) fits closely over the epiotic cartilage and gives the appearance of an epiotic bone.

Some of the features said to distinguish halosaurs from notacanths in the older literature are not truly distinctive, because the genus *Halosaurus* shows a number of "notacanth characters" (*e.g.* constriction of the notochord by the vertebral centra) not shown by the only halosaur that has been extensively described anatomically, *Halosauropsis macrochir.*

The notacanths have lost maxillary teeth, which are retained by halosaurs, but it is not quite true that the maxilla of notacanths fails to border the mouth. In the Notacanthidae the maxilla lies on the border of the mouth medial to the premaxilla; and in the very peculiar suctorial mouth of *Lipogenys*, the rear of the maxilla is not only bent downward, as in Notacanthidae, but bent forward nearly to meet its fellow, so that the maxilla nearly excludes the dentary from the *lower* border of the mouth and is the chief support of the lower oral rim.

Aside from the enlarged lateral-line canals and the low course of the canal upon the flanks, the halosaurs seem to be the more primitive of the two groups. The notacanths are unknown as fossils, since Arambourg (*2*) has shown that the Upper Cretaceous *Pronotacanthus* does not belong to this group. The halosaurs, however, are known from the Upper Cretaceous of Europe, where *Echidnocephalus* (*19*, *31*, *32*) and *Enchelurus* (*20*, *32*, *33*) represent the group. *Echidnocephalus* is so extremely similar to the living genus *Halosaurus* that it would be quite reasonable to lump the two together if it were not for the nomenclatorial problems that would arise: *Echidnocephalus* Marck (*19*) 1858 is an older name than *Halosaurus* Johnson 1863, for the discovery of the Cretaceous fossils preceded the discovery of the living fish. *Enchelurus* differs from other Halosauridae in having a more posteriorly placed dorsal fin (partly opposite the anal); this is an interesting resemblance to the notacanths, which also differ from living Halosauridae in the more posterior position of the dorsal fin. The Miocene genus *Laytonia* (*6*) seems to be a direct synonym of *Halosaurus*, since the diagnostic feature attributed to it (normal and large preopercular bone) is true of all halosaurs, in spite of the erroneous descriptions by Gill (*10*) and Günther (*16*).

Greenwood *et al.* (*14*) refer the Heteromi (under the name Notacanthiformes) to the superorder Elopomorpha, including also the eels, the albuloids, and the Elopidae and Megalopidae. The correctness of this relationship is attested by a number of anatomical resemblances between these fishes. Some, probably the majority, of these resemblances are primitive features that have been lost in nearly all other teleosts, but some of these resemblances appear to be shared specializations, presumably inherited from a common ancestor. The diagnostic features of the "Elopomorpha" are discussed below.

THE ROSTRAL COMMISSURE AND ALLIS'S LOOP. In the vast majority of teleost fishes the infraorbital sensory canal, innervated by the buccal nerve of the lateralis system (conventionally regarded as a ramus of the facial nerve), extends no farther for-

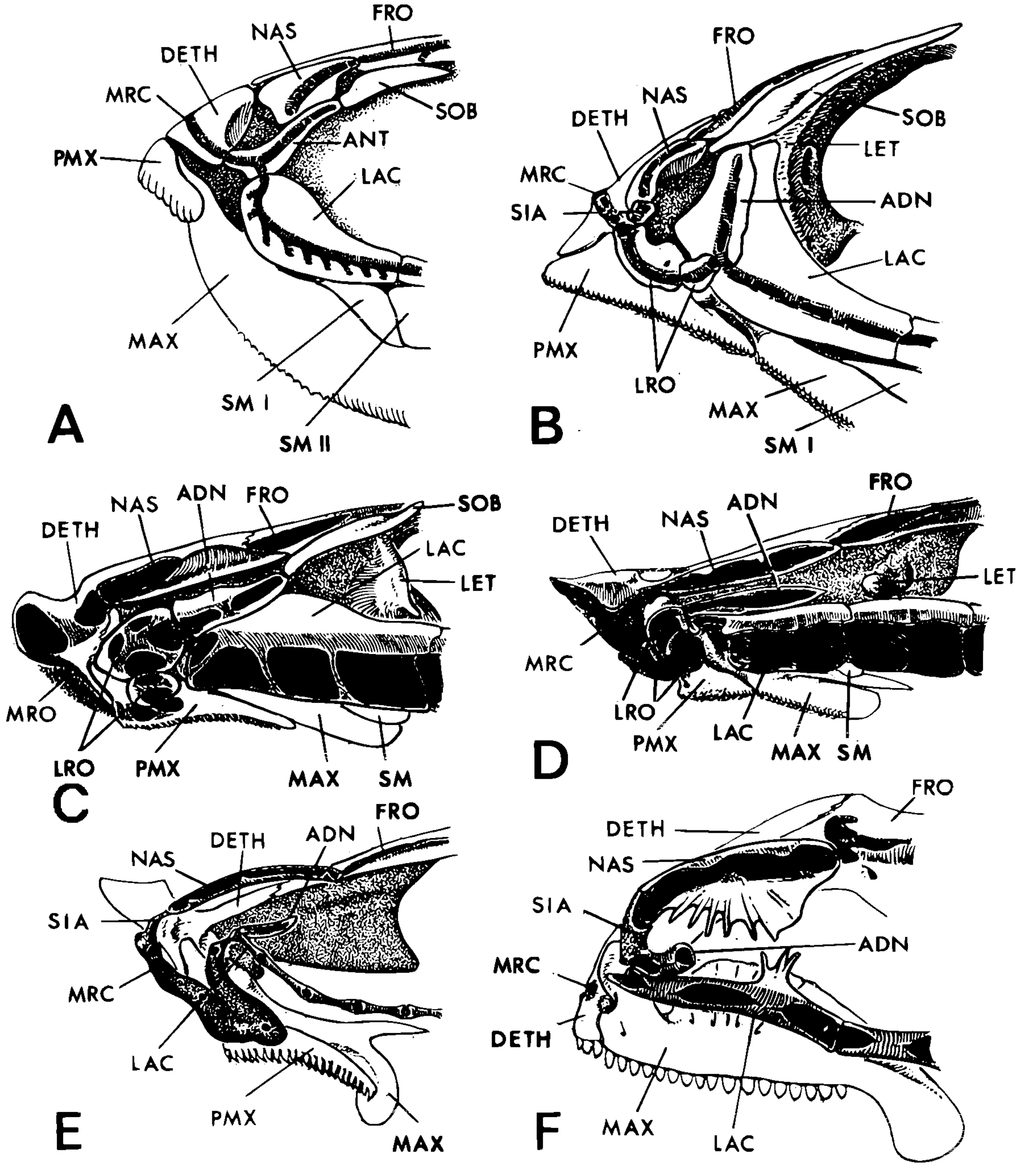


Figure 1. The dermal bones of the snout and rostral sensory canal system of a pholidophoroid and of "elopomorph" fishes. a, *Pholidophoroides crenulata*, a pholidophoroid of the English Lower Jurassic, after (25: 395). b, *Elops saurus*. c, *Albula vulpes*. d, *Halosaurus guentheri*. e, *Notacanthus chemnitzi*. f, *Simenchelys parasiticus* (Order Apodes). Note that in the pholidophoroid the supraorbital canal is separate from the rostral commissure, but that in the "elopomorphs" there is a supraorbital-infraorbital anastomosis, either directly (c, d, and some specimens of *Elops*) or by a membranous tube (e, f) or a small ossification (b, a specimen of *Elops* in author's collection). This anastomosis of the two canals anterior to the nostrils is here termed Allis's loop. In the eel illustrated, the connection is membranous, but in others (*e.g. Anguilla, Conger*) the connection is ossified. The

ward than the lachrymal bone, as the term is used for teleosts, without implying homology with the lachrymal bone of tetrapods. Gardiner (*9*) has defined the position of the teleost lachrymal as follows:

> In teleosts and pholidophorids the lachrymal always articulates with the edge of the lateral ethmoid, its ventral edge lies lateral to the maxilla but not necessarily touching it, and the palatine articulates with its inner surface.

This definition will not work for notacanths because the lateral ethmoid is absent and the mobile palatine is quite free of the bones of the surface of the snout, but in halosaurs the definition is quite usable, aside from the failure of the palatine to form any definite articulation with the suborbital bones. The only portion of the lateral ethmoid cartilage remaining in halosaurs is the portion attached to the suborbital bone overlying the anterior end of the blade of the maxilla. The lateral ethmoid of halosaurs has the form of a slender and U-shaped cylinder of cartilage, passing backward ventral to the olfactory nerve and then arching forward to reach the lachrymal bone (Günther's [*16*] figure of the skull of ***Halosauropsis macrochir*** shows only the medial end of the lateral ethmoid, and the delicate distal end seems to have been cut in preparation.)

In the "Elopomorpha" the infraorbital canal is continued forward of the lachrymal beneath the nares by a rostral commissure that seems quite homologous to that of palaeoniscoid, holostean, and pholidophoroid fishes (see Figs. 1 and 2). In ***Elops*** and megalopids the commissure is complete and runs straight across the dermal ethmoid (rostral of paleontologists) in a bony tube (*24*), but in ***Albula*** and ***Pterothrissus***, the commissure is bent into a horseshoe (concave upward) that extends down from the dermal ethmoid onto the anterior face of the premaxillae; the premaxillae bear canal-supporting ossifications. (My own observations on ***Pterothrissus*** and ***Albula*** do not completely confirm Gosline (*12*), for I find that the supraorbital canals do not end blindly at the tip of the snout, but bend sharply downward to connect with the canal overlying the premaxillae. Gosline's "cavity in the mesethmoid by means of which the supraorbital sensory canals of either side join" seems closed over by a thin membrane in my material, and it is at this point that the canal bends sharply ***downward***, not inward.) The premaxilla is pierced by the nerve for the rostral commissure.

Unlike many fishes below the teleost level (*9*), the "elopomorph" rostral commissure, which is innervated by the buccal nerve, forms a smoothly continuous anastomosis with the anterior end of the supraorbital canal, born by the nasal bone and innervated by the superficial ophthalmic nerve. So complete is this anastomosis that when the canals alone are considered, without reference to the innervation, the rostral

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(Figure 1, continued.)

pattern of the canals in C and D, where the canals have become cavernous, is more easily made out in E. Abbreviations: ADN, adnasal bone; ANT, antorbital bone; DETH, dermal ethmoid (rostral) bone; FRO, frontal bone; LAC, lachrymal bone; LET, lateral ethmoid bone or cartilage; LRO, lateral rostral bone(s); MAX, maxillary bone; MRC, median part of rostral commissure canal; NAS, nasal bone; PMX, premaxillary bone; SIA, supraorbital-infraorbital canal anastomosis; SM, supramaxillary bone; SM I, anterior supramaxillary bone; SM II, posterior supramaxillary bone; SOB, supraorbital bone.

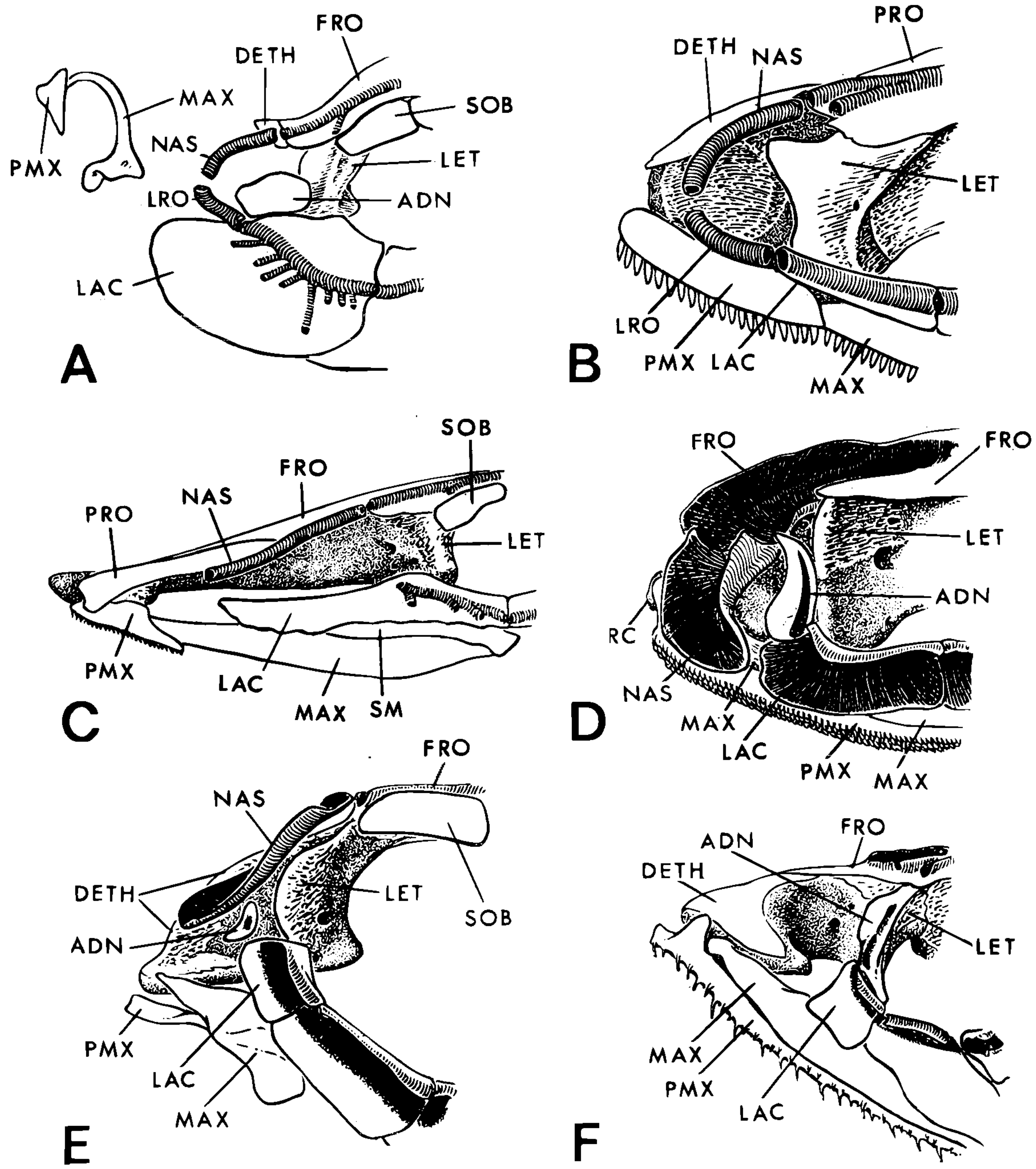

Figure 2. The dermal bones of the snout and rostral sensory canals of some non-"elopomorph" teleost fishes. A, *Phractolaemus ansorgi*, a chanoid (after *28*). B, *Hiodon alosoides*, a notopteroid (?). C, *Esox lucius*, an esocoid. D. *Nannobrachium cf. nigrum*, a myctophid (Order Iniomi). E, *Bathylagus euryops*, an argentinoid. F, *Yarrella blackfordi*, a gonostomatid stomiatoid. Abbreviations as in Fig. 1, as well as: PRO, proethmoid bone; RC, rostral cartilage. In A and B there is a connection between the supraorbital and infraorbital sensory canals anterior to the nostrils, suggestive of the Allis's loop of "elopomorphs", but there is no canal upon the dermal ethmoid bone and the canal in the lateral rostral continues back into the canal of the lachrymal, rather than into a canal on the adnasal. The proethmoid of C possibly represents a lateral rostral that has lost its sensory canal. The cavern-

commissure appears to be a connection of the supraorbital canals, rather than a forward continuation of the infraorbital canals. This is most strikingly seen in eels, where Allis (*1*) noted that the anterior neuromasts of the snout, although lodged in what appears to be only a downward arc of the front of the supraorbital canal, are innervated by the buccal nerve (the nerve of the infraorbital canal). These neuromasts on the snouts of eels are well anterior to the nasal sac and the maxilla, and so are to be compared with the rostral commissure of *Elops* and sub-teleosts, rather than with the infraorbital canal of most teleosts. However, in eels the rostral commissure is incomplete and there is no communication across the dermal ethmoid, although an isolated median sensory organ may be a vestige of former communication.

Although the presence of a rostral commissure is merely a primitive feature and a resemblance to pholidophoroids, the pholidophoroids studied by Nybelin (*25*) do not show the smooth connection of the rostral commissure and supraorbital canal. I here give the name "Allis's loop" to the arc formed in *Elops*-like fishes by the anterior end of the supraorbital canal and the part of the rostral commissure lateral to its anastomosis with the supraorbital canal. It is rather characteristic of "Elopomorphs", in contrast to Pholidophoroids, that this loop seems to form a continuous structure, while the medial (anteriormost) part of the rostral commissure (absent or isolated in eels) seems an adjunct, connecting the right and left Allis's loops, either as a straight transverse canal (*Elops*) or as a U-shaped figure overhanging the premaxillae (*Albula*) (Fig. 1).

As in a variety of primitive teleosts (*12*), *Elops*, *Albula*, and their relatives have a dorsally and backwardly directed snag of the infraorbital canal that overlaps the rear of the olfactory chamber and runs upward behind the nostrils, dorsal to the lachrymal. This canal, the adnasal canal, makes a sharp (usually acute) angle with the main part of the infraorbital canal, but acts as the backward continuation of Allis's loop, continuing the arc of the latter. Indeed, in pholidophoroids (*9*, *25*) the rostral commissure, the adnasal canal ("antorbital branch of infraorbital sensory canal") and main infraorbital canal all meet on a single bone, the antorbital, with the rostral commissure and adnasal canal nearly in a line and the main infraorbital canal nearly perpendicular to them. In "Elopomorphs", as in other teleosts, the antorbital of pholidophoroids has fragmented, so that the adnasal canal is born on a separate bone, the adnasal of Derschied (*7*), while the rostral commissure is born by one or more elements, called lateral rostrals by Nybelin (*24*). In eels (*1*; personal observations on *Conger* and *Anguilla*) it is hard to say whether or not an adnasal canal is present, for although no canal runs upward in front of the eye from the anterior end of the main infraorbital canal, it is quite possible that the rear of the Allis's loop represents an adnasal canal in continuity with the rostral commissure.

(Figure 2, continued.)

ous expansion of the sensory canals in D results in a close approximation of the supraorbital canal upon the nasal to the infraorbital canal upon the lachrymal, although the canals are distinct. In E, the adnasal has become isolated from the main infraorbital canal of the lachrymal (but the adnasal and lachrymal are in contact in some other Argentinoidea). In F, the adnasal has become a bracing strut upon the lateral ethmoid.

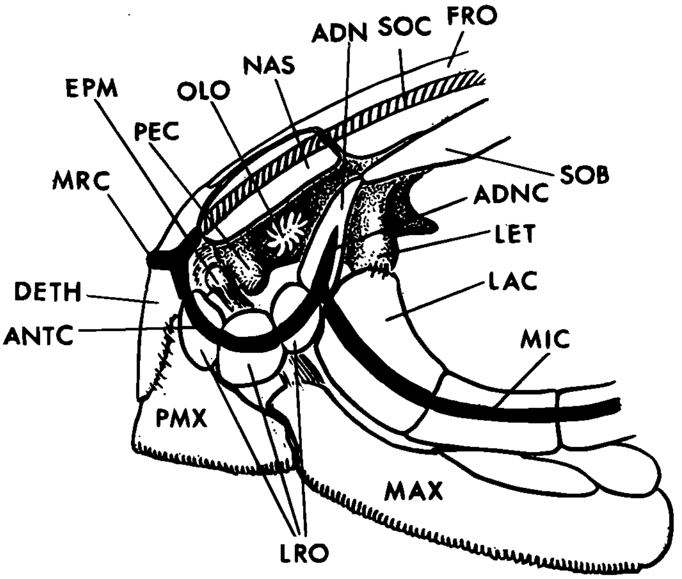

FIGURE 3. Scheme of the sensory canals and dermal bones of the snout of "elopomorph" fishes. Abbreviations are as in Figs. 1 and 2, as well as: ADNC, adnasal canal. ANTC, antorbital canal. EPM, ethmoid process of maxillary bone. MIC, main part of infraorbital canal. OLD, olfactory organ. PEC, preëthmoid cornu. SOC, supraorbital canal. Sensory canals supplied by the buccal nerve, black; sensory canals supplied by the superficial ophthalmic nerve, hatched. The lateral rostrals (LRO) and adnasal (ADN) together represent the antorbital bone of pholidophoroids (see Fig. 1, A) and the portion of the rostral commissure lying on the lateral rostrals may be called the antorbital canal (ANTC). As in pholidophoroids, the antorbital canal runs smoothly into the adnasal canal, but is approximately perpendicular to the main part of the infraorbital canal (MIC). The angle between the antorbital and main infraorbital canal lies directly over the base of the ethmoid process of the maxilla, allowing considerable free vertical movement of the maxilla at this region. Because the dermal ethmoid (DETH) meets the premaxilla (PMX) on a nearly vertical line (fusion takes place in eels) the premaxilla has little mobility in the vertical plane, although (eels excepted) it has some transverse motion. The antorbital canal, closely bound by skin to the premaxilla, thus moves in a plane nearly perpendicular to that of the main infraorbital canal, bound by skin to the maxilla, when the mouth is opened. The continuity of the infraorbital canal may even be broken between the adnasal and the lachrymal in some eels, or between lateral rostral and adnasal in some notacanths. In albuloids and Halosauridae the adnasal and its canal become horizontal and parallel to the main infraorbital canal, as a result of lengthening of the snout in this region, but the angulation between the antorbital and main infraorbital canals is even sharper than in other "elopomorphs". In eels, the median part of the rostral commissure (MRC) becomes isolated; while in albuloids and Heteromi this part of the snout is projected forward as a preoral snout. The continuity of the supraorbital canal with the rostral commissure system forms Allis's loop.

In halosaurs, as noted by Gosline (*12*)[1], the pattern of canals on the snout is very similar to that of *Albula* and *Pterothrissus*, which also agree with halosaurs in the cavernous nature of the canals on the head. Although Gosline says the supraorbital and infraorbital canals end blindly at the tip of the snout, I find in all halosaurid genera that the supraorbital canal passes downward and backward through a paired perforation in the tip of the dermal ethmoid to enter a sac-like canal that overlies the premaxilla (but is supported by independent ossicles, rather than by the premaxilla itself); the rear

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[1] Gosline cites as his specimen of a halosaur "*Halosauropsis* (USNM 53615)". This specimen is of the fish here termed *Aldrovandia affinis*, since I restrict the genus *Halosauropsis* to *H. macrochir*.

of this canal upon the premaxilla makes an upward loop at the maxillo-premaxillary articulation (as figured by Gosline for *Pterothrissus*) and is continued back by the main infraorbital canal and by the adnasal canal. In *Halosaurus* the adnasal canal is well developed with a pore and neuromast, although not as cavernous as are the other canals; but in *Halosauropsis* and *Aldrovandia*, the canal, although present, is reduced and lacks a pore. The premaxilla is pierced by the nerve for the rostral commissure, as in albuloids.

The portion of the dermal ethmoid of halosaurs lining the canals seems to ossify separately from the deeper membrane bone (as is generally the case with the canal tube and membrane bones of teleosts), and some specimens may show a partial or complete suture between the canal lining and the main bone (just as the figured specimen of *Halosaurus guentheri* shows a suture between the canal tube element of the frontal and the main body of the frontal itself). It seems likely that this was the case with Günther's (*16*) figured skull of *Halosauropsis*, prompting Berg (*3*) to suggest that there is "an unpaired 'rostral' before the mesethmoid".

In notacanths the canals are not cavernous, except for a large sac lying upon the premaxillae and innervated by the buccal nerve. This sac seems clearly homologous with the middle portion of the rostral commissure of halosaurs and albuloids, but it is not always connected with the supraorbital, adnasal, or main infraorbital canals. The canal-supporting sclerifications (they do not appear to be true ossifications) do not overlie the premaxilla, and there do not appear to be any 'lateral rostrals'. The adnasal is represented by the anteriormost sclerification of the infraorbital canal and is nearly perpendicular to the sclerification just behind (probably representing the lachrymal). Thus the notacanths do not always show the continuous Allis's loop seen in halosaurs, but the sac-like rostral commissure is in the same position as the Allis's loop of halosaurs and is at least as close to the end of the supraorbital canal as to the suborbital canal. In possession of a rostral commissure that lies upon the premaxillae, the notacanths are very similar to albuloids and halosaurs and unlike other teleosts.

The presence of a rostral commissure is nearly, but not quite, diagnostic of "Elopomorpha". At least one chanoid fish, *Phractolaemus*, has a small tubular bone continuing the infraorbital canal anterior to the lateral ethmoid. This connects with the anterior end of the supraorbital canal, which is born by a tubular nasal that curves downward anterior to the nares (*28*). This pattern is very much like that of eels, but in *Phractolaemus*, as in other chanoid fishes, there is no adnasal canal, even though the adnasal bone is present.[2]

Hiodon, at least *H. alosoides* (personal observation), also has an Allis's loop formed by a decurved nasal and a single, tubular lateral rostral, very much like that of *Phractolaemus*; and as in chanoid fishes, there is no adnasal canal. The relationships of *Hiodon* are obscure, but the following characteristics all suggest that *Hiodon* may share a common ancestry with the chanoid fishes: the resemblance to *Phractolaemus* in snout canals;

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[2] The bone termed "lacrimal" by Thys van den Audenaerde would be called a lateral rostral in our terminology; the lachrymal of *Phractolaemus*, in our terminology, is called "sousorbitaire II" by Thys, and the adnasal is called the "antorbitaire" by Thys.

the absence of an ethmoid condyle on the maxilla; forward extension of the lateral ethmoid lateral to the olfactory cavity (so that the olfactory rosette lies on the posteromedial, rather than medial, face of the cavity); *Chanos*-like exoccipital wings flanking the foramen magnum and flexure of the parasphenoid; great extension of the postorbital sensory canal forward of its anastomosis with the supraorbital canal as in *Chanos* (*13*); and large and lid-like extrascapular that nearly conceals the true parietal.

No other groups of teleosts show any bone-enclosed remnants of the rostral commissure and Allis's loop, but one group of fishes may have saved the lateral rostral bone, even though the sensory canal has been lost. The paired dermal proethmoid bone of esocoid fishes has the same position above the premaxilla as the lateral rostral of "elopomorphs", and it is possible that the esocoid proethmoid is a lateral rostral that has lost its canal.

THE POSTERIOR VENOUS FORAMEN OF THE TRIGEMINO-FACIAL RECESS. In the great majority of teleosts, the head vein leaves the braincase through the opening of trigemino-facial recess for the hyomandibular nerve. Generally the vein is ventral to the nerve, and sometimes (*e.g. Argentina*, some berycoids) the hyomandibular foramen is divided into a dorsal nervous and a ventral venous foramen. In the "Elopomorpha" there is at least a small vein passing through the hyomandibular foramen of the prootic, homologous to the usual venous channel of teleosts; but in addition, there is a more posterior branch of the main head vein that passes through a quite separate foramen in the prootic, behind (not beneath) the hyomandibular foramen. This foramen is present in elopids, megalopids, albuloids, eels, and Heteromi, and is almost confined to this assemblage (Fig. 4). A small posterior venous foramen exists, however, in the Osteoglossidae. The pneumatic foramen (for the otic portion of the swim bladder) of *Hiodon* and Clupeoidea has much the same position as the posterior venous foramen of "Elopomorpha" and conceivably is derived from the venous foramen, although its contents are now quite different.

MEDIAL CONTACT OF TRUE PARIETAL BONES. All of the "Elopomorpha" have large parietal bones that meet (or, in some eels, fuse) on the midline of the skull behind the frontals. These are *true* parietals that do not bear the transverse supratemporal commissure, but lie anterior to the series of bones (extrascapulars) bearing that commissure. Contact of true parietals on the midline also occurs in some salmonoids and in *Hiodon*, but is a much rarer condition than the literature would indicate, for many of the teleost fishes said to have a median parietal contact actually show a median contact of extrascapulars, as evidenced by the supposed "parietals" carrying the supratemporal commissure. Examples of fishes with a median contact of extrascapulars that has been mistaken for median parietal contact are: Notopteridae, Osteoglossoidei, *Aulopus*, *Argentina*, *Chanos*, Characidae, and Gymnotidae. It is also possible that some fishes (*e.g.* Mormyridae) that appear to have true parietals in median contact actually show a contact of median extrascapulars that have lost their canal as a result of degeneration of the median part of the supratemporal commissure.

THE LEPTOCEPHALUS LARVA. The previously discussed characteristics of the "Elopomorpha" are essentially primitive and pholidophoroid-like features that have

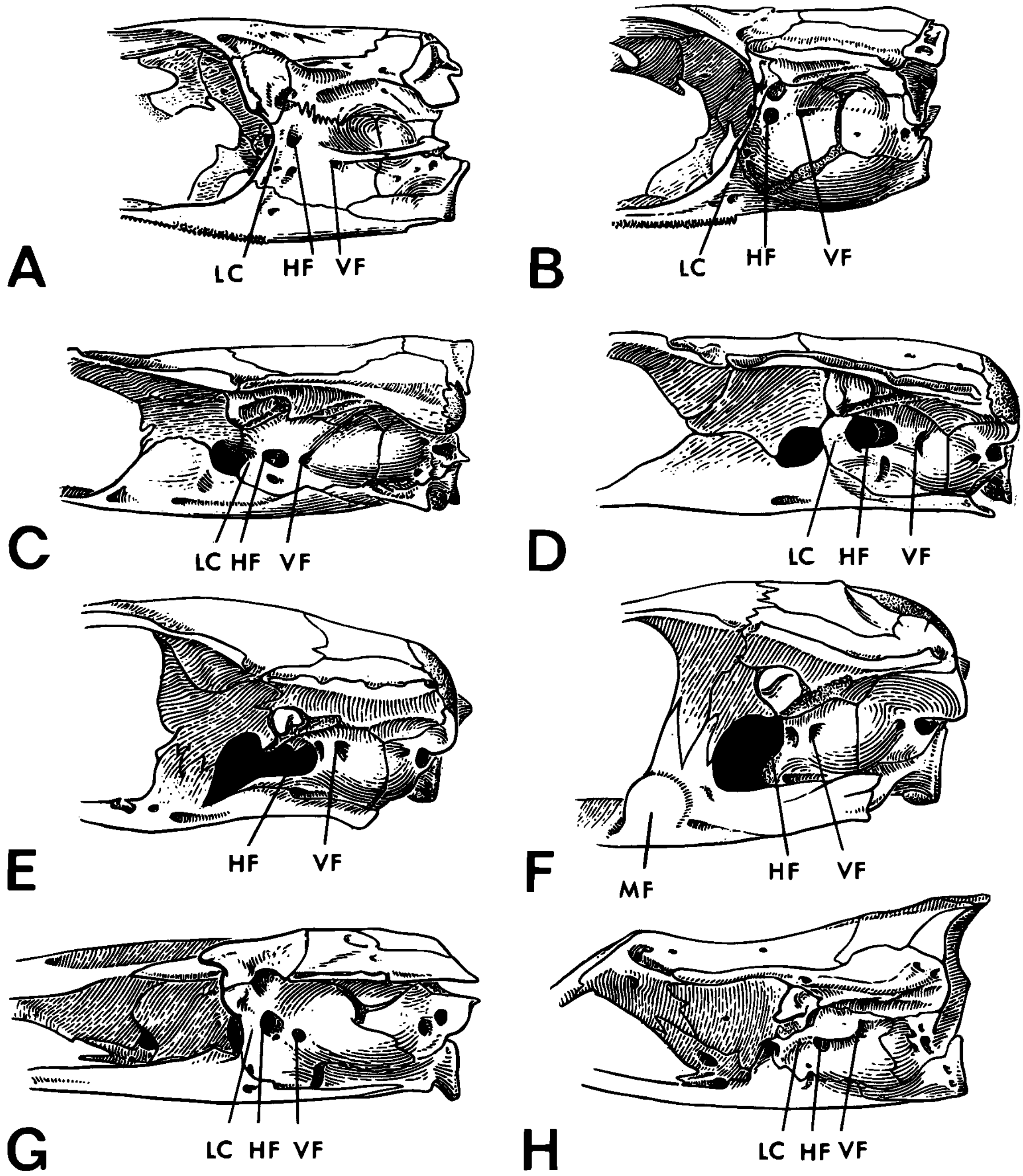

FIGURE 4. Lateral view of the braincase of some "elopomorph" fishes. A, *Elops saurus* (Order Isospondyli: Family Elopidae). B, *Pterothrissus gissu* (Isospondyli: Pterothrissidae). C, *Halosaurus guentheri* (Heteromi: Halosauridae). D, *Polyacanthonotus africanus* (Heteromi: Notacanthidae). E, juvenile *Notacanthus chemnitzi* (Heteromi: Notacanthidae). F, *Lipogenys gilli* (Heteromi: Lipogenyidae). G, *Serrivomer beani* (Apodes: Serrivomeridae). H, *Simenchelys parasiticus* (Apodes: Simenchelyidae). The venous foramen (VF) characteristic of the "elopomorphs" lies posterior to the foramen for the hyomandibular nerve (HF) and is defined by a bar of bone quite separate from the bar of bone (lateral commissure, LC) separating the foramen for the hyomandibular nerve from the foramen for the mandibular and buccal nerves. This is seen most clearly in E and F, where the venous foramen is well defined, in spite of the absence of a lateral commissure (not yet formed, because of juvenile condition). The facet on the parasphenoid for the metapterygoid (MF), diagnostic of the Lipogenyidae, is shown in F.

been retained by the elopomorphs and lost by most other teleosts. This is not the case with the peculiar and diagnostic leptocephalus larval stage. The elopid, megalopid, and albuloid fishes are known to have a leptocephalus larva (see Part 3), as do eels (including the Lyomeri). The larva of notacanths is unknown, but Harrisson (*17*) has described a leptocephalus that is without doubt that of a halosaur (it has the characteristic head of a halosaur), probably *Aldrovandia affinis* (see p. 45). Mead (*22*) has also described a leptocephalus as that of a halosaur, but Harrisson doubts this allocation.

A leptocephalus larva is characterized by the following combination of characters (*17*): body much compressed and ribbon-like, conspicuously deeper than the head; head relatively very small; eyes flat and close to side of head; anal (and urinogenital) papilla close to tip of tail; a long dorsal fin fold.

CERTAIN NEGATIVE CHARACTERS. Aside from the above-noted characters that unite the "Elopomorphs" and distinguish them from other fishes, the "elopomorph" group may be characterized by the absence of the specializations of some other groups that have been confused with them.

Thus, the supratemporal canal in elopomorphs runs along the lateral border of the pterotic, while that of the stomatioid and alepocephaloid fishes is set far in from the border of the pterotic, medial to the level of the hyomandibular facet.

In the "elopomorph" fishes the lateral-line canals remain extracranial and without direct contact with the perilymph or labyrinth of the ear. Thus there is no formation of an intracranial recessus lateralis (characteristic of *Denticeps* and the clupeioid fishes) or of perforation of the skull roof by the posterior portion of the supratemporal canal, as in Notopteridae. However, in halosaurs, the cartilaginous roof of the otic capsule is perforated, so that the posterior semicircular canal lies just beneath the supratemporal commissure, and the sensory commissure and semicircular canal are separated by only a thin lamina of extrascapular bone.

In the "Elopomorpha" the premaxillae (absent in eels) are attached directly to the ethmoid, without the interposition of a rostral cartilage. In this they differ from the acanthopterygian and anacanthine fishes, as well as from the atheriniform fishes and the more primitive Iniomi (the advanced alepisauroid iniomes appear to have lost the rostral cartilage secondarily).

The specializations of the Heteromi. In basic structure the Heteromi are much like the albuloids, but they have advanced considerably beyond the albuloids in two major trends: (1) the caudal fin has been reduced and its locomotor function taken over by the tail itself; (2) the palate has been freed from the ethmoid region and the musculature lifting the palate considerably enlarged, with accompanying modification of the braincase in the region of origin of this musculature.

LOSS OF THE CAUDAL FIN. In halosaurs with an unregenerated tail tip, there is no specialization of the rear end of the body axis for the support of a caudal fin. The anal fin continues to the tip of the tail without interruption, although there is a progressive reduction, from before backwards, of the membrane between the anal rays, so that the most posterior part of the anal fin consists of nearly bare rays forming a long fringe on the ventral profile of the filament-like tail. Internally, toward the middle of the tail, ossification of the vertebrae decreases, and in the posterior portion of the tail the vertebrae are represented by their neural and haemal arches and by delicate rings around the notochord, each centrum being represented by an indefinite number of these rings. At the tip of the tail the vertebrae are absent altogether and the notochord projects freely. There are, therefore, no special hypural bones, but the last five or so "anal rays" are attached directly to the notochordal sheath and appear to be caudal rays. At least, these last rays are suggestively similar to the uppermost rays of a primitive teleost caudal fin, the rays attaching to the tip of the "urostyle". (For discussions of teleost caudal structure, see references *11*, *12*, *13*, and *14*.)

One striking characteristic of a teleost caudal skeleton (that is, the skeleton supporting the caudal fin) is the lack of any obvious correspondence between the haemal arch, neural arch, and central elements. Primitively in teleosts (*11*, *12*) there are three centra (terminal, postterminal I, and postterminal II) in the adult, but a much larger (six to nine) number of hypurals representing the haemal arches. By this criterion, lack of numerical correspondence, all vertebrae in which the centra have become reduced to rings not showing one-to-one correspondence with the neural and haemal arches could be considered as part of a urostyle that is not bent up from the body axis. In the absence of any flexure to mark off a distinct caudal-support region and the absence of any interruption of the apparent "anal fin", it is quite impossible to distinguish "terminal and postterminal centra", but some confirmation of the idea that the rear of the "anal" fin is actually caudal comes from the lateral line. The lateral line does not extend to the tip of the fleshy body axis in any of the Heteromi, but extends down to the "anal fin", generally at about one abdomen-length behind the vent, in halosaurs, and ends short of the tip of the fleshy tail in notacanths.

It thus would appear that the caudal fin has become merged with the anal and lost most of the characteristics of a caudal to become like an anal fin throughout. It is most unfortunate that Harrisson's (*17*) leptocephalus of a halosaur had lost the tip of the tail, but it is interesting that this specimen lacks any indication of an anal fin fold. As in other leptocephali, the urinary papilla lies far posterior to the presumptive position of the adult vent, and the adult anal fin would occupy a position that is far anterior to the larval vent. The anal fin of elopoids and albuloids (see Part 3: pp. 125, 136) first forms as a small lobe just anterior to the lower lobe of the caudal fin, and subsequently moves forward. The long anal fin of halosaurs probably originates in the larva in continuity with the caudal and extends its way forward as the vent moves forward during metamorphosis, as in albuloids and elopoids; but unlike albuloids and elopoids, the halosaurs do not sever connections between the caudal and the anal, and the morphological characteristics of an anal fin predominate over those of a caudal in the subsequent development of the entire (compound) fin.

What has been said of the halosaur caudal and anal fins probably applies to notacanths as well.

It should be noted that specimens of Heteromi with an unregenerated tip of the tail are quite rare. In a regenerated tail, the last few vertebrae are slightly turned upward and a pulpy (notochordal?) axis extends back beyond the last ossified vertebra to bear the pseudocaudal rays. Even though these last vertebrae may be caudal vertebrae that normally bear haemal arches, the haemal arches are absent (presumably resorbed), and no hypural-like support is formed. (For an X-ray photograph of the regenerated tail of *Notacanthus*, see *29*.) Regenerated "caudal fins" have a vertical, rather than longitudinal, base and the rays are much more crowded than on the unregenerated part of the anal.

The great frequency of regenerated tail tips among Heteromi suggests that easy loss of the tail to predators may be a protective defense to these fishes, analogous to the easy loss of the tail in lizards and salamanders. This would suggest, in turn, a functional advantage for loss of a distinct caudal fin in Heteromi. The Heteromi retain, in adult life, the means of locomotion of a leptocephalus larva: undulation of the posterior body axis. The advantage of this mechanism over propulsion by an oar-like caudal fin is that undulation of the body axis is effective even when the tip of the axis has been bitten off, whereas loss of the caudal fin almost immobilizes a fish of normal form.

THE HIGHLY MOTILE PALATE OF THE HETEROMI. In the halosaurs, the autopalatine cartilage is absent, unless it is represented by a small nubbin of cartilage between the anterior end of the pterygoid cartilage and the maxilla at the level of the maxillo-premaxillary articulation. In any case, there is no articulation between the autopalatine and the ethmoid region. The dermopalatine bone, which is well developed, is anterior to the ectopterygoid and entopterygoid, and is only loosely connected to them; because of the reduction of the autopalatine, the dermopalatine is, in fact, free of the rest of the skull except for this loose articulation of its posterior end with the palatal arch and an equally loose articulation with its fellow on the midline. Contraction of the very large and powerful levator muscle of the palatal arch draws the arch forward. Because of the connection by a nubbin cartilage between the maxilla and the pterygoid cartilage, the forward movement of the palatal arch moves the region of the maxillo-premaxillary articulation forward. This has the effect of rotating the premaxillary tooth row from a diagonal or nearly longitudinal position to a transverse position. The dermopalatine is similarly rotated to a transverse position, for its rear is attached to the pterygoid cartilage and the premaxilla and dermopalatine are thus connected like the straightedges of a draftsman's parallel-rule.

Because the maxilla has a condylar connection with the ethmoid region, anterior and medial to the connection between pterygoid cartilage and maxilla, the forward movement of the palatal arch rotates the maxilla from a longitudinal to a diagonal position, swinging the rear of the maxilla outward. Since the rear of the maxilla is bound to the coronoid process of the lower jaw, this laterad rotation of the maxilla results in a laterad rotation of the dentary tooth rows and a broadening of the symphysial angle between the two dentaries. Thus, the freeing of the palatal arch from the ethmoid region allows it to function as a highly effective lever in broadening the gape and swinging tooth rows forward. The hyomandibular is hinged to the cranium by a longitudinal contact of considerable length, permitting transverse rotation of the hyomandibular, but not longitudinal rotation. It is the mobile hinge between the hyomandibular and symplectic (the only connection between the palatal arch and hyomandibular) that permits forward movement of the palatal arch.

The contact of the dermopalatines on the midline excludes the vomer from the roof of the mouth and the vomer is quite toothless. It might be asked, what is the selective advantage of retaining the dermopalatines at the expense of the vomerine dentition? The probable answer is that the vomerine teeth are fixed to the cranium and would not be moved by contraction of the levator pterygoideus (also called levator arcus palatini). The halosaur jaw mechanism allows each tooth row of the jaws and palate to be brought forward, at least at its lateral end, by the contraction of the levator pterygoideus during opening of the mouth. When the mouth is closed and the levator is relaxed, the teeth of the ectopterygoid move straight backward towards the gullet, while the premaxillary, maxillary, dentary, and dermopalatine tooth rows rotate backward and inward. A slip of the adductor mandibulae, the retractor maxillae slip, pulls upon the nubbin of cartilage at the maxillo-premaxillo-pterygoid cartilage connection, and thus acts as the antagonist to the levator pterygoideus.

The outward rotation of the rear of the maxilla produced by this complicated mechanism has a functional significance beyond broadening of the gape, for it acts to unsheath the spine at the rear of the maxilla. When the mouth is closed, this spine lies flat against the side of the head, concealed beneath the overhanging and voluminous infraorbital sensory canal. The outward rotation of the maxilla, produced by contraction of the levator pterygoideus, coupled with the downward rotation of the maxilla produced by opening of the mouth, brings the maxillary spine outward and downward to project freely at the side of the head. It is possible, in fact, that the erection of the maxillary spine has been the major functional advantage leading to the evolution of the mouth apparatus of the Heteromi, for most fishes have developed a method of broadening the gape when the mouth is opened, without developing any such complicated mechanism.

The mouth apparatus of Notacanthidae is basically similar to that of halosaurs, but an emphasis has been placed on the anteriormost tooth-bearing elements: the premaxillae and the dermopalatines. The premaxilla is extended back along the lateral surface of the maxilla and the latter bone has become toothless; correspondingly, the dermopalatine has extended backward, behind its pivot on the palatal arch, along the lateral surface of the ectopterygoid, and the ectopterygoid has become toothless.

The toothless and suctorial mouth of *Lipogenys* seems to have evolved from a notacanthid-like mouth, but the maxilla has extended downward to form much of the posteroventral border of the mouth, and the palatal arch has developed a sliding articulation with the parasphenoid. Although fleshy lips, rather than teeth, are moved, the mechanics of the mouth are essentially as in Halosauridae and Notacanthidae; and as in the other Heteromi, there is a maxillary spine.

As might be expected from its mechanical importance, the levator pterygoideus of Heteromi is exceptionally large. In fishes generally, this muscle arises from the sphenotic process; but surprisingly, although the levator is unusually large in Heteromi, the sphenotic bone is unusually small in this group (it fails to reach the inner surface of the cranium and is a mere tubercle on the outer surface). In *Halosaurus* and the notacanths the levator arises from the lamina-like pterosphenoid anterior to the sphenotic, and from the frontal immediately dorsal to the pterosphenoid; in the Halosauropsinae the origin of the levator has extended forward on the ventral surface of the frontal between the eyes. This unusually forward position of the origin of the levator in Heteromi permits the muscle to act as a protractor, rather than a simple lifter, of the palatal arch. The lamina giving origin to the levator constitutes essentially the whole of the pterosphenoid in Heteromi, and is braced by a strong ascending wing of the parasphenoid that sutures to its ventral border. The relations of this pterosphenoid lamina and the supporting wing of the parasphenoid to the cranial nerves indicate that the pterosphenoid and parasphenoid wing of Heteromi is homologous to a mere muscular ridge on the skull of other, related fishes, and that most of the pterosphenoid of other fishes has been lost.

In most teleosts, all but the posteriormost edge of the pterosphenoid is flexed inward, so that the pterosphenoid forms an anterior, rather than a lateral, wall for the cranial cavity. The prootic and pterosphenoid together bound a foramen for the mandibular, buccal, and superficial ophthalmic nerves, or else the pterosphenoid is narrowly excluded from this foramen. Dorsal to this large foramen there is usually a small foramen in the pterosphenoid for the trochlear nerve, and both this foramen and the large mandibular-buccal-ophthalmic foramen face forward into the orbital cavity and lie anterior and medial to the apex of the lateral (ascending) wing of the parasphenoid. The dorsal border of the ossified pterosphenoid is continued by cartilage (the "epiphysial bar") across the roof of the cranium to meet its fellow (in *Tarpon* and *Megalops* this "epiphysial bar" is ossified, so that the pterosphenoid bones meet on the roof of the braincase beneath the frontals). A muscular ridge on the pterosphenoid runs upwards, near the posterior border of the bone, from the mandibular-buccal-ophthalmic foramen to the sphenotic; this muscular ridge, associated with the levator pterygoideus, marks off the lateral from the anterior (orbital) surface of the braincase.

In Heteromi, the mandibular and buccal nerves pass through a foramen bounded dorsally by the pterosphenoid, posteriorly by the prootic, and ventrally and anteriorly by the parasphenoid. The superficial ophthalmic nerve does not pass through this foramen, but runs medial to the extensive contact between pterosphenoid and parasphenoid to enter the orbital cavity through the broad anterior cranial aperture, as does the trochlear nerve. Thus, the major part of the pterosphenoid of Heteromi is interposed between the buccal and superficial ophthalmic nerves (where there is no bone in most teleosts) and none of the pterosphenoid extends medial to the superficial ophthalmic and trochlear nerves (where the bulk of the pterosphenoid lies in most teleosts). Furthermore, the "epiphysial bar" of Heteromi does not arise from the entire dorsal border of the bone, but arises instead from a narrowed area well posterior to the anterior border of the pterosphenoid; a rib-like thickening of the pterosphenoid, more conspicuous on the inner than on the outer surface, curves upward and forward from the mandibular-buccal foramen to the root of the "epiphysial bar".

The peculiar relationships to nerves of the pterosphenoid of Heteromi can be explained if this rib-like thickening of the bone is considered the only remnant in Heteromi of the body of the pterosphenoid of other teleosts. This would imply that only the postero-lateral edge of the pterosphenoid has been retained and the portion medial to the trochlear and superficial ophthalmic nerves has been lost, as have the other neurocranial elements, orbitosphenoid and basisphenoid, that separate the orbital from the cranial cavity in most primitive teleosts. The most conspicuous part of the pterosphenoid of Heteromi, the part giving origin to the levator pterygoideus, would seem to be a new and peculiar structure, formed by great hypertrophy of the muscular ridge running from the mandibular foramen to the sphenotic in other teleosts. This muscular ridge would seem to have been greatly extended forward as a broad lamina in the Heteromi, thus extending forward the origin of the levator pterygoideus. This forward extension of the pterosphenoid has been met and braced by an upward extension of the parasphenoid that does not correspond to the lateral wing of the parasphenoid of other fishes, since it is more anteriorly placed, anterior to the buccal nerve.

It would follow from this interpretation that the anteriormost part of the "cranial cavity" of Heteromi, *i.e.* the portion of the cavity bounded laterally by the pterosphenoid lamina and ascending wing of the parasphenoid, is not truly cranial, but corresponds to the rear of the orbital cavity of other teleosts. The eye is relatively small in Heteromi and quite degenerate, without macroscopically visible scleral cartilage or bones, falciform process, or retractor lentis muscle. Such degeneration of the eye is not surprising in deep-sea fishes, and it must be suspected that it was the degeneration of the eye that made possible the forward extension of the levator pterygoideus and the accompanying modifications of the mouth apparatus in the early evolution of the Heteromi.

CERTAIN OTHER PECULIARITIES OF THE HETEROMI AMONG "ELOPOMORPH" FISHES. In what may be called the herring-shaped "elopomorphs", *i.e.*, *Elops*, megalopids, and albuloids, the more ventral part of the epaxial musculature is continued forward onto the skull to originate from the dorso-lateral surface of the otic capsule, dorsal to the horizontal semicircular canal (ensheathed in the endochondral part of the pterotic) and lateral to the posterior semicircular canal (ensheathed in the epiotic) and to the anterior semicircular canal (ensheathed in the sphenotic or epiotic or both).[3] This forward extension of the epaxial musculature is roofed over by dermal bones, principally the posttemporal, the extrascapulars (tabulars), and the dermal component (intertemporal) of

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[3] In *Megalops* and *Tarpon* this musculature is continued even farther forward than the otic capsule and reaches the (ossified) "epiphysial bar" of the pterosphenoid.

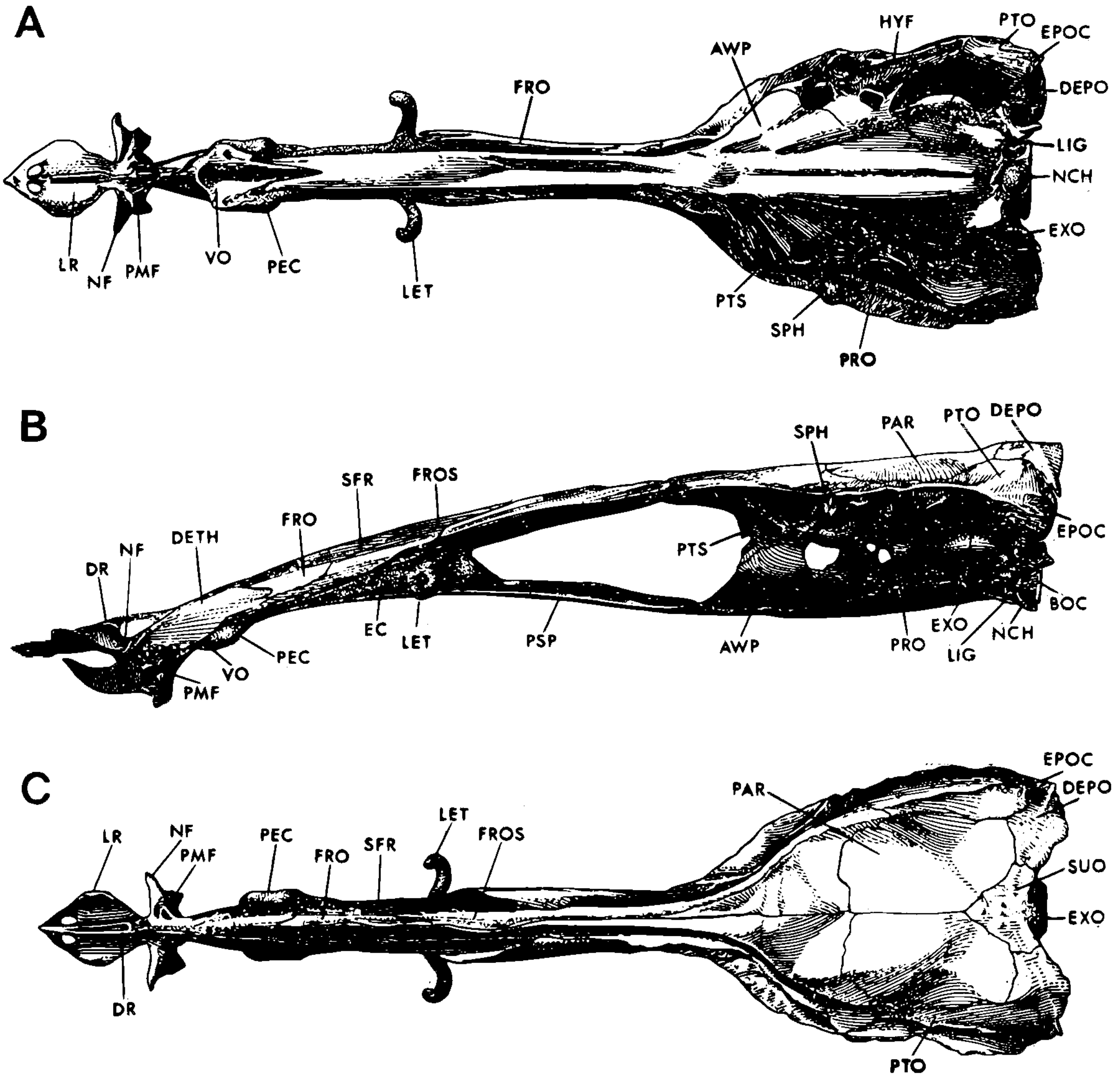
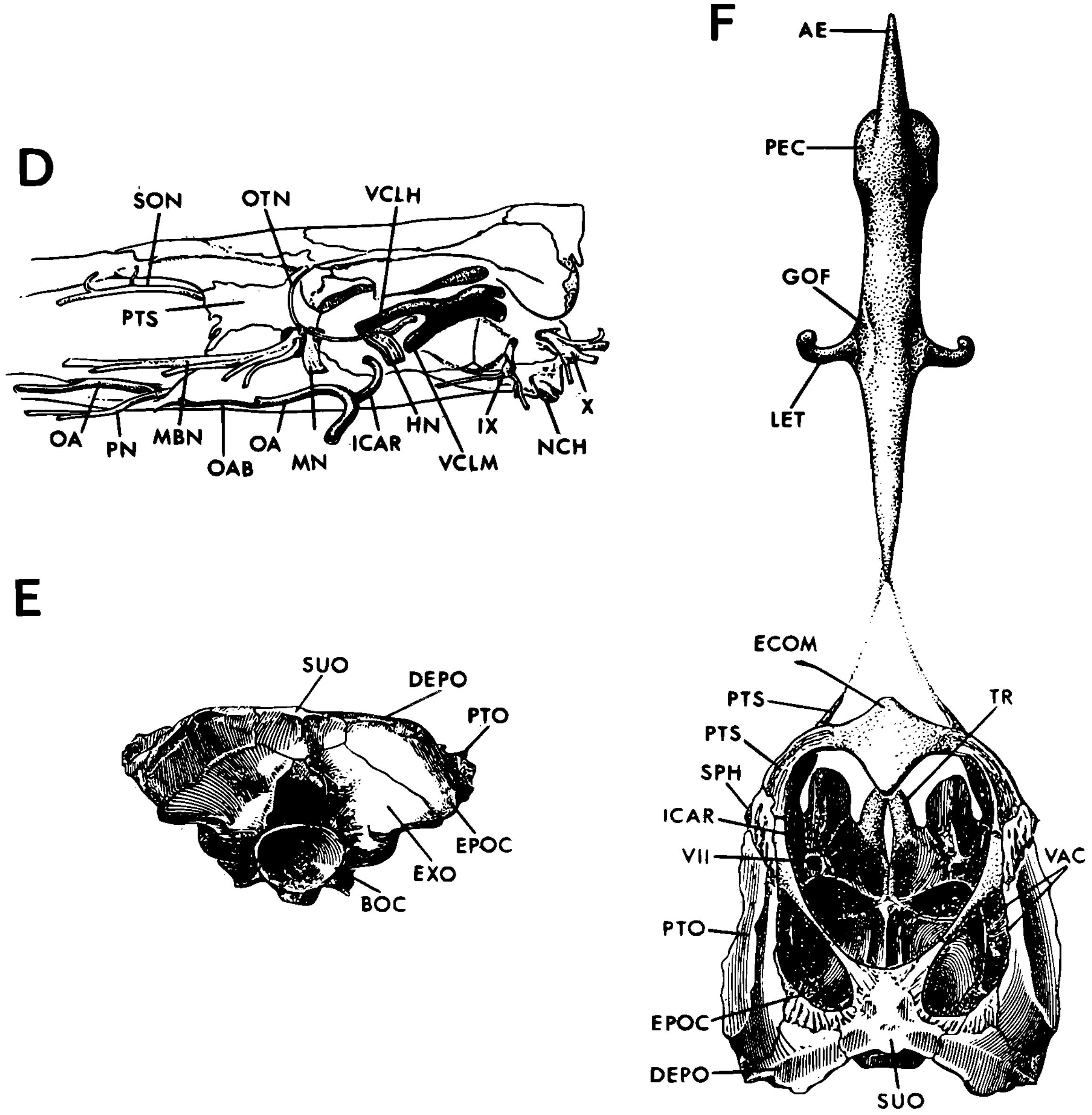


Figure 5. Neurocranium of one of the Heteromi (*Halosaurus guentheri*, Family Halosauridae), to show some of the cranial characters of the order. A, ventral view. B, lateral view. C, dorsal view. D, diagram of major vessels and nerves, to show contents of cranial foramina. E, occipital view. F, dorsal view, with frontals, parietals, parasphenoid, and dermal ethmoid removed to show underlying cartilage. Abbreviations: AE, apex of ethmoid cartilage; AWP, ascending wing of parasphenoid; BOC, basioccipital; DEPO, dermal ossification (= medial extrascapular) of epiotic; DETH, dermal ethmoid; DR, dorsal crest of rostral commissure support on dermal ethmoid; EC, ethmoid cartilage; ECOM, epiphysial commissure; EPOC, cartilage of epiotic; EXO, exoccipital; FRO, frontal bone, deeper layer; FROS, ossification of frontal around sensory canal; GOF, groove for olfactory tract; HN, hyomandibular nerve; HYF, facet for hyomandibular bone; ICAR, internal carotid artery (or its foramen); IX, glossopharyngeal nerve; LET, lateral ethmoid cartilage; LIG, process of basioccipital for ligament to cleithrum-supracleithrum articulation; LR, lateral wing of rostral commissure support on dermal ethmoid; MBN, conjoined maxillary and buccal nerves; MN, mandibular nerve; NCH, tip of notochord; NF, facet for support of nasal bone on dermal ethmoid; OA, orbital artery; OAB, orbital artery, minor branch perhaps a vestige of the efferent pseudobranchial artery; OTN, otic nerve; PAR, parietal; PEC, preethmoid cornu; PMF, facet for premaxilla on dermal ethmoid; PN, palatine branch of facial nerve; PRO, prootic; PSP, parasphenoid;



PTO, pterotic; PTS, pterosphenoid; SFR, suture within frontal between its deeper layer and ossification around sensory canal (an abnormality of the figured specimen); SON, superficial ophthalmic nerve; SPH, sphenotic; SUO, supraoccipital; TR, remnant of trabecula; VAC, vacuity in otic capsule; VCLH, vena capitis lateralis, branch accompanying hyomandibular nerve; VCLM, vena capitis lateralis, main branch; VII, foramen for facial nerve; VO, vomer; X, vagus nerve.

the pterotic. There is thus formed a deep pit on the occiput, the posttemporal fossa roofed by dermal bones and with a medial wall and a floor formed by the endochondral cranium. Such a fossa is not a peculiarity of elopomorph fishes, nor is the forward extension of the epaxial musculature; these are primitive osteichthyan features and many teleosts show such a "roofed posterior temporal fossa".

Indeed, the forward extension of the epaxial musculature upon the otic capsule is the general rule among teleosts, but in all but a few primitive groups the dermal bone roof of this fossa is defective, leaving much or all of the anterior extension of the muscle exposed.

In the Heteromi, the posttemporal fossa has been lost in an unusual way: the posterior semicircular canal, and with it the epiotic, has extended laterally to come in contact with the dermal roof, occluding the posttemporal fossa and producing a broad semicircular occiput. The supratemporal commissure runs directly external to the posterior semicircular canal (unusual, for generally the commissure bisects the angle between the anterior and posterior semicircular canals) and the epiotic is largely or entirely cartilaginous. In notacanths, the cartilage of the epiotic separates the posterior semicircular canal from the supratemporal commissure, as the extrascapulars seem to be only sclerified and not truly ossified. In halosaurs, the lateral extrascapular is ossified and fits over the epiotic cartilage (so that it might easily be mistaken for an epiotic ossification), but the roof of the otic capsule is perforated, so that the epiotic cartilage does not intervene between the semicircular canal and the supratemporal commissure. In both halosaurs and notacanths, the space in the cranium that would normally be occupied by the posttemporal fossa is filled by the inflated and perilymph-filled otic capsule, for in the Heteromi the capsule does not fit tightly around the labyrinth dorsally. The cartilage of the otic capsule is defective here, so that the perilymph comes in direct contact with the dermal roof of the skull.

The Heteromi also differ from the herring-shaped "elopomorphs" in the position of the pectoral fin. In the herring-shaped "elopomorphs", the pectoral fin lies close to the ventral profile of the body, ventral to the gill clefts and presumably ventral to the backward stream of water from the gill clefts. In Heteromi, the pectoral fin is situated high on the side of the body, dorsal to the stream of water from the pharynx; at least, this is the adult position, although Harrisson's halosaur leptocephalus has the pectoral somewhat lower, about level with the gill clefts, suggesting that the pectoral fin migrates higher on the sides during ontogeny.

The high position of the pectoral fin in Heteromi may be associated more with jaw mechanics than with respiratory currents. In *Elops*, the rectus cervicis musculature that depresses the floor of the pharynx and jaw arises from the anterior surface of the cleithrum and the shoulder girdle thus separates the rectus cervicis from the myotomes of the body wall. In both *Albula* and *Pterothrissus*, however, there is a posterior and ventral extension of the origin of the rectus cervicis onto the superficial aspect of the cleithrum, beneath the root of the pectoral fin. The Heteromi have greatly enlarged such an extension, and the broad rectus cervicis passes over the entire cleithrum beneath the pectoral and originates from the outer surface of the myotomes of the body wall. The high position of the pectoral fin thus permits a very extensive rectus cervicis muscle in the Heteromi. Tucker and Jones (*29*) have shown that *Notacanthus* can bend the head and anterior vertebral column downward, and I have seen halosaurs with a similarly deflected head. The only muscles that are properly placed for bending the head downward are the rectus cervicis group. Making room for the enlargement of these muscles for downward bending of the head during bottom feeding may be the chief adaptive reason for the high pectoral fin in the Heteromi. All the Heteromi are benthic bottom-feeders.

The cleithrum, in Heteromi, is unavailable for the origins of the extensor muscles of the pectoral fin because it is covered over by the rectus cervicis muscles. Thus the pectoral fin musculature arises from the endochondral girdle, which is expanded into a plate. This plate consists only of the hypocoracoid and hypercoracoid, for the mesocoracoid (present in the herring-shaped "elopomorphs") is absent. The absence of the mesocoracoid in Heteromi is probably a consequence of the elevated position of the endochondral shoulder-girdle, dorsal to the level of the body cavity. When present, the mesocoracoid usually lies in the more lateral part of the transverse septum, between the pericardial and peritoneal sections of the body cavity.

The brain of Heteromi (see *30* for figures of brains of various Heteromi, as well as of other fishes) is unlike that of the herring-shaped "elopomorphs" in the great forward development of the cerebellum, which extends over the optic lobes.

The swim bladder of Heteromi (*21*) is unlike that of the herring-like "elopomorphs" in having a long duct that is not patent anteriorly. My own observations are that the duct extends forward from the bladder as a patent canal, close to the coeliac artery, to the dorsal wall of the coelom above the oesophagus. Here the duct becomes a tough ligament extending downwards to the oesophagus. This ligament occupies the position of the open duct of the herring-shaped "elopomorphs". Accompanying this closure of the duct, so that air can no longer enter or leave the bladder directly, the Heteromi have developed two conspicuous unipolar retia mirabilia that lie in the walls of the posterior (patent) section of the duct and the immediately adjacent section of the bladder itself.

Relationship to the Apodes. Marshall (*21*) was much impressed by the similarity between Heteromi and true eels in the structure of the swim bladder. Apart from this resemblance, there are a number of other reasons for believing the Heteromi to be especially related to the Apodes. The occiput of eels is constructed along the same plan as that of Heteromi, with all the epaxial muscles attached on or medial to the sheath of the posterior semicircular canal. The cerebellum of eels is at least incipiently produced forward over the optic lobes. Both eels and Heteromi totally lack oviducts. The pectoral fins of eels are placed high on the sides, above the rectus cervicis, their musculature arising from the endochondral girdle; the latter lacks a mesocoracoid. Eels have a leptocephalus larva, lack a distinct caudal fin, lack lateral ethmoids, have at least the Allis's loop of the rostral commissure, and have a venous foramen posterior to the hyomandibular foramen of the prootic.

Anguilla, *Simenchelys*, and *Conger*, at least (and very likely the other Apodes, to judge from the skull), show a striking similarity to Heteromi in having the pterosphenoid extend between the buccal and superficial ophthalmic nerves. However, in spite of this resemblance to the Heteromi—that the pterosphenoid forms a false sidewall to the cranium—eels differ from Heteromi in retaining the true sidewall of the brain case. The pterosphenoid is well developed medial to the exit of the superficial ophthalmic nerve and there is an ossified orbitosphenoid.

The mechanics of the mouth in eels is in some respects the exact opposite of that in Heteromi. Whereas in Heteromi the palatal arch is unusually mobile and is connected to the hyomandibular by a kinetic symplectic, eels have an unusually rigid connection between the palatal arch and the hyomandibular through direct suture between quadrate and hyomandibular, the sympletic being absent. In Heteromi, the adductor mandibuli arises entirely from the suspensorium, and the brain case has been modified to accommodate an enlarged levator pterygoideus; but in eels, the brain case has been modified to become the origin for much of the adductor mandibulae.

Thus, while the resemblances between Apodes and Heteromi are so strong that it is almost certain the two groups have a common ancestry, the divergence between the Heteromi and Apodes has been considerable and neither group can be derived directly from the other. However, some of the peculiarities of eels might best be explained if it is assumed that the earliest eels began with the incipient peculiarities of the Heteromi, but that subsequent evolution in Apodes took an almost opposite adaptive trend. Such a character as the total absence of the symplectic in eels could be interpreted as a means of erasing the exceptionally mobile palate of Heteromi in returning to a rigid suspensorium. Eels lack premaxillae, and the failure of their right and left Allis's loops to show direct connection might well be because they are descended from a form in which the medial part of the rostral commissure lay upon the premaxillae, as in albuloids and Heteromi.

Exclusion from the Heteromi of Certain Groups Referred there by Earlier Authors. The external appearance of notacanths is quite suggestive of Mastacembelidae, particularly in such features as the row of isolated spines along the back and along the ventral profile of the tail, the prominent snout overhanging the mouth, the reduced eye covered by a spectacle, the elongated and eel-like form, and the presence of a sharp spine below and slightly anterior to the eye. Earlier authors included the notacanths among the mastacembelids; probably the last author to do so in a formal classification was Cope (*5*).

When the internal structure of mastacembelids is compared with that of notacanths, however, the resemblance vanishes. (See Regan, *27*, for an account of Mastacembelidae; my own comparisons have been based on *Mastacembelus congicus* and *Macrognathus aculeatus*.) Thus, in Mastacembelidae the premaxillae are not attached directly to the dermal ethmoid (as they are in notacanths) but to a rostral cartilage. In Mastacembelidae, the lateral ethmoid is strongly ossified and firmly articulated with the palatoquadrate cartilage and the investing ectopterygoid bone, and the dermal palatine is separated from its fellow by a strong vomer that is incorporated into the roof of the mouth. Unlike the single-headed hyomandibular of Heteromi, the hyomandibular of mastacembelids has a peg-like sphenotic head separated from the long pterotic facet. The suborbital spine of notacanths is born by the maxilla, but that of mastacembelids is born by the lachrymal.

Whereas notacanths, like halosaurs, have large parietals that meet to exclude the frontals from the supraoccipital, the frontals of Mastacembelidae are in contact with the supraoccipital and probably mastacembelids lack true parietals. (The bone generally called "parietal" in mastacembelids carries the lateral portion of the supratemporal commissure and seems to be a lateral extrascapular.) The exoccipital of mastacembelids contributes to the occipital "condyle" (more accurately, cotyle), forming a ring-like lip around the basioccipital to define a deep cup that receives a cartilaginous condyle of the first vertebra.

In all these features, Mastacembelidae show a percomorphan affinity, and none of the characteristics of the "elopomorphs" (*i.e.*, rostral commissure, venous foramen behind the foramen in the prootic for the hyomandibular nerve, leptocephalus larva) are found in the mastacembelids.

Boulenger's (*4*) reference of the Carapidae ("Fierasferidae") to the Heteromi is also without good anatomical basis. *Carapus* has a small rostral cartilage, as in Iniomi, Anacanthini, Acanthopterygii, etc., whereas there is no indication of such a cartilage or of its former presence in the Heteromi. *Carapus* makes no approach to the peculiarities of the mouth apparatus seen in Heteromi, and the Heteromi show no trace of the modifications of the ribs to support the swim bladder seen in *Carapus*. *Carapus* does not show any of the diagnostic features of the "elopomorph" group of fishes to which the Heteromi belong.

Boulenger (*4*) also referred the fossil Dercetidae to the Heteromi. The more detailed knowledge of this Cretaceous family contributed by Arambourg (*2*) makes it seem quite unlikely that the Dercetidae are related to the Heteromi. The most important differences may be summarized:

1. The premaxillae of the dercetids are produced anterior to the ethmoid as a beak; but it is quite characteristic of the Heteromi that the dermal ethmoid is produced anterior to the jaws as a snout overhanging the mouth.
2. In the dercetids, there is a membrane bone above the orbit, identified as the supraorbital by Arambourg, but possibly the dermosphenotic; neither supraorbital nor dermosphenotic occur in the Heteromi.
3. The orbit is limited anteriorly by a large and ossified lateral ethmoid in the dercetids, but this element is greatly reduced and totally cartilaginous in Heteromi.
4. Rather than being freely movable elements suspended free beneath the ethmoid region, the palatines of dercetids are large triangular bones braced against the dermal bone roof of the ethmoid region.
5. The lower jaw lacks a coronoid process in the dercetids, although this process is very prominent in Heteromi.
6. The dercetid interopercle is triangular and of considerable vertical height; the interopercle of Heteromi is strap-like or hourglass-shaped and longitudinal in position.
7. The tail is relatively short in dercetids, with the number of caudal vertebrae much less than the number of abdominal vertebrae; but the tail is longer than the precaudal body in Heteromi, where the caudal vertebrae outnumber the abdominal.

8. The abdominal vertebrae of dercetids show strong transverse processes of the centra, these processes being divided into a longer, rib-bearing anterior spine and a shorter ribless posterior spine. No such transverse process occurs in Heteromi, where the ribs are born on conical autogenous parapophyses that fit by their bases into pits in the centra.

9. The vertebral centra of the dercetids are elongated and constricted in the middle, the elongation being particularly great just behind the head. In the Heteromi, the centra are short and cylindrical, and slightly shorter behind the head than at the mid-abdominal region.

10. In the dercetids, the shoulder girdle appears to be attached directly to the skull by the supracleithrum, whereas in halosaurs the attachment is by the posttemporal, and in notacanths the girdle is free of the skull.

11. The dercetids are characterized by a series of trifid spinous plates along the side of the body and tail, unknown in any Heteromi, while normal scales are absent in dercetids but present in all Heteromi.

None of the diagnostic features of the Heteromi are visible in the Dercetidae. However, all of the above differences except 4 and 11 suggest that the Dercetidae, rather than being related to the Heteromi, might be related to the Belonidae, which they also resemble in having a dentition of large fangs interspersed with small teeth.

Range. All Heteromi are oceanic, and the group is generally regarded as part of the deep-sea fauna. This is probably true of halosaurs, but the notacanths are not exclusively deep-sea fishes, for *Notacanthus* has been caught on the Grand Banks at a depth of only 70 fms (*18*). On the other hand, the type specimen of the halosaur *Aldrovandia rostrata* was taken from the Corner Rise in the mid-Atlantic at a depth of 2750 fms (*15*). There is no reason to doubt that this specimen actually came from the bottom, since Harrisson (*17*) found, by an X-ray examination, a bottom-living tanaid crustacean in the hind gut.

There is reason to believe that in spite of the rarity of Heteromi in museum collections, the group is common or even abundant in deep water. Thus, the observers in the bathyscaphe off Portugal in the Atlantic found a halosaur the most common fish observed during two dives of 924 and 1202 fms, respectively, in the Setubal Canyon (*26*).[4] In spite of this abundance, I can find no published record of any halosaur being trawled in the vicinity of the Setubal Canyon.

Halosaurs have been recorded from every ocean except the Arctic and Antarctic, (see *17* for summary of halosaur records), but are unknown from the Mediterranean except for a single record from off Algeria (*8*). The bathyscaphe observers who found halosaurs so common off the Atlantic coast of Portugal failed to see them in Mediterranean dives (*26*), and there are no recorded specimens. *Halosauropsis macrochir*

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[4] Although Pérès gives a specific identification of the halosaurs seen as *Halosaurus johnsonianus*, it seems impossible, at least from the published photographs, to identify these fish more accurately than to family, and although it is probable, it is not certain that only one species of halosaur was observed.

has been taken from the Prince Edward (Marion) Islands (*16*) on the edge of the Antarctic Ocean at a latitude of 46°46′ S.

Besides their occurrence in the oceans where halosaurs occur, notacanths are known from the Mediterranean and also the Arctic Ocean (*29*). The Heteromi thus appear to be almost world-wide in distribution.

Classification. The treatment of the Heteromi has fluctuated between placing halosaurs and notacanths in separate orders (*e.g.*: *3*, *10*) and placing the Halosauridae, Notacanthidae, and Lipogenyidae as families of the Heteromi without other subdivision of the order (*e.g.*: *4*, *14*, *23*). The differences between Halosauridae, on the one hand, and Notacanthidae and Lipogenyidae on the other, seem great enough to warrant division of the order into two suborders.

The supposed intermediate position (*4*) of *Lipogenys* between halosaurs and notacanths does not bear close inspection, for while the dorsal fin of *Lipogenys* does not have the peculiar mastacembelid-like form seen in Notacanthidae, it is quite different in details of structure from the dorsal fin of halosaurs and seems to be a *Notacanthus*-like fin in which the anterior spines have become crowded together. In details of head structure *Lipogenys* is less like halosaurs than are *Notacanthus* and *Polyacanthonotus*, and, indeed, it is this last genus which comes closest to the halosaurs in head structure, shoulder girdle, and visceral arrangement. *Polyacanthonotus* has numerous "spines" that show traces of articulations (*21*) and seem to be only partially transformed rays. Such "spines" can easily be derived from the rays of halosaurs, particularly from the unbranched and nearly unconnected rays that occur in the middle and posterior regions of the anal fin of halosaurs. In the halosaur genus *Aldrovandia*, the 1st dorsal ray is reduced to a short spine, and similar reduction of the other dorsal rays would produce a notacanth-like fin.

Two suborders, characterized in the following key, are recognized here.

Key and Synopsis of the Suborders and Families of Heteromi

Note: Since the halosaurs are known to have a leptocephalus larva, it is quite likely that the notacanths also have a leptocephalus, and that the vent moves forward at metamorphosis. Certain of the characters used in this key can be explained as the result of greater forward migration of the vent during metamorphosis in notacanths. These characters, marked with an asterisk (*), would not be expected to hold in very young, still-metamorphosing specimens.

1a. Maxillary and premaxillary both toothed (very young individuals may lack maxillary teeth); dermopalatine and ectopterygoid both toothed, the former bone entirely anterior to the latter; one supramaxillary; sensory canals of head all cavernous (but the adnasal canal only moderately so); suborbital and lateral rostral bones (supporting the infraorbital canal and rostral commissure) broad and well ossified; dermal ethmoid with a transversely expanded and perforated anterior tip (traversed by the downward extension of the supraorbital canal to meet the rostral commissure); nasal ossified, its anterior end resting on a transverse expansion of the dermal ethmoid bone that also bears a facet for the premaxilla; lateral extrascapular (bearing the lateral portion of the supratemporal commissure) large and well ossified, fitting so closely over the (mostly cartilaginous) epiotic as to appear to be the epiotic bone; posttemporal bone well ossified and connecting skull with supracleithrum; body lateral line (except for a few inconspicuous scales behind skull and above roof of pectoral) cavernous and running low on flank near ventral profile; lateral ethmoid represented by a curved bar of cartilage extending laterally beneath the olfactory nerve to meet one of the suborbital bones; olfactory organs of the two sides of head completely separated from each other by the dermal ethmoid bone and ethmoid cartilage; no fontanelle between frontal bones; dorsal and anal fins each with not more than one anterior spine-like (unarticulated) ray; urinary bladder lying within the peritoneal cavity, in dorsal mesentery above hind gut*; paired kidneys anterior to vent large, at least as well developed as the unpaired post-peritoneal kidney*; intestine straight, without loop-like convolutions*; insertion of pelvic fin slightly to markedly nearer opercular slit than vent*; dorsal fin (except in the Cretaceous genus *Enchelurus*) entirely anterior to vent*; stomach Y-shaped, with the fundus prolonged backward as a distinct caecum; scales large, in fewer than 30 longitudinal rows on each side of body; branchiostegal membranes completely separate, the left overlapping the right, from level of hypohyal and of 1st branchiostegal ray backward.

Suborder Halosauroidei
One family, Family Halosauridae, p. 32.

1 b. Maxillary toothless, nearly excluded from mouth by premaxilla (the latter toothed in all but *Lipogenys*): ectopterygoid toothless, the dermopalatine toothed (most) or not (*Lipogenys*) and produced backward along lateral surface of ectopterygoid; no supramaxillary; sensory canals of head all of small caliber (except for rostral commissure, which may be sac-like); suborbital and lateral rostral elements not truly ossified, but former represented by slender and tube-like sclerifications; tip of dermal ethmoid compressed, without transverse expansion, entirely medial to sensory canals; nasal sclerified but not ossified, not supported by dermal ethmoid but lying in the membranous wall of the olfactory organ; lateral extrascapular represented only by a sclerified tube that is quite separate from the (mostly cartilaginous) epiotic; posttemporal represented only by a sclerified tube with its rear resting upon the free dorsal end of the supracleithrum; body lateral line normal, not cavernous, running along the groove between expaxial and hypoaxial muscle-masses, at least anterior to vent (may run close to ventral profile on tail in *Polyacanthonotus*); no lateral ethmoid cartilage; medial walls of the two olfactory organs nearly or quite in contact with each other on midline above dermal ethmoid; a fontanelle on midline between the frontals (sometimes extending back between the parietals, as well); dorsal and anal fins each with at least five unarticulated and spine-like rays anteriorly; urinary bladder lying behind the peritoneal cavity in retroperi-

toneal position*; main bulk of kidney behind peritoneal cavity, the paired extension along the abdominal vertebral column a ribbon-like vestige*; intestine with at least one loop-like convolution*; insertion of pelvic fin much nearer to vent than to opercular slit*; much or all of dorsal fin posterior to vent*; stomach U-shaped, without distinct backward prolongation of the fundus as a caecum; scales small, in 50 or more longitudinal rows on each side of body; branchiostegal membranes joined, at least anteriorly, the juncture extending well posterior to hypohyal. Suborder Notacanthoidei.

2a. Premaxillary, dermopalatine, and dentary toothed; downwardly bent rear of maxilla behind corner of mouth, the dentaries extending forward between the decurved maxillary blades to form a conspicuous lower jaw; gill clefts of normal chevron-like form, nearly equal to gills in vertical extent, with well-developed gill rakers; true first pharyngobranchial absent, the branchial basket suspended by a ligament from first epibranchial to opercular and hyomandibular; rear of metapterygoid extending horizontally along inner face of hyomandibular, well ventral to parasphenoid; all dorsal rays unarticulated and spine-like except the last, which is cleft into a spine-like anterior and a soft (usually articulated) posterior branch; cleithrum, supracleithrum, and urohyal well ossified; primary shoulder girdle with well-developed scapular fenestra or emargination, containing a disc-shaped hypercoracoid and an hourglass-shaped hypocoracoid ossification, and with a long cartilaginous postcoracoid process; interoperculum with an expansion appearing ventral to preopercular; mandibular sensory canal with pores on preopercular and on side of lower jaw; pleural ribs tendon-like, feebly (usually not at all) ossified.
Family Notacanthidae, p. 124.

2b. No teeth; lower jaw much shortened, not reaching level of the decurved posterior ends of the maxillaries, so that the latter touch (but are separated by a fissure) on the posteroventral border of the sucker-like mouth, with the true lower jaw appearing to be a "tongue" within this mouth; gill clefts reduced to small round or oval openings, much exceeded in dorsal and ventral extent by the gills, the gill rakers absent; true first pharyngobranchial present (as a cartilage, the entire branchial basket being cartilaginous) and suspending the branchial basket through a ligamentous connection to the base of the skull medial to hyomandibular; rear of metapterygoid with a gliding articulation against the parasphenoid; several of the posterior dorsal rays articulated; no cleithrum or supracleithrum, the urohyal a thin and feeble ossification on the dorsal surface of a tendon to the hypohyals; primary shoulder girdle an imperforate band of cartilage containing disc-like hypercoracoid and disc-like hypocoracoid ossifications, with very short postcoracoid process; interoperculum a narrow ossification in ligament from subopercular to lower jaw, concealed laterally by preopercular; mandibular sensory canal with pores only on preopercular; well ossified, but short, pleural ribs on abdominal vertebrae.
Family Lipogenyidae, p. 208.

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Addendum to Order Heteromi

In a paper that appeared too late for inclusion in the preceding text, D. G. Smith (Copeia, 1970: 1–9) reports leptocephalus larvae of the "*Tiluropsis*" type (a form name, not intended to have nomenclatorial standing) and the similar "*Leptocephalus giganteus*" from localities in the western North Atlantic and Gulf of Mexico; previously, this kind of leptocephalus had been reported from the eastern North Atlantic (along with the very similar "*Tilurus*" type) and ("*Leptocephalus giganteus*") from New Zealand and South Africa. The "*Tiluropsis*" "*Tilurus*", and "*Leptocephalus giganteus*" larvae appear to be closely related and Smith argues convincingly that they probably represent larvae of the "Notacanthiformes" (Heteromi of present work). Most convincing is the presence of pelvic fins (unknown in eels) in conjunction with a terminal caudal filament suggestive of the tail of adult halosaurs (quite unlike the tail of elopoid and albuloid larvae of comparable development and also unlike at least the great majority of eels). The brain of the western North Atlantic "*Tiluropsis*", as figured by Smith, differs from that of adult Heteromi in the small cerebellum that does not at all conceal or separate the optic lobes, but this could well be merely an ontogenetic difference. Unlike Harrisson's leptocephalus, the head has not yet acquired any of the distinctive characters of Heteromi and still retains a leptocephalus dentition of fang-like teeth.

Smith refers these larvae to the Halosauridae and may well be correct, but at present there is no real reason to exclude them from the Notacanthidae or Lipogenyidae and I would prefer to refer them simply to the Heteromi, family unknown.

Suborder Halosauroidei

Family Halosauridae

SAMUEL B. McDOWELL

Rutgers University, Newark

Characters. The diagnostic structural features of Halosauridae have been given above in the *Key and Synopsis of the Suborders and Families of Heteromi* (p. 27). Obvious recognition features for the rapid identification of a halosaur are the following:

The body is elongated and essentially eel-like, with the spatulate snout projecting conspicuously beyond the mouth, and with a long anal fin running along the ventral profile of the attenuated tail; no distinct caudal fin in unregenerated specimens, and the pseudocaudal (formed in specimens with a regenerated tip of the tail) formed of closely set and parallel rays directed backward as a terminal streamer, without forking or paddle-like expansion of the fin; dorsal fin with its base subequal to, or shorter than, its longest ray in length, entirely anterior to anal fin in living genera, the dorsal profile of the tail without spines, rays, or a defined adipose fin (but the larval fin fold may persist as a long, scaleless strip of soft skin along the midline of the upper side of the tail); dorsal and anal without conspicuous spines, although the 1st dorsal ray and 1st anal ray may each be reduced to a short unarticulated spine lying against the base of the articulated ray just behind; pectoral high on side, just behind upper end of branchial slit; pelvic fins far behind head in abdominal position, but nearer to the head than to the vent and either just beneath the beginning of the dorsal fin or anterior to the dorsal; pelvic fins close together, connected by a membrane at least at extreme base, this connecting membrane connected to belly by a median vertical membrane (the membrane connecting the bases of the pelvic fins is really a scale pocket, for a median scale overlapping the innermost rays of both fins, but this scale is usually rubbed off in preserved material); lateral line of body enlarged and cavernous, running close to ventral profile, level with the cavernous canal beneath the eye (in addition to the conspicuous canal on the lower flank, there is an exceedingly inconspicuous canal, which is narrow and normal in structure, running for three to five scales from the rear of the head to just above the root of the pectoral fin; as in many other fishes, a well-developed recurrent (gustatory) nerve runs backward and upward from the head to run parallel to the base of the dorsal fin; the recurrent nerve lies just beneath the thin skin and appears as a a whitish line on some preserved specimens, where it could be mistaken for a lateral line).

The elongated body, projecting snout, and the positions of the fins are diagnostic and have been used reliably to identify a halosaur in underwater photographs (*31*) and observation of living fishes from the bathyscaphe (*27*, *36*). The more elongated body and absence of any dorsal fin upon the tail distinguish halosaurs from macrourids, and the short-based dorsal fin and abdominal pelvic fins distinguish halosaurs from brotulids. The combination of a conspicuous anal with a high and short-based dorsal fin distinguishes halosaurs from eels when the pelvic fins are not visible.

Observations on Living Halosaurs. Although it is quite easy to recognize a member of the Halosauridae by sight, even under poor light, reliable identification to species or even to genus is probably impossible without close examination of a specimen. Accordingly, the few observations of living halosaurs are considered here in the family account.

Marshall and Bourne (*31*) have given observations, made by underwater automatic photography in the Gulf of Aden, of a halosaur they identify as *Halosaurus parvipennis* (regarded here as a synonym of *H. carinicauda*, an Indian Ocean species closely related to *H. guentheri* of the North Atlantic). This identification is probably correct. They give the following description of feeding behavior (*31*: 239):

> The present photographs and others show that halosaurs adopt a slightly inclined posture like that of a macrourid. Again, this is to be expected. Halosaurs also have a long tail and an anal fin with long rays, but the single dorsal member has a short base. Undulations of the tail and anal fin will again drive the animal forward and incline it head-down to the sediments. The photographs often show halosaurs with short wave undulations passing down the posterior half to a third of the tail. But longer wave, eel-like undulations have also been seen.
>
> A head-down attitude is apt in a fish with jaws suspended underneath the snout. All halosaurs and most macrourids have such jaws, which are more easily able to pick food organisms off the bottom. Moreover, the head, which ends in a triangular snout, can be used to root in the oozes, so turning up food organisms. The reinforced snout of a macrourid or a halosaur is thus a decidedly useful structure.

The observations from the bathyscaphe (*27*, *36*) are in agreement with these observations and the halosaurs observed (off the coast of Portugal) have been identified as *Halosaurus johnsonianus*, an identification that may well be correct. The published photographs from the bathyscaphe show the "longer wave, eel-like undulations", quite different in appearance from the "short wave undulations" confined to the rear of the tail shown in Marshall and Bourne's photograph. It should be noted that in halosaurs, the rear of the anal fin has the rays nearly unconnected by membrane, forming a hair-like fringe that probably offers little resistance to the water. The "short wave undulations" are probably used for remaining almost stationary while exploring the bottom for food, whereas the long-wave, eel-like undulations are probably used for rapid movement from place to place.

The Snout. Although Marshall and Bourne suggest that the characteristic projecting snout of halosaurs is used to "root in the oozes", it is unlikely that halosaurs use the snout as a plow except in soft sediment, since the bone supporting the snout is very delicate and thus quite unlike the rigid and sturdily built snout of a sturgeon. More likely, the snout of halosaurs is used primarily as a sensory probe, and it is formed mainly by the rostral commissure of the lateral-line system and the thin bones supporting the rostral commissure.

In addition to the relatively large and few pores of the rostral commissure, which open into the cavernous underlying canal and correspond to the neuromasts, the ventral surface of the halosaur snout is studded with numberous papillae, each papilla bearing a tiny distal pore. These papillae are not innervated by the buccal nerve, as are the neuromasts of the rostral commissure, but by a nerve that branches off from the anterior face of the hyomandibular branch of the facial nerve just external to the passage of the hyomandibular nerve through the hyomandibular bone. The position of these nerve fibres, on the anterior face of the hyomandibular nerve, strongly suggests that they are gustatory and that the pores in the tiny papillae of the snout are taste-buds. The halosaur snout is probably an efficient detector of food, both acoustically using the rostral commissure, and chemically, using the taste-buds.

The Olfactory Organ. Unlike eels, the olfactory organ of female and juvenile halosaurs is not particularly large or well developed, and is of the usual type seen among teleosts as described by Burne (*11*). The olfactory rosette is oval, with a linear central raphe that runs forward and slightly upward to become bound to the anterior wall of the anterior nostril. From this central raphe the olfactory laminae radiate in two series: a ventral series of laminae that are placed on the vertical medial wall of the nasal cavity, extending downward; and a dorsal series that are placed on the horizontal roof of the cavity, extending outward. The laminae are longest and largest posteriorly, shortest anteriorly. The number of laminae in each series is slightly more than a dozen in *Halosaurus* and *Halosauropsis macrochir*, or fewer, about eight in each series, as in *Aldrovandia affinis* and *A. gracilis.* Each lamina is expanded distal to its middle into a triangular linguiform process of pulpy appearance. Distal to the linguiform process, each lamina becomes a thin and transparent membrane.

The anterior nostril opens onto the center of the rosette and the posterior nostril opens immediately behind the anterior nostril onto the enlarged posterior laminae. Externally, the anterior nostril has a posterior flap that surrounds the nostril to form a short tube, and internally a curtain-like scoop grows inward from the posterior margin of the anterior nostril and directs water onto the anterior part of the olfactory rosette.

In all halosaurs that are adequately known, remarkable changes take place in the olfactory organ of males with fully distended testes (*33*). It was first noted by Grey (*23*) that "*Aldrovandia pallida*" (here considered a synonym of *A. affinis*) shows sexual dimorphism in the anterior nostrils, that of the female being colorless with a scarcely noticeable tube or flap, whereas that of the male has a relatively long and prominent black tube. This modification, which is not seen in males with relatively small testes, is accompanied by a modification of the olfactory rosette: the linguiform process of each lamina becomes much enlarged and lobulated, so that the entire rosette comes to look like a sprig of broccoli. Whether this change is permanent or only a temporary "nuptial change" is unknown, but the change in the olfactory rosette appears to be characteristic of all male halosaurs with large testes.

So far as the modification of the nostrils is concerned, there are taxonomically useful differences between the species. *Halosauropsis macrochir* is like *A. affinis*: the anterior nostril is brownish in the female, in keeping with the general deep pigmentation, but that of the male is enlarged and jet black. The male *Halosaurus guentheri* also shows an enlarged and blackened anterior nostril.

In *Halosaurus oveni* and *H. radiatus*, as well as in *Aldrovandia gracilis*, the anterior nostril of the male becomes enlarged but is unpigmented.

In *Aldrovandia phalacra*, it is the posterior nostril that becomes enlarged in the male (*33*) and changes from a small crescentic slit to a large oval opening that exposes most of the broccoli-like olfactory rosette (this was clearly depicted in Vaillant's (*42*) plate, but received no comment in his text). The type, and probably only known specimen, of *A. rostrata* is a mature male with the posterior nostril enlarged as in *A. phalacra*. These modifications of the olfactory organ in male halosaurs strongly suggest that the male finds the female by scent. Females do not have any macroscopically visible special glands to secrete an attractant, and probably it is in the general mucus that such an attractant is released.

Food and Feeding Mechanism. Harrisson (*25*) has summarized published information on the food of halosaurs, as well as contributing observations of his own, and concluded that small crustacea probably form the chief item of diet. My own observations confirm this. Nearly all the halosaurs that I have opened for examination of the stomach have contained crustaceans. Very frequently the crustacea are reduced to a "shrimp paste" that is nearly unrecognizable, except for a fragment of a leg; this may be the result of powerful digestion in the stomach. This, however, seems unlikely because polychaet worms may sometimes be found nearly intact within such a mass of "shrimp paste", and intact crustaceans may even be found in the hind-gut (*e.g.*, the tanaid found in the type of *Aldrovandia rostrata* [*25*]). More likely, this "shrimp paste" represents detritus already decomposed before eaten by the halosaur.

Halosauropsis macrochir may eat small squid, *Rossia* (*13*) and I have found cumacean crustacea in four out of nine *Halosauropsis* with identifiable stomach-contents; but even this species, probably the largest and certainly the largest-mouthed of the halosaurs, often has small crustaceans, probably copepods, in its stomach. In the other halosaurs, small crustacea also predominate in the diet, although polychaets, small snails, molluscan (pelecypod?) veligers, small clams, sipunculids, echinoderms, and (in two *Halosaurus guentheri* examined) questionably identified anthozoans have been found.

The peculiar kinetic palate of halosaurs has been described (p. 16) in the general account of the Order Heteromi. It should be noted that even when fully distended, the mouth of even *Halosauropsis macrochir* is not large and the halosaurs are not equipped to engulf large prey. Teeth are born by the maxilla (exact in very young, presumably newly metamorphosed, specimens), premaxilla, dermopalatine, ectopterygoid, and dentary bones. In *Halosaurus*, but not in *Halosauropsis* or in *Aldrovandia*, there is a dermal placque bearing teeth on the basihyal ("glossohyal"); *Halosauropsis*, but not the other genera, has a scattering of minute teeth on the entopterygoid.

All halosaurs resemble the elopoid and albuloid fishes, and differ markedly from the Notacanthoidei, in having the lining of the pharynx provided with tooth-bearing dermal bones. On the roof of the pharynx, two (most) or three (*Halosauropsis*) of these toothed placques are clustered together to form a paired upper pharyngeal tooth plate, supported by (but separable from) the third and fourth pharyngobranchial cartilages. On the floor of the pharynx there is an elongated median toothed dermal placque (parabasal) closely bound to the basibranchials; and, more posteriorly, a pair of broad triangular placques are firmly connected to the fifth ceratobranchials to form the lower pharyngeal bones. These flat, tooth-bearing plates are serially homologous with the gill rakers and grade into them. The gill rakers are dermal bones, produced out into finger-like processes and bearing minute teeth, either over their entire mesial surfaces (most) or in distinct clusters (the longer rakers of *Halosauropsis*). As usual, each gill arch except the last bears an anterior row of longer gill rakers extending into the gill cleft in front, and a posterior row of short and tubercle-like gill rakers extending into the cleft behind.

All of the teeth of halosaurs, including those on the gill rakers and pharyngeal bones, are very small. They are hinged and clustered in villose patches in which it is difficult to distinguish definite rows.[1] There is no formation of any cutting edge by a row of teeth (such as seen in Notacanthidae).

The true, calcified teeth are equalled in size and approximated in form by uncalcified papillae on the lining of the mouth, pharynx, and esophagus. Probably these papillae represent rudimentary teeth. Although true teeth do not occur on the parasphenoid (as they do in elopoids and albuloids), the parasphenoid region of the lining of the mouth is provided with these soft, toothlike papillae.

Just as the small, villose teeth on the bones of the mouth of halosaurs are well adapted to "combing" small prey into the pharynx, but poorly adapted to catching or holding large prey, the pharyngeal dentition and pharyngeal musculature of halosaurs is adapted to feeding on small, rather than large, organisms. There is no retractor pharyngeus muscle (such as seen in alepisauroids, for example) running from the vertebral column to the upper pharyngeals and used to pull large prey towards the stomach. However, the musculature and skeletal support of the upper pharyngeal plates permits

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[1] In the specific descriptions, the number of longitudinal rows of teeth in each tooth patch are given. It should be understood that these are somewhat arbitrary estimates, useful in showing the relative widths of various tooth patches, not descriptive of precisely defined rows of teeth.

inward and backward rotation of the anterior ends of these plates (thus, the motion of the upper pharyngeals is analogous to the motion of the premaxillae and of the dermopalatines). The 4th pharyngobranchial is a small, longitudinal cylinder, tightly bound to the tooth-bearing plate and attached posteriorly to the 4th epibranchial and anteriorly to the 3rd pharyngobranchial. But the 3rd pharyngobranchial (bound also to the tooth-bearing plate) is free of the preceding (2nd) branchial arch and conspicuously enlarged. Its free dorsal end does not extend forward and inward, as do the dorsal ends of the 1st and 2nd pharyngobranchials, but instead is bent forward and outward. Unlike the other pharyngobranchials, the 3rd pharyngobranchial is joined to its fellow on the opposite side by a strong transverse muscle, the transversus dorsalis pharyngealis. Contraction of the transversus dorsalis pharyngealis pulls the divergent free dorsal ends of the 3rd pharyngobranchials together, and in so doing, both constricts the pharynx and rotates the upper pharyngeal plates inward and backward. Because the 3rd branchial arch is not connected dorsally with the 2nd arch, the upper pharyngeal plate has a freedom of movement that is analogous with the freedom of movement of the palatal arch resulting from its loss of connection with the ethmoid region.

It has been suggested (*25*: 466) that, "It is likely that the sloping levator-arcus-palatini muscles [*i.e.*, the muscles here called levator pterygoideus] in *Aldrovandia* help rock the palatoquadrate back and forth, and a grinding mechanism of this type would seem well suited to triturating lamellibranchs." However, the teeth of halosaurs are not at all suited to triturating food, either in the mouth or in the pharynx, but serve to increase the friction of the lining of the oral-pharyngeal cavity for moving food backward to the esophagus and stomach. I have found small lamellibranchs in the stomach and intestine of halosaurs, with the thin shell unbroken, and BMNH 1905.9.29.10 (type of *Halosaurus niger*, a synonym of *Halosauropsis machrochir*) has a delicate and bullate pteropod (?) shell in the pharynx.

The stomach of halosaurs is of the caecal type, with the fundus produced into a backwardly extended blind sac. The walls are moderately thick and muscular (but not gizzard-like) and do not seem particularly extensible. Full stomachs differ from empty stomachs mainly in the diameter of the caecum of the fundus, not in its backward extent, and I have never seen a halosaur stomach extended backward past its normal position by food. Halosaurs do not seem adapted to gorging themselves on a bulky mass of food at a single meal. In contrast, the stomachs of notacanths and, particularly, *Lipogenys*, may be extended back to the rear of the peritoneal cavity when gorged with food; to make this comparison fair, however, it should be noted that the peritoneal cavity of halosaurs is relatively much longer than that of notacanths, as indicated by characters marked with an asterisk in the *Key and Synopsis of the Suborders and Families of Heteromi.*

The muscular pyloric arm of the stomach extends forward to meet the duodenum at an acute angle. The duodenum, like the rest of the intestine, is straight and longitudinal, with from four to twenty pyloric caeca. The number, arrangement, and pigmentation of the pyloric caeca are very useful in the taxonomy of halosaurs. The tips of the caeca do not lie free in the body cavity (except the extreme tips in *Halosauropsis*), but are held in place by mesentery and branches of the hepatic portal vein. In most halosaurs the caeca form a regular row, like the teeth of a comb, but in *Halosauropsis* they are so crowded at their bases as to form a series that is so deeply zig-zag in arrangement as to appear double, and the tips are irregularly disposed. *Halosauropsis* further differ from the others in lacking pigment on the caeca; in most halosaurs the caeca are black, like the rest of the digestive tract, but in *Halosaurus oveni*, *H. ridgwayi*, and *H. radiatus* (the subgenus *Halosaurus*) the distal part of each caecum is colorless.

The liver has a single, relatively narrow lobe lying ventral to the stomach, to the left of the pyloric arm of the latter.

Lateral-line System. The cavernous lateral-line canals, both on the flanks and on the head, of halosaurs are quite characteristic. Lendenfeld (*29*) has studied and figured the histology of the lateral line of the flank, but misidentified certain structures in the mistaken belief that the lateral line was a row of photophores comparable to that of stomiatoid fishes. The delicate sheath of the flank canal is usually damaged in specimens, and because of its transparency, is not easy to study when well preserved. The dark pigmentation of the canal sheath of adult *Halosauropsis macrochir* makes the canal easier to study in this species; a good account of the canal sheath of *Halosauropsis* has been given by Koefoed (*28*). The canals and neuromasts of the head of *Halosaurus* have been described by Garman (*18*) and the peculiarities of the preopercular canal have been clarified by Marshall (*30*).

Halosaurs possess one short lateral-line canal that has not been mentioned in the literature, and which is of quite normal form, without cavernous expansion. This canal runs from the posttemporal backward for three to five scales, to end above the base of the lobe supporting the pectoral fin. It is very similar to the flank canal of notacanths and is formed basically of a narrow membranous tube, born on the superficial surface of the supporting scales, with its pores in pairs: one facing dorsally and one facing ventrally. The dorsal pore is separated from the ventral pore only by a thin longitudinal band of membrane which is easily torn; probably (but not certainly) the confluence of the dorsal and ventral pores into a single opening, which I have observed occasionally, is the result of such damage. The canal is not surrounded by the bone of the scale, but lies in a longitudinal gutter formed by bordering ridges of bone; sclerified, but uncalcified, flaps extend from these ridges to fold around the canal between the pores.

The conspicuous flank canal of halosaurs is basically similar to this short canal, but is enormously expanded, with the ventrally directed pores much enlarged but the dorsally directed pores remaining small and inconspicuous (they have been missed by previous workers). The canal runs low on the flank and the scales bearing neuromasts are moderately (Halosaurinae) or greatly (Halosauropsinae) enlarged. The branch of the vagus innervating the canal lies just internal to the scales and is conspicuous through the transparent skin of preserved specimens.[2] The nerve of the lateral line has a thick sheath, leading Lendenfeld (*29*), in his histological study, to identify this sheath as a slime canal. The neuromasts are very large and diamond-shaped and each scale supporting a neuromast is perforated near its center by the nerve of the neuromast. The enlarged canal sheath is entirely superficial to the ossified part of the scale, but each neuromast-bearing scale has a pair of sclerified flaps, one extending downward from above and the other extending upward from below, that support the membranous outer wall of the canal sheath.

As noted above, the dorsal pores of the canal remain small slits, but the ventral pores are greatly enlarged and extended as short tubes. In *Halosaurus*, each tube of a ventral pore is fused to the tube just in front and the tube just behind. This is true also of the abdominal part of the canal in *Halosauropsis* and the entire canal of *Aldrovandia affinis* and *A. phalacra*. On the tail of *Halosauropsis*, and on the entire flank canal of *A. gracilis* and *A. mediorostris*, the neuromast-bearing scales are more broadly separated, so that the short tubes of the ventral pores are not in contact; here, the posterior wall of the pore fuses to the outer sheath of the main canal just behind the pore. Consequently, in either case, the canal is not a simple tube with large holes in its wall (as, for example, in Cetunculi), but is sacculated.

In very young, but metamorphosed halosaurs, the flank lateral line may not reach the level of the anus, although the head canals are developed, and the flank canal seems to be the last one to develop. Even in adults, the canal does not reach the end of the body axis, but ends near the base of the anal fin about one abdomen-length behind the vent. The flank canal is not connected to the canals of the head, but begins behind the opercular slit, level with the cavernous canals upon the preopercular, and thus acts as a functional continuation of the cavernous canals on the side of the head.

The mandibular canal, innervated by the hyomandibular nerve, lies upon the preopercular, articular, and dentary bones. The pores are in a single series and the canal is not sacculated. On the lower jaw, particularly anteriorly, the pores are relatively small, but on the preopercular bone the pores are very large. The outer wall of the canal is formed entirely by skin, and on the preopercular bone this wall is so easily torn that the pores are countable on only a small minority of specimens. On the preopercular bone, the mandibular canal extends backward as an horizontal continuation of the canal upon the jaw, extends upward and forward to form a U-shaped loop (convexity directed backward), then turns upward to end in a pore at the upper end of the preopercular bone. The backwardly-directed loop upon the preopercular is quite unusual (but seen in *Denticeps* [*11*]) and is responsible for the peculiar form of the preopercular, as pointed out by Harrisson (*25*). The part of the preopercular bearing this loop is extended backward to border the opercular slit, exceeding the opercular bone in backward extent. Harrisson was unable to trace the canal on his halosaur

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[2] The lateral-line scales are mostly or entirely rubbed off in most specimens, but the large nerves of the neuromasts can be seen in the scale pockets, particularly when temporarily stained with tincture of iodine or methylene blue. I have found it easier to count lateral-line nerve stubs than to count the scales themselves in making counts of lateral-line scales.

leptocephalus, because of damage to the specimen, but found the preopercular to have the same backward extension to the margin of the opercular slit that is so diagnostic of adult halosaurs. This is one of the strongest bits of evidence that his leptocephalus is a halosaur.

The upper limb of the preopercular loop of the mandibular canal is horizontal and precisely in line with the main portion of the infraorbital sensory canal; indeed, with damaged material, the upper limb of the preopercular loop of the mandibular canal may appear to be a backward continuation of the infraorbital canal.[3]

The other canals of the head are connected with one another by anastomoses, but can be distinguished by the innervation of their neuromasts. The infraorbital canal, innervated by the buccal nerve, is divisible into four sections: the rostral commissure, the adnasal canal, the main infraorbital canal, and a vertical postorbital canal.

The rostral commissure has already been discussed in the general account of the Order Heteromi. In halosaurs, the commissure hangs down from the dermal ethmoid as a capacious U-shaped sac that overlies the premaxillary bones, as in albuloids. Although the rostral commissure of halosaurs differs from that of albuloids in being supported by separate lateral rostral bones rather than by the premaxillae themselves, the nerve branch for the commissure pierces the premaxilla. The albuloids probably differ from halosaurs only in fusion of the lateral rostral with the premaxilla. The rostral commissure of halosaurs pierces a diamond-shaped transverse expansion of the tip of the dermal ethmoid, and runs backward on the dorsal surface of the dermal ethmoid to anastomose with the anterior end of the supraorbital canal, borne by the nasal. On the dorsal surface of the dermal ethmoid, the left and right arms of the rostral commissure are brought together, but do not join, since a thin membrane separates them. The actual continuity of the canal across the midline lies below the diamond-shaped terminal expansion of the dermal ethmoid, on the ventral surface of the projecting snout.[4] The outer walls of the rostral commissure are formed entirely of skin, and the pores are (by halosaur standards) small, no larger than the posterior nostril.

The main part of the infraorbital canal is much inflated, with a membranous outer wall. Its inner and dorsal wall is formed by the suborbital bones, which have their dorsal edges curled outward over the canal. The pores are large and easily torn, making it impossible to count them on many specimens. Although the main part of the infraorbital canal, which overlaps the maxillary bone, lies on the same horizontal level with lowermost part of the rostral commissure, the continuity with the rostral commissure is formed in a much more dorsal position almost level with the nostrils. Ventral to this continuity, the wall of the rostral commissure is joined to the wall of the main portion of the infraorbital canal to form a diagonal membrane sloping downward and backward.

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[3] This appears to have misled Garman (*18*) into figuring the infraorbital and mandibular canals as connected on the cheek, as in crossopterygian and dipnoan fishes, and too has misled Marshall (*30*) into ascribing the upper part of the mandibular canal to the infraorbital canal, as a peculiar extension of the latter onto the preopercular bone.

[4] In spite of published descriptions to the contrary, I find *Albula* and *Pterothrissus* to be like halosaurs in this respect, with a thin membrane separating the left and right arms of the canal on the dorsal surface of the dermal ethmoid.

The main portion of the infraorbital canal ends in a very large and backwardly-directed pore just anterior to the preopercular. The infraorbital canal is then continued upward at a right angle to the main portion, by a much narrower vertical canal that anastomoses with the supratemporal canal at the anterior end of the pterotic bone. This vertical portion of the infraorbital canal is not cavernous and is born by two or three infraorbital bones that form a connected chain in *Halosaurus* but are isolated in the skin in Halosauropsinae. The pores of this portion of the canal are quite small.

The adnasal canal joins the infraorbital canal at the communication between the rostral commissure and the main portion of the canal. The canal then extends backwards and only slightly upward, lateral to the olfactory organ and dorsal to the main portion of the infraorbital canal. The canal, which is born by the adnasal bone, ends blindly posteriorly beneath the nostrils in *Halosauropsis* and *Aldrovandia*, but ends in a pore beneath the nostrils in *Halosaurus*.

In Harrisson's (*25*) leptocephalus the infraorbital canal is inflated and essentially like that of the adult, even though the flank canal is not developed. Harrisson's figure does not indicate a pore beneath the nostrils, but his statement, "A pore just anterior to the nasal capsule marks the posterior limit of the adnasal canal," leads me to suspect his larva is *Halosaurus* rather than *Aldrovandia*.

The supraorbital canal, innervated by the superficial ophthalmic nerve, is borne by the nasal, frontal, and parietal bones and is considerably narrower than the flank, infraorbital, and mandibular canals. Its outer wall is formed by the skin. Near the rear of the frontal bone, the supraorbital canal gives off a laterad and caudad snag that merges smoothly with the supratemporal canal on the front of the pterotic. Behind this snag, the canal is vestigial, often without a pore (but with one neuromast in *Halosaurus*) and leaves no impression on the bone. Two (rarely three) pores and two neuromasts lie on the nasal bone and the nasal is constricted between the neuromasts and nearly divided into an anterior and a posterior bone (as in the albuloid *Pterothrissus*). The frontal bears two or three pores and neuromasts. Harrisson (*25*) says of his halosaur leptocephalus: "... a series of pale elongate ovals marks the position of the supraorbital lateral-line canal." The development of the supraorbital canal thus seems to lag behind that of the infraorbital canal.

The supratemporal canal, innervated by the otic nerve, is carried by the pterotic bone in an open bony gutter, with the skin forming the outer (dorsal) wall of the canal. Anteriorly the supratemporal canal is smoothly continuous with the supraorbital canal, but meets the infraorbital canal at almost a right angle. The canal bears two or three pores and neuromasts and continues posteriorly, without demarcation, into the posttemporal canal. Harrisson's figure suggests the supratemporal canal is not yet developed in his leptocephalus.

The posttemporal canal and supratemporal commissure are innervated by a branch of the vagus. The posttemporal canal is longitudinal and borne by the posttemporal bone, while the transverse supratemporal commissure lies upon the supraoccipital (which is thus probably a "dermosupraoccipital", involving a medial extrascapular fused to the underlying cartilage bone) and lateral extrascapular (which fits closely upon the epiotic cartilage). It joins the posttemporal canal on the posttemporal bone. In most halosaurs, but not in *Halosauropsis*, there is a median pore of the supratemporal commissure, which is complete across the occiput. There is in all halosaurs a paired pore, lying on the lateral extrascapular. The longitudinal posttemporal canal has one pore, and there is another pore on the common canal formed by fusion of the supratemporal commissure with the longitudinal posttemporal canal. Posteriorly, the posttemporal canal is continued by the short notacanth-like canal to the root of the pectoral, described above.

The canals on the halosaur head are essentially like those of albuloid fishes, with the added peculiarity of a loop of the mandibular canal upon the preopercular. The canals of the head, particularly the infraorbital and mandibular canals, resemble the flank canal. They are cavernous and are provided with exceptionally large neuromasts that are easily visible to the naked eye.

Supposed Luminous Organs. Günther (*24*) and Lendenfeld (*29*) attributed a light-producing function to the neuromasts of halosaurs, although without any circumstantial observations of luminescence in live fish. Günther appears to have been influenced by the striking color contrast between the pale neuromasts and deeply pigmented skin of *Halosauropsis macrochir*, although he correctly identified the row of neuromasts as the lateral line. Lendenfeld appears to have been misled by histological study of a badly preserved specimen (he identified the lateralis branch of the vagus nerve as the lateral-line canal!) and concluded (*29*: 313): "... there can be no doubt that the small spindle-shaped organ [*i.e.*, the neuromast] attached outside to the scale is phosphorescent. It appears very similar to the suborbital organ of *Opostomias micripnus*."

Günther's and Lendenfeld's ideas seem to have influenced most later work. Thus, Goode and Bean (*22*) erected the genus *Aldrovandia* for halosaurs with greatly enlarged lateral-line scales and stated that these scales were provided with photophores. Collett (*13*) erected the genus *Halosauropsis* for *H. macrochir* in the belief that this species differed from other halosaurs in possessing "organes photodotiques" and that the black pigmentation of the lateral-line sheath, characteristic of this species, was part of a mechanism for directing the light downward. Garman (*18*) did not question the luminescence of halosaur neuromasts (which he recognized as such), but noted the similarity of the neuromasts in all halosaurs and, unlike Collett, concluded that all halosaurs are luminous. He even speculated on the function of this supposed luminescence (*18*: 296): "The positions of their lanterns on the lower portions of the head and body indicates a probable habit of illuminating the mud for a short distance around the individual in its search for prey."

However, belief in the luminescent function of halosaur neuromasts has not been universal. Vaillant (*42*) was noncommittal and said the state of the material collected by the TALISMAN and TRAVAILLEUR did not permit giving an account of the nature of the whitish spots on the scales. Brauer doubted the light-producing nature of the neuromasts and suggested (*9*: [2]: 118–119) that Günther and Lendenfeld may have been influenced to attribute light-producing functions to many deep-sea fishes by the belief that deep-sea fishes ought to have photophores.

It seems beyond doubt that the organs along the lateral line, both of head and body, are neuromasts, as indicated by their innervation and by their similarity to the neuromasts of other fishes (particularly the neuromasts on the head of albuloids). The question remains, do these neuromasts of halosaurs have an additional light-producing function? Their structure does not suggest it, for while in *Halosauropsis macrochir* these organs are covered by pigmented skin (in the adult, but not in juveniles), in no halosaur is there a backing of pigment or a differentiated reflector layer. Although these organs are associated with large sensory (lateralis) nerves, no macroscopically visible motor nerves go to them. (Twigs of the hyomandibular nerve, probably gustatory fibres, go to the sheaths of the infraorbital, including alinasal, and mandibular canals, but not to the neuromasts of these canals.) Alcock (*6*: 240) figured a halosaur under the heading, "glow fishes whose phosphorescence is probably under the direct control of the will," but such an interpretation is not consistent with the absence of motor innervation. Hormonal stimulation, however, is not excluded by this argument.

But the assumption of hormonally-induced luminescence of halosaur neuromasts is unnecessary. Myctophids have large neuromasts on the head very similar to those of halosaurs, and it is not these neuromasts that light up, but rather the photophores of quite different construction. The giant neuromasts on the head of *Albula*, a well-known fish that is not known to be luminescent, are very similar to the neuromasts of halosaurs. There does not seem to be any difference in construction between the neuromasts of the supraorbital canal of *Halosaurus* and the other neuromasts, yet the supraorbital neuromasts of *Halosaurus* are covered by scaly and opaque skin. It is also hard to reconcile the development of light-producing organs for scanning the bottom, as suggested by Garman, with the degenerate condition of the eye in halosaurs. Unlike the probably related albuloid *Pterothrissus* (personal observation), halosaurs lack any macroscopic trace of a falciform process, retractor lentis muscle, or scleral cartilage.

Photographs of living halosaurs in their natural environment (*27*, *31*, *36*) do not show any pale spots suggestive of light organs, nor has Dr. Harvey Bullis (personal communication) observed luminescence in the numerous halosaurs trawled up by the OREGON. It may even be questioned whether light organs are to be expected in halosaurs. Most of the reported cases of bioluminescence are from the bathypelagic or even surface pelagic fauna; bioluminescence appears to be rare among the benthic fishes.

Günther (*24*) and Lendenfeld (*29*), besides attributing a light-producing function to neuromasts, also considered the suprabranchial organ as luminescent. The suprabranchial organ has not received attention from later workers. It is a whitish mass lying dorsal to the gill clefts in the branchial chamber, on the outer side of the supracleithrum. Both Lendenfeld's sections and my own[5] show the organ to be com-

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[5] I am most grateful to Mrs. Lisa Hamilton Walters for her care in preparing these sections.

posed of numerous lymphocyte-like cells interspersed with fibrous (eosinophilic) needle-like structures. Except for the latter, the histology is quite similar to that of a mammalian tonsil. The needle-like structures appear to be identical with the small fibrous rods (branchial rays) that support the individual filaments of the gills, which lie just ventral to the suprabranchial organ. In some specimens of *Halosaurus*, the position of the suprabranchial organ is taken up by dorsal extensions of the true gills. Probably the suprabranchial organ of halosaurs represents a degenerate group of gill filaments, possibly a larval gill, with the branchial rays still persistent, but the remainder of the filaments broken down to a mass of lymphocytes. The organ shows no histological resemblance to a photophore and is covered by the opercular bone, which is covered on its inner (branchial) surface by the black lining of the branchial chamber. The Notacanthoidei, which have never been suggested to be luminous, also have a suprabranchial organ like that of halosaurs.

Scales and Squamation. The scales of halosaurs, unlike those of Notacanthoidei, are relatively large and regular in arrangement, with well-defined longitudinal and vertically diagonal rows. Even where the normal body scales become adjacent to greatly enlarged lateral-line placques (*Halosauropsis* and *Aldrovandia*), there is a stable pattern (differing from species to species) of contacts between normal scales and lateral-line placques.

David (*15*) has characterized the scale structure of halosaurs. The nucleus of the scale is large, egg-shaped, and smooth, and is surrounded by strong, curved circuli and fine radiating apical lines. In the dorsal and ventral sectors of the scale, the circuli are strong and straight, paralleling the parallel dorsal and ventral margins of the scale. The basal (anterior) sector of the scale shows a radiating series of central folds, crossed by numerous circuli that undulate to follow the contours of the folds. The basal border of the scale is nearly straight, but is scalloped at its intersection with each of the basal folds. The apical (posterior) border is more or less rounded.

The shape of the enlarged lateral-line scales of most *Aldrovandia* (*A. affinis* excepted) would differ from this in the greater curviture of the basal (anterior) margin, so that the scale is oval rather than rectangular with rounded corners. Otherwise, the lateral-line scales are similar to the others except for a perforation near the center for the lateral-line nerve.

The scales of the rows just dorsal and just ventral to the lateral-line row are peculiar in that they are narrowed, with their posterior apex drawn out into a rounded-off point that is bent in the direction of the lateral line.

The scales of the mid-dorsal row frequently do not correspond to the transverse rows of the flank, but are considerably fewer in number. Sometimes these mid-dorsal scales bear terminal flaps of sclerotised, but uncalcified, material. These scales are probably modified because they were formed in the region of the dorsal fin-fold of the leptocephalus larva.

Scales are found over the entire body and tail, and also form a lateral fringe on at least the base of each anal and dorsal ray. The bases of the pelvic rays bear small scales, but the pectoral rays are unscaled. The fleshy base of the pectoral is scaled on its lateral surface, but its medial surface and the region of the flank against which it lies are without scales. The isthmus has numerous scales, smaller than those of the rest of the body, but the branchiostegal membranes are scaleless.

In all halosaurs there are scales on at least the side of the head, overlying the jaw muscles and levator operculi, but the sheath of the infraorbital canal (including the rostral commissure) and of the mandibular canal are without scales. In all halosaurs there is a concealed row of scales buried beneath the main infraorbital sensory canal, actually deep to the suborbital bones. Probably this row is to be regarded as originally ventral to the sensory canal, but buried by the ventral expansion of the canal.

In *Halosaurus*, the top of the head and the opercular bone bear scales, and there is a row of scales along the side of the lower jaw. In *Halosauropsis*, however, the scales on the top of the head and the lower jaw have been lost, and in *Aldrovandia* the scales on the opercular bone have been lost as well.

Reproduction and Development. The sexes of halosaurs are separate, and there is a sexual dimorphism in the olfactory organ, as noted above. The female totally lacks oviducts and the eggs are shed through an abdominal pore located between the anal and urinary openings. The ovaries hang down into the abdominal cavity as simple laminae, without the curling of their free edges. In ripe females, the entire abdominal cavity is distended by the numerous small yellow eggs that may lie free within it. In males, there is a paired testicular duct that opens posteriorly into the urinary sinus just below the urinary bladder. Each testicular duct bears two testicular masses, an anterior testis, anterior to the level of the base of the pelvic fins, and a posterior testis, anterior to the anus. (I have observed this unusual feature in *Pterothrissus gissu*, as well.) Although each ovary of a ripe female appears to be continuous, unripe females resemble the male in having the gonad of each side divided into an anterior, prepelvic portion and a posterior, preanal portion.

The larva is known to be a leptocephalus (*25*). The only leptocephalus positively known to be that of a halosaur was taken in an Isaacs-Kidd midwater trawl (mean depth, 601.5 fms) during the autumn of 1961, off Madeira, between 29°59′N, 22°56′W and 29°50′N, 22°57′W. This leptocephalus seems to have just begun metamorphosis, since the gut ends blindly 22 segments anterior to the urinary papilla and the mandibular and infraorbital sensory canals, including the rostral commissure, are in an essentially adult state. A summary of Harrisson's description of this leptocephalus is given below:

> Total length (tail tip missing), 190 mm (estimated total length with intact tail, 194 mm); head from snout to basis cranii, 9.5 mm; greatest depth of body, 7.3 mm; ratio head length: total length, *ca.* 1:20; ratio head length: length to pelvic fins, *ca.* 1:3; ratio maximum head depth: maximum body depth, 1:2.
>
> Total myotomes, *ca.* 250; myotomes to urinary papilla, 207; gill rakers, 1st arch, 9 + 1; branchiostegals, 10; dorsal rays, none (a continuous finfold); pectoral rays, 10: pelvic rays, 8; anal rays none (no trace of an anal finfold); lateral line undeveloped.
>
> Dorsal finfold beginning far behind pelvic fins, near midbody, running to end of preserved tail; pectoral fin placed below midline of side but [from figure] above most of gill cleft; preoperculum contributing extensively

to margin of gill cleft (as in adult halosaurs); supraorbital canals not very close together; levator pterygoideus behind eye (as in *Halosaurus*); adnasal canal with pore just anterior to nasal capsule; larval teeth (such as found in eel leptocephali) absent, no other teeth mentioned or figured; no maxillary spine mentioned or figured; no scales.

Harrisson refers this larva to *Aldrovandia affinis*. However, the presence of a pore on the adnasal canal and the failure of the levator pterygoideus muscles to extend between the eyes are features not seen in adult or juvenile *Aldrovandia*, but are characteristic of adult *Halosaurus*. The failure of the supraorbital canals to run close together is a difference from most *Halosaurus* and a resemblance to *Aldrovandia*, but *Halosaurus johnsonianus*, which is known to occur not far from Madeira, has the supraorbital canals separated by slightly more than the width of one canal. I think it most probable that this larva is *Halosaurus johnsonianus*, but it is quite possible that *Aldrovandia* passes through a *Halosaurus*-like stage.

Harrisson found three pale zones, and two dark zones with the beginning of a third, in the otolith. If these represent annual rings, as seems probable, then halosaurs would be eel-like in remaining in the leptocephalus stage for about 3 years.

Metamorphosed but small and obviously juvenile halosaurs lack scales and may have a lateral line that fails to extend to the anus. The lateral-line scales are the first to develop. The anteriormost branchiostegal may be preceded by unossified ligament-like rays, suggesting that additional branchiostegals may be formed after metamorphosis. Even adult halosaurs may have unossified pectoral rays in the flesh just ventral to the conspicuous rays. Possibly the number of pectoral rays increases during post-metamorphic life. In very small halosaurs, the premaxilla is toothed, but the maxilla may be toothed only anteriorly or even lack teeth entirely, indicating that the adult dentition is formed first on the premaxilla and then extends backward on the maxillary bone. The gill-raker count given for the leptocephalus is considerably lower than that known for any adult halosaur, but it is not certain that the rakers of the larval fish persist as the rakers of the adult.

Social Organization. Unlike notacanths, halosaurs are frequently, perhaps usually, trawled up in groups of more than one individual. The observations from the bathyscaphe (*36*) indicate that they are at least sometimes gregarious, although they do not appear to show the close and orderly formation associated with schooling, as in such fish as mackerel. Grey (*23*) records the capture in one bottom haul by the OREGON (St. 1303, 28°47′N, 87°50′W, 1150–1200 fathoms, May 26, 1955) of 21 *Aldrovandia gracilis* and 20 *A.* "*pallida*" [= *A. affinis*]. It is not certain that this indicates a mixed aggregation of two species, since the two species may have entered the trawl at different times, but it suggests the possibility of such mixed aggregations. In the same general area, *Halosaurus guentheri* has been taken with *Aldrovandia affinis*, and with *A. gracilis*.

Aggregations of halosaurs are often not homogenous in age, and the haul at OREGON St. 1303 included young and adults of both species. Since it is now known that halosaurs pass through a pelagic leptocephalus larval stage, the question arises, how do young (*i.e.*, newly transformed) individuals become attracted to the vicinity of older individuals of their own species? The question cannot be answered at present.

In the case of *Halosaurus guentheri*, aggregations I have examined are homogeneous as to sex (33), either consisting of males or of females and juveniles. This indicates some sort of social organization in this species, but in the case of *Aldrovandia affinis*, *A. gracilis*, and *A. phalacra*, males and females have been taken together on several occasions.

Measurements and Counts Used in this Study. Because very few halosaur specimens retain their original complete tail, standard length and the number of anal rays are useless for comparative purposes. The weakness of the ribs in the body wall and the distension of the abdomen by eggs in ripe females make standard depth a difficult measurement to repeat with any accuracy on the same specimen. The tip of the snout of halosaurs is supported by very fragile, not infrequently broken, bone, and it is undesirable that any measurement including the snout tip be used as the divisor of a ratio. The following measurements and counts are used here in the species accounts:

GNATHOPROCTAL LENGTH: The distance (straight line) from the tip of the lower jaw to the anal opening.

PREANAL DEPTH: The depth (taken with calipers) of the base of the tail just anterior to the base of the anal fin, expressed as per cent of gnathoproctal length. The body is firmly supported by haemal arches and the anal interhaemals at this point, and this measurement is a reasonable index of depth of the body.

HEAD LENGTH: Taken with calipers or dividers, placing one point at the tip of the lower jaw and the other point at the upper end of the opercular cleft; expressed as per cent of gnathoproctal length.

SNOUT LENGTH: Taken with calipers or dividers, placing one point at the tip of the dermal ethmoid bone, the other point on the anteriormost border of the transparent spectacle over the eye; expressed as per cent of gnathoproctal length.

PREORAL SNOUT LENGTH: Taken with calipers or dividers, placing one point on the tip of the dermal ethmoid, the other point on the most anterior end of the premaxillary tooth patch; expressed as per cent of gnathoproctal length.

LENGTH OF SPECTACLE: Taken with calipers or dividers, placing one point on the most anterior, the other point on the most posterior part of the border of transparent window over the eye; expressed as per cent of gnathoproctal length. The spectacle is somewhat longer than the true eye beneath it, and "length of spectacle" is not the same measurement as "diameter of eye".

DEPTH OF HEAD: Taken with calipers at the level of the jaw articulation on specimens with the mouth naturally closed; expressed as per cent of gnathoproctal length. When the mouth of the halosaurus is open, the floor of the pharynx is depressed to varying degrees and a meaningful measurement of head depth cannot be taken.

DISTANCE FROM OCCIPITAL COMMISSURE TO ORIGIN OF DORSAL: Taken with a straight-edged ruler from the transverse sensory commissure (supratemporal commissure) to the base of the 1st dorsal ray; expressed as per cent of gnathoproctal length.

DISTANCE FROM EDGE OF PREOPERCLE TO ORIGIN OF PELVIC: Taken with calipers or dividers from the most posterior point on the border of the opercular flap (this point always formed by the preopercular in halosaurs) to the anterolateral corner of the pelvic fin insertion.

DORSAL RAYS: All rays are counted, including the 1st ray of *Aldrovandia*, where this ray is reduced to a short, unarticulated spine. The last ray of the dorsal fin of halosaurs is usually cleft to the base into an anterior and a posterior portion; but both halves have a common insertion on a pterygiophore and a common muscle attachment; these two halves of a single ray are not counted separately.

PECTORAL RAYS: The dorsalmost "ray" of the halosaur pectoral is a stiff and unbranched spine, articulating directly with the hypercoracoid, rather than with a pterygial bone, and with a musculature of its own. This spine is regarded here as a fulcral spine and not counted as a ray (the presence of a fulcral spine articulating directly with the coracoid arch on the anterior or dorsal margin of the pectoral fin is not a peculiarity of halosaurs, but a very common feature among actinopterygian fishes). Small, rudimentary pectoral rays are found nearly or quite buried in the flesh on the ventral margin of the fin; these are included in the fin-ray counts.

PELVIC RAYS: The small fulcral spine just dorsal to the outer edge of the pelvic fin is not included in this count, since it is not directly connected with the pelvic girdle or pelvic musculature.

LATERAL-LINE SCALES TO ORIGIN OF PELVIC FIN: This is a count of scales (or scale pockets) actually bearing neuromasts (or showing the stub of a nerve to a neuromast), taken from the first such scale behind the gill cleft to (and including) the scale just over the base of the outermost pelvic ray.

LATERAL-LINE SCALES TO LEVEL OF ANUS: Similar to above count, but extended back to include the scale just above the anal opening.

SCALES ABOVE LATERAL LINE: This count is taken just anterior to the base of the dorsal and made in zig-zag fashion down to, but not including, the lateral-line scale. The median dorsal scale just anterior to the dorsal is included. (In most specimens, this must be a count of scale-pockets, rather than of scales. I have found temporary staining with methylene blue makes this count considerably easier.)

SCALES ACROSS BELLY: The number of longitudinal scale rows, counted in zig-zag fashion, from (but not including) one lateral line to the other; taken just behind the pelvic fins.

BRANCHIOSTEGAL RAYS: This count is made (usually) by dissection, occasionally by soaking the specimen in glycerine to make the branchiostegal membrane sufficiently transparent to reveal the anteriormost rays; a number of rays are concealed beneath the preopercular, and these rays are included in the count; the interopercular and subopercular are not included in the count, and some dissection may be necessary (usually merely peeling away some of the loose lining of the branchial chamber) to distinguish between branchiostegals, interopercular, and subopercular.

TOTAL GILL RAKERS ON ANTERIOR FACE OF 1ST BRANCHIAL ARCH: This count includes rudimentary rakers bordering the 1st gill cleft, as well as the prominent rakers. At the ventral extremity of the gill cleft the row of rudimentary rakers may become continuous with small patches of teeth on the floor of the pharynx; only those rakers actually on the gill-cleft margin are included.

GILL RAKERS ON ANTERIOR BORDER OF LAST CLEFT: Only those rakers actually on the border of last gill cleft are included. The last gill cleft is more easily accessible than the 1st, and this count is nearly as useful as the count of rakers on the 1st arch, and is an easier count to make.

PYLORIC CAECA: Only distinct sacculations are counted. (The anteriormost part of the duodenum may form a loose fold at its junction with the pyloric arm of the stomach, and care must be taken to avoid counting this fold as a caecum.) A midline cut, from the level of the anterior end of the pelvic bone to the base of the isthmus allows access to the pyloric caeca with a minimum of disturbance of the other viscera. This cut also gives access to the stomach, for examination of its contents, and to the anterior gonads, for determination of sex. Cuts made on one side to give access to these viscera generally have to be so long that the specimen is considerably damaged.

Classification. At first glance, all halosaurs look much alike, perhaps because the peculiarities in which they agree in differing from other fishes divert attention from the differences between halosaur species. When these latter differences are considered, however, the halosaurs fall into two groups, here considered subfamilies. One group, containing the living genus *Halosaurus* and the Upper Cretaceous genera *Echidnocephalus* and *Enchelurus*, has a narrow interorbital region constructed as in Notacanthoidei, with the levator pterygoideus lying entirely behind the eye and with the membranes defining the cranial cavity fused on the midline between the eyes to form a median interorbital septum. As in Notacanthoidei, the maxillary spine is long or very long and the ossified part of the blade of the maxilla is extended well behind the root of the spine; and again as in Notacanthoidei, the tip of the dermal ethmoid has a median dorsal crest; the adnasal canal is well developed; and the lateral-line scales are in approximately one-to-one ratio to the vertebrae, ribs, and myotomes in the abdominal region. So far as is known, the notochord of the species of this group is greatly constricted by the vertebral centra, as in most fishes, including notacanths.

The other group of halosaurs is considerably modified, assuming that the most primitive halosaur would be the (as yet hypothetical, and presumably Cretaceous) common ancestor of halosaurs and notacanths. The interorbital region has been broadened, permitting the origins of the levator pterygoideus muscles to extend forward between the eyes and become even larger than in *Halosaurus* and the notacanths. The membranes defining the cranial cavity between the orbits remain totally separate, so that the cranial cavity completely separates the orbital cavities (the group thus differs from *Halosaurus* in much the way that the Bathysauridae differs from the Synodontidae). The maxillary spine is short, and posterior to its root the maxillary blade is represented only by a pad of unossified connective tissue. The median crest on the dermal ethmoid is absent, and the adnasal canal is reduced and without a pore. The lateral-line scales are much enlarged and reduced in number, so that there is only one lateral-line scale for every two or three vertebrae, ribs, and myotomes in the abdominal region. The ossification of the vertebral centrum is reduced to a cylinder of bone around the unconstricted notochord.

Within this second group, the large-mouthed and very broad-headed species *macrochir* appears generically separable from the others, and two genera are recognized here: *Halosauropsis* Collett, July 1, 1896, for *macrochir*; and *Aldrovandia* Goode and Bean, August, 1896. (For discussions of the true date of publication of Goode and Bean's *Oceanic Ichthyology*, see *12* and *18*: 296). These two genera are here placed in a subfamily, the Halosauropsinae.

The characters of the subfamilies and genera are given in the following key.

Key to Subfamilies and Genera of Halosauridae

1 a. Blade of maxillary bone ossified posterior to root of maxillary spine; length of lower jaw much less than distance from jaw articulation to posterior edge of preoperculum; one lateral-line placque for every transverse scale row on body and tail; dorsal surface of head scaled at least as far forward of level of nostrils; adnasal sensory canal with a pore beneath the nostrils; dermal ethmoid bone with an ossified median keel; spleen visible ventrally, to the left of the caecal extension of fundus of stomach; no distinct 5th epibranchial cartilage; origin of levator pterygoideus on pterosphenoid and frontal just dorsal to pterosphenoid, behind eye; paired membranes around olfactory nerves (planum supraseptale) fused on midline to form a median interorbital septum membrane ventral to olfactory nerves. Subfamily Halosaurinae.

  2 a. Dorsal fin opposite anterior part of anal fin.
    Genus *Enchelurus* v.d. Marck 1863.
    Upper Cretaceous.

  2 b. Dorsal fin entirely anterior to the anal fin.

    3 a. Six pelvic rays. Genus *Echidnocephalus* v.d. Marck 1858.
    Upper Cretaceous.

    3 b. Eight to ten pelvic rays. Genus *Halosaurus* Johnson 1863, p. 51.

1 b. Blade of maxilla not ossified behind base of maxillary spine so that the base of the spine is smoothly continuous with the concave posterior margin of the bone; length of lower jaw subequal to distance from jaw articulation to posterior edge of preoperculum; one lateral-line placque for every two or three transverse scale rows on body and tail; vertex without scales anterior to supratemporal commissure; adnasal canal without a pore; dermal ethmoid bone without median keel; spleen dorsal to stomach, above pyloric arm of latter, not visible from below; a spheroidal 5th epibranchial cartilage separate from 4th epibranchial and from 5th ceratobranchial; origins of levator pterygoideus muscles extended forward on

ventral surface of frontals between eyes; no median orbital septum membrane, the paired planum supraseptale membranes extending from frontal to parasphenoid.

Subfamily Halosauropsinae.

3a. First dorsal ray segmented and as long as the 2nd ray; opercular bone-bearing scales; pyloric caeca long and unpigmented, clustered into two longitudinal series (or a deeply zig-zag single series) at their bases, their tips irregularly disposed around stomach; sheath of lateral line pigmented black in adult (unpigmented in young); entopterygoid with a sparse shagreen of rudimentary but calcified teeth; upper pharyngeal tooth patch formed by three appressed dentigerous placques; outer (opercular) surface of 1st epibranchial with ossified, denticulated placques; frontal of adult expanded over orbit as a projecting wing, the brain case broadest across the frontals; anterior margin of pterosphenoid crimped in to restrict the orbitocranial aperture; dorsalmost branchiostegal ray broadened, similar to subopercular.

Genus *Halosauropsis* Collett 1896, p. 74.

3b. First dorsal ray reduced to a short, unarticulated spine, much shorter than 2nd dorsal ray; opercular bone without scales (but scales present on outer surface of levator operculi muscle, just dorsal to opercular bone); pyloric caeca blackish, like intestine, arranged in a single longitudinal series, relatively short and club-shaped, their tips straight; sheath of lateral line never pigmented; no entopterygoid teeth (but uncalcified papillae may be present); upper pharyngeal tooth-patch formed by two appressed dentigerous placques; no denticulate placques on outer (opercular) surface of 1st epibranchial; frontal not extended as wing over orbit, the brain case broadest at sphenotics or at occiput; anterior margin of pterosphenoid not crimped in; dorsalmost branchiostegal ray similar to adjacent branchiostegal, conspicuously narrower than subopercular.

Genus *Aldrovandia* Goode and Bean "1895" [= 1896], p. 87.

Genus *Halosaurus* Johnson 1863

Halosaurus Johnson, Proc. zool. Soc. London, 1863: 406. Type by monotypy, *Halosaurus owenii* Johnson = *H. oweni* Johnson. Johnson, Ann. Mag. nat. Hist., (3) 14, 1864: 74 (duplicate publication of above).

Generic Synonyms:

Halosaurichthys Alcock, Ann. Mag. nat. Hist., (6) *4*, 1889: 454. Type by monotypy, *Halosaurichthys carinicauda* Alcock.

Laytonia David, Geol. Soc. Amer. Spec. Pap. No. 43, 1943: 13–17. Type by author's designation, *Laytonia californica* David, Miocene, Sepulveda Canyon, California.

Generic Characters. Scales on dorsal surface of head, the scaled area extending forward at least to the level of the nostrils; opercular bone scaled; each transverse scale row on body and anterior part of tail containing a lateral-line scale, the lateral-line scales only slightly enlarged and approximately in a one-to-one ratio with the vertebrae, ribs, and myotomes; frontal bones conspicuously narrowed between orbits, so that the orbits face outward and upward; skull broadest at sphenotics or occiput; tip of dermal ethmoid with an ossified median dorsal crest; pterosphenoids not crimped in to restrict orbitocranial aperture; eyes separated by a median and unpaired interorbital septum membrane ventral to the paired planum supraseptate membranes that separate olfactory nerves from orbital cavity; origin of levator pterygoideus confined to pterosphenoid, sphenotic, and the frontal immediately dorsal to the pterosphenoid, the muscle lying entirely behind the eye; maxillary spine long to very long, the ossified blade of the maxilla extended well posterior to the root of the spine; superior pharyngeal toothpatch formed of two appressed dentigerous placques; no dentigerous placques on external surface of 1st epibranchial; adnasal canal with a pore beneath the nostrils; supratemporal commissure with a median pore overlying supraoccipital; 1st dorsal ray at least half as long as 2nd, segmented; 1st anal ray usually segmented and more than half as long as 2nd; dorsal fin entirely anterior to anal; pelvic fin with a fulcral spine and eight to ten rays; pyloric caeca pigmented, at least basally, and arranged in a single longitudinal row; last (dorsalmost) branchiostegal no broader than other branchiostegal rays.

Synonymy. The genus *Halosaurichthys* was proposed by Alcock (*1*) for *H. carinicauda*, based on a single specimen taken from the Andaman Sea in 490 fms. The supposed generic distinction was based on the extensive membranous connection between the pelvic fins and on the presence of an "adipose fin", represented by a black fold of skin along the midline of the back and tail. However, nearly complete joining of the pelvic fins by membrane occurs as a variation in *Halosaurus guentheri*, and a black fold along the dorsal midline of tail is quite frequent in *Halosaurus*, particularly in smaller and presumably younger specimens, and can now be interpreted as a persistence of the dorsal fin fold of the leptocephalus larva. Alcock's figure (*7*) shows the fold to be torn, with a tatter lying free, vaguely suggestive of a salmonoid adipose fin, and this may have misled him. At any rate, his later account (*5*) makes no mention of a free adipose fin and the dorsal fold is stated to contain scales. In this later account, Alcock appears to have retracted his generic name, for he describes the fish as *Halosaurus carinicauda* and he notes that this species and his *Halosaurus parvipennis* (*3*) from the Arabian Sea are "very closely related". Norman (*34*) has suggested that *carinicauda* and *parvipennis* are synonymous, and there is nothing in Alcock's figure and descriptions to contradict this suggestion, particularly if a Bali Sea specimen recorded by Weber (*43*: 92, 94–95, 616; figured and described in *44*: 2–3) as *Halosaurus carinicauda* is correctly identified. *Halosaurus carinicauda* (including *parvipennis*) is very closely related to *Halosaurus guentheri*, perhaps even conspecific with the latter, and Alcock's reasons for erecting the genus *Halosaurichthys* appear invalid. However, Alcock's name is available for a recognizible subgenus of *Halosaurus* (see below).

The genus *Laytonia* David (*14*), proposed for a Miocene fossil from what is now part of Los Angeles, California, also appears to be a synonym of *Halosaurus*. The supposed difference between "*Laytonia*" and living Halosauridae in the preopercular region is non-existent and was based on Günther's (*24*) misinterpretation of the preopercular