PROCEEDINGS
OF THE
California Academy of Sciences

FOURTH SERIES

VOLUME XXXVIII

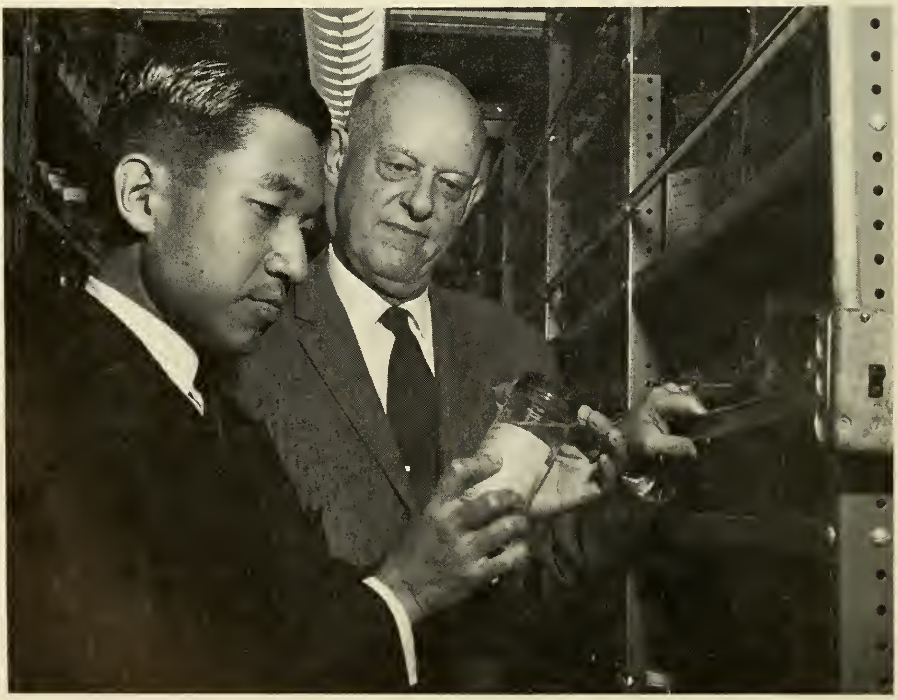
Festschrift for George Sprague Myers

In Honor of His Sixty-fifth Birthday

SAN FRANCISCO
PUBLISHED BY THE ACADEMY
1970

Washington Biologist's Field Club;
Plummers Island, Md., 1933
Photo by A. K. Fisher

Retirement Photo 1970



With HIH Crown Prince Akihito in the Stanford Collection 1967
Palo Alto Times Photo

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CONTENTS

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INTRODUCTION

The faculty appointment of George Sprague Myers as a Stanford associate professor in 1936 and full professor in 1938 marked the resurgence of what had informally been recognized as the Jordan school of ichthyology. In the thirty-four years since that time more than 104 graduate and special students as well as a large number of undergraduates, have come under Professor Myers' guidance. Although the majority of these students were involved in the study of fishes, a very respectable number specialized in amphibians and reptiles. During this same period the *Stanford Ichthyological Bulletin* came into prominence as did a series of important herpetological reports published as *Occasional Papers of the Natural History Museum of Stanford University.*

On behalf of the many students and colleagues who have carried out their studies at the Stanford Natural History Museum, the authors participating in this volume respectfully dedicate this Festschrift to George Sprague Myers in appreciation of his helpful leadership in the field of systematics of the lower vertebrates.

EARL S. HERALD
August 1970

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ON THE NATURAL HISTORY OF GEORGE SPRAGUE MYERS[1]

By

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At a very young age, George Sprague Myers manifested those qualities which were to remain his mark of distinction—an extraordinary sensitivity to the beauty of order in Nature, a boundless capacity to learn about what interested him, and a zest for collecting, arranging, and reasoning how things must fit together. Given such an endowment, the place where he was born and spent his boyhood—Jersey City, New Jersey—and the epoch of his birth—early part of the twentieth century—were peculiarly right for guiding him towards and into his life work. For at that time many of the nineteenth century systematic zoologists were still flourishing (David Starr Jordan, for example) and there were plenty of roads from Jersey City leading to their doors and also to back country that was still unspoiled and beckoning.

Jersey City in 1905, the year of Myers' birth, was already well established as part of what was to grow into the great Atlantic megalopolis. Like its neighboring satellite communities, it did not share any part of New York's splendor,

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[1] I am deeply grateful to Mrs. Mary S. McKenzie, for providing information on the family background and early history of her nephew; and also to Dr. Alan E. Leviton through whose good offices I have been permitted to consult and use several autobiographical fragments which Myers wrote at various times and deposited along with his extensive file of biographical information on zoologists at the California Academy of Sciences.

yet was close enough to attract the most unbeautiful features of industrial development.

The house where Myers was born and spent much of his boyhood was a three-story brick structure at 283 Grove Street, directly opposite the front of the city hall. Even in 1905, this was part of a dwindling genteel neighborhood in the process of being eaten away by slums that were surrounding it.

The biota of the Grove Street house was typical of relic residential sections in northeastern crowded cities. Near the woodshed in the back yard grew a large Rose-of-Sharon bush, a lilac which annually put out a few flowers, some South American spider plants (*Cleome*). There were a few *Ailanthus* trees in nearby back yards, and an ancient linden that grew out of a hole in the flagstone sidewalk near the curb. Of insects that aroused some interest in young Myers, albeit a short-lived one, were bees of various sorts. "What could you do with a bee?" he asked. The only birds were English sparrows. Mammals consisted of cats, dogs, rats, and bats which issued at dusk from a nearby church. One of the cats was a pet, the first of a series which Myers has had almost continuously ever since.

Myers' introduction to fish life was a minnow, probably *Chrosomus neogaeus*, living in a spring on a farm to which he was taken during a summer trip to Maine at the age of seven. Next he met some entrancing goldfish in a pet shop where his mother and Aunt Mary often took him during their visits to New York. He actually got to possess one or two goldfish in a bowl at various times. These experiences were no more remarkable than any other young city boy might have during his natural history phase. To young Myers, however, this was no phase, but rather a prologue to his great lifelong interest. This really began at age 12, when he first attended the Jersey City Aquarium Society's annual exhibition in the public library. Enthralled by the colorful fresh-water fishes from all over the world, he promptly joined the Society and began to accumulate aquariums in which he kept not only exotic fishes but also native ones (*Umbra*, *Fundulus*, *Enneacanthus*, etc.). These he caught on trips made by train or trolley car to various places in northern New Jersey. At the same time he collected and kept amphibians and reptiles, these being as interesting to him as fishes. When he was about 15 years old, attending Lincoln High School in Jersey City, he sought advice of his biology teacher about a trip he was planning to the Pine Barrens of Lakehurst, New Jersey, to collect the beautiful rare tree frog *Hyla andersonii*. The teacher, rather out of his depth, suggested that Myers discuss his problem with Dr. G. K. Noble at the American Museum of Natural History in New York. By following that advice, Myers became introduced to the world of research zoologists. Noble, impressed, of course, introduced him to A. I. Ortenburger; and when the two had become well enough acquainted with this interesting young fellow, they took him on the last of Noble's Lakehurst trips to study the life history of *Hyla andersonii.* Through Noble, Myers came to know Karl P. Schmidt, and, in the Museum's fish department, John Treadwell Nichols, Arthur W. Henn, and Eugene W. Gudger. It was not long before he was spending so much time on his cold-blooded vertebrates that his school work slipped badly, for he took full advantage of the proximity of New York to meet most of the old guard zoologists at the Museum, the Zoo, and the Aquarium—Henry Fairfield Osborn, Bashford Dean, F. A. Lucas, Walter Granger, W. D. Matthew, Frank M. Chapman, Carl Akeley, Robert Cushman Murphy, Roy Chapman Andrews, C. H. Townsend, William Beebe, John Tee-Van, and Charles M. Breder. And when a young fellow from the University of Virginia was selected by Noble to go with Andrews to collect reptiles in China, Noble and Myers went out to Plainfield, New Jersey with him to teach him how to collect salamanders. His name was Clifford H. Pope.

One day in 1924 while at the Museum, Myers was introduced to Dean Carl H. Eigenmann of Indiana University, the principal worker on the systematics of the fresh-water fishes of South America. Myers had then published a few short papers on fishes and had become especially interested in those of tropical America. The result was an invitation by Eigenmann to come to Indiana as a student and have part of the cost defrayed by part-time work in caring for the Indiana fish collection.

Myers had not done well in high school, and lacked several credits for graduation. Moreover, with the examples before him of several then well-known zoologists who had had no university preparation, he was uncertain even whether to go to college. However, he says that Noble gave him a thorough tongue-lashing about his refusal to get the necessary schooling, and this, coupled with Eigenmann's offer, decided him to go. In lieu of his missing high school credits, Dean Eigenmann arranged to have him granted credit for the research he had already accomplished. He has always felt a great deal of gratitude to Noble and Eigenmann, without whose help his professional career might have been aborted.

At Indiana, he neglected his academic studies to accomplish some field work and to complete a synopsis of the amphibians and reptiles of Indiana. At the same time he got a superb introduction to South American fishes, and also to curatorial methods for preserved research collections. Aside from Eigenmann, the man on the Indiana faculty who had the most influence on Myers (though Myers took no formal courses from him) was the entomologist, Professor Alfred C. Kinsey (later the student of human sexuality), whose forward-looking views of evolution and systematics were then finding expression in studies of cynipid wasps. From Kinsey, Myers began to gain a very broad view of systematics as a synthesis of the comparative aspects of all other biological disciplines, a view that finally found expression in a review paper in 1930.

After Myers had been at Indiana one year, Eigenmann fell ill and was taken first to Florida and then to the San Diego region of California for his health. Since he obviously would not be able to return to the University, there seemed little reason for Myers to remain. However, he unpacked the large Ternetz South American collections as they arrived, and, with Eigenmann's permission, described some of the novelties.

Stanford University, founded in 1891, had become a center of research on fishes and their habits through the influence of the university's first president, David Starr Jordan, and the first chairman of its zoology department, Charles H. Gilbert. In 1926, both men had been long retired, but Jordan was still active and he had noticed the papers published by Myers. When he heard of Eigenmann's illness, Jordan wrote to Myers asking whether he would like to transfer to Stanford with the same sort of part-time assistantship he had had at Indiana. Jumping at the opportunity, Myers arrived in California in September, 1926.

It was shortly after his arrival at Stanford that I first met him there. As a biologist at the California State Fisheries Laboratory at Terminal Island, I had just begun a study of the California barracuda, and took advantage of an opportunity to spend a few days at the Natural History Museum to search its library and to study the sphyraenid material in the fish collection. The Museum at that time was a center of quiet excitement such as I will never forget, for many of the biology faculty members focused their interests there, and the principal interest was the study of fishes. There is a vivid picture in my mind's eye of a pleasant, fine-looking, young man, an undergraduate, working as an assistant in the Museum. "May I help you?" he asked. "Perhaps," I replied, cataloging him as a library assistant. When I told him what I wanted, he poured a steady stream of information *out of his head*: "Of course, you must already have the essential papers about *Sphyraena argentea* and *S. ensis*. You may have missed *Sphyraena idiastes*. We have the original 1903 description by Heller and Snodgrass." And so on through the whole family Sphyraenidae around the world. No, he was not working on sphyraenids himself. Never had. It seemed to me as I talked to this enthusiastic modest fellow that he knew everything about everything. He was already a learned person when most people are scratching about, trying to make up their minds what they want to learn about.

The area surrounding the Stanford lands was then open country, and the University community (affectionately known as "The Farm" by faculty and student alike) moved at a relatively leisurely pace. Under Jordan's influence it had been, and still was, a great center for studying systematic zoology, especially fishes. Jordan was still working on fossil fishes. John Otterbein Snyder was chairman of the zoology department, with Edwin C. Starks as morphologist, Harold Heath as invertebrate zoologist, G. C. Price as embryologist, and Isabel McCracken, R. W. Doane, and G. F. Ferris as entomologists. Aside from courses in other departments, Myers came to know Snyder, Starks, Heath, and Ferris best, as well as H. G. Schenk and S. W. Muller in the geology department, in which he eventually took his doctorate minor.

The Dudley Herbarium, the Entomological Collections, and the Zoological Collections were then housed—temporarily, it was said—in the south end of the Stanford Museum where they remained as the "Natural History Museum," and later the "Division of Systematic Biology," for the entire period of Myers' active association with the University. Professor LeRoy Abrams was in charge of the Herbarium, Ferris of the insects, and Snyder of the Zoological Collections.

Although Snyder was his special mentor and friend, Myers visited Jordan, at Jordan's warm invitation, at least once a week. Snyder, like Gilbert before him, had almost deserted systematics to work on the migrations of salmon and steelhead trout. In 1928, Willis H. Rich was appointed to the department, to teach ecology and fishery biology.

A biweekly seminar in fishery biology in 1928–29, attended by Snyder, Rich, Frank Weymouth, Starks, and about a dozen serious students including Myers, most of whom were to become leaders in the study of fishes, was a whirlwind of lively discussion and argument among and between students and professors, such as I have rarely experienced since.

Because the Stanford group then most interested in the theory of systematics was led by Schenk in geology, Myers gravitated to that quarter. In connection with one of Schenk's seminars, Myers published a review of a recent botanical revision in Schenk's *Micropaleontology Bulletin*, in which the ideas he had developed after contact with Kinsey at Indiana and Schenk at Stanford were synthesized into a view of systematic biology that was unusually broad for its day. When it is recalled that Myers was then an undergraduate student, without much knowledge of what was then being done on theoretical systematics by several isolated men or groups in America and Europe, his statement is remarkable.

Myers' university work went slowly, not only because of his part-time employment but also because he was able only slowly to force himself to neglect extracurricular work in ichthyology and herpetology enough to get good marks. One objection to granting him a bachelor's degree was that he had not taken enough required courses in English. Snyder later confided to me (with much amusement), that he had demolished this hurdle simply by waving in the faces of the objecting English Department's faculty members a handful of the publications Myers had produced since he entered college, saying, "Look, see how much *he* has written!" He had published a good deal by the time he was granted his A.B. degree in June, 1930, seven years after he entered Indiana as a freshman. After that, things went more rapidly. He obtained an A.M. in 1931, and his Ph.D. in June, 1933.

Of his Stanford student years, Myers has said that he learned more morphological zoology from Harold Heath and Tage Skogsberg at the University's Hopkins Marine Station (where he spent the summer of 1929), than from all others. Nevertheless, Snyder, Starks, and Rich ranked high in his training years. For four years he saw and talked with Jordan almost weekly, gaining a great wealth of information about ichthyological workers and history.

In 1928, Dr. Albert W. Herre, a former pupil of Jordan, was appointed to a non-faculty position as Curator of the Zoological Museum at Stanford with an arrangement by which he would be retired only upon the President's pleasure. Myers says that he owes much broadening and maturing to Herre's influence, not only while he was a student, but also after he returned to Stanford in 1936.

In 1933, Myers was appointed Assistant Curator in charge of the Division of Fishes at the U.S. National Museum, with a first assignment to pack and ship many National Museum fishes that had been at Stanford in the hands of the late Charles H. Gilbert. He arrived in Washington in March, 1933.

At the National Museum, Myers took charge of the most important ichthyological resarch collection in America but one which had suffered from nearly 40 years of impoverishment and neglect. Moreover, the great financial depression of the 1930's had worsened the situation so much that for the first two years of Myers' tenure, the Division lacked even the services of a typist. Besides Myers, the staff consisted only of one elderly but enthusiastic scientific aid, Earl D. Reid[2], and a laborer who cared for the alcoholic collections. For the next three years, Myers and Reid spent most of their time in sorting, bottling, and registering an enormous backlog of specimens and putting the Division's offices, files, and records into working condition. During most of this period they trained and supervised squads of up to a dozen temporary workers at a time, these having been supplied free to government bureaus by successive federal agencies set up to relieve unemployment.

Although there was precious little time for research during these three years, Myers and Reid initiated a survey of the fresh-water fishes of Virginia. The only help from the impoverished Museum was for bottles and alcohol, but using Reid's old automobile and paying all other expenses themselves, they made many collections from the Dismal Swamp to the mountains of western Virginia.

Myers says that in Washington he had the best and most cooperative superior administrators that a curator could have. His immediate superior was the late Leonhard Stejneger, Head Curator of Zoology and Curator of the Division of Reptiles and Amphibians, whose kindliness and enormous memory he has always remembered with pleasure. The other was Alexander Wetmore, then Assistant

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[2] Myers always expressed the greatest admiration for Reid, who was invalided out of the U.S. Marine Corps after being wounded in the eyes while in Nicaragua. Reid became a doorman in the Museum and worked his way to the Civil Service subprofessional grade of Aid by taking night courses in zoology at George Washington University.

Secretary of the Smithsonian and Director of the National Museum, whose administrative ability and thoughtfulness for his staff were boundless.

In 1936, Myers was invited back to Stanford, and after considerable thought, accepted a position as Associate Professor of Biology and Head Curator of Zoological Collections, with the provisions that he be advanced to Professor by 1938, that half his time be spent on curatorial duties and half on teaching, and that Dr. Herre's employment as Curator of Zoology not be terminated as the department head had planned. With Herre's retention assured, Myers assumed his new position in September, 1936.

George Myers has told me many times that his most important contributions to ichthyology and herpetology have been the help and guidance he has been able to give to the long line of graduate students who worked with him at Stanford. When he began teaching in 1936, no formal course dealing with more than the barest rudiments of taxonomic ichthyology appears to have been given anywhere. In those days, prospective taxonomists were supposed to pick up knowledge of their field without any formal guidance. The Stanford fish course initiated by Charles H. Gilbert and continued by John O. Snyder had consisted solely of identifying specimens with the aid of Jordan and Evermann's "Fishes of North and Middle America." Myers has told me that his own background in ichthyology and vertebrate evolution was very defective as a consequence, so that between 1936 and 1938 he found it necessary to prepare himself by doing a great deal of reading and studying. The books of Goodrich and Romer and the papers of C. Tate Regan proved to be of the greatest help. In 1938, for the benefit of a small group of students, including W. A. Gosline and E. S. Herald, he attempted a general summary of fish classification and evolution, with emphasis on the literature and history and on major groups down to the family level. This first attempt developed into a more formal course, called "Advanced Systematic Ichthyology," which was usually given every other year, alternating with a shorter, somewhat less advanced course in herpetology. This course in ichthyology formed the genesis of other more or less similar courses, such as that given by W. A. Gosline first at the University of Michigan and later at the University of Hawaii. Myers also gave annually a course at first called "Vertebrate Paleontology" and, later, "Evolution of the Vertebrates," and a short course on zoogeography. Myers' most popular course, planned and given by himself and his botanical colleague, Professor Ira L. Wiggins, was a general survey of plant and animal ecology, including ecology of man. It was given for two or three years in the late 1940's primarily for non-biologists. In this course, Myers was one of the first to emphasize the rapidly increasing danger to the human race caused by the unrestricted growth of human population. Unfortunately, other work forced Wiggins to withdraw from the course, and, as Myers felt himself incompetent to handle the botanical side, the course was regretfully dropped.

Myers has maintained that graduate teaching is greatly helped by the presence of a "critical mass" of at least four enthusiastic students working under one professor on different dissertations in related fields. The presence of such a group was barely attained in his laboratory when World War II intervened. Students vanished, and he was sent to Brazil for two and one-half years. It was not reattained until the late 1940's; but from that time until well into the 1960's a "critical mass" was continuously present, rising at one point to as many as 12 or 13, usually two or three of them herpetologists and the rest ichthyologists. As he says: "Those were the most exciting and rewarding years that I have experienced. As a matter of principle, no graduate student was assigned a doctorate problem, or encouraged to choose one closely related to any of my own research. They were forced to select their own, my only requirements being that the problem be reasonably interesting and difficult but not impossibly time-consuming, and that it be concerned with areas within which I felt myself fairly competent to judge quality of performance. The atmosphere was never dull. Everybody helped and taught everybody else, the professor learning as much from the students as they did from him. Chores in the old Natural History Museum, such as registering and care of material, helping with the editing of the *Stanford Ichthyological Bulletin,* and the like, were often done almost as much by those who were not paid to do the work as those who were. My own contribution was largely that of arbiter, critic, walking bibliographer, ruthless editor of often poorly expressed, first attempts to write up scientific results, father-confessor, cheerleader, and especially as the provider and keeper of a laboratory atmosphere conducive to hard work, cooperation, enthusiasm, and high attainment. There was little of the formality that often separates professor from student. Evening seminars or meetings often ended in a nearby Bierstube, and I was usually invited to student parties. Former students have often remarked on the uniqueness of human relations in the Museum and recall them with nostalgia —as do I. Yet, I must have commanded a modicum of respect for I have noted with some amusement that none of my former graduate students ever tried to address me by my first name (a common enough thing in the U.S.A.) until 10 or 15 years after obtaining their doctorates; and several have never been able to bring themselves to do so. But when the number of graduate students rose to eight, ten, or a higher number, I got comparatively little research of my own done, for I was available to all of them almost every day—an arrangement at which some other groups of graduate students, both at Stanford and elsewhere, marvelled. Yet near the height of my graduate student load, economic necessity forced me to write extensively for —and manage—a popular aquarium magazine (*The Aquarium Journal*). This very difficult regime went on for two years (1952–54) until my Stanford salary rose enough to make it possible to give up most such writing."

The Stanford fish collection was originally small, consisting largely of duplicates from the field work of Jordan and his pupils. Through the years it grew slowly through an unexpressed policy of growth in diversity without amassing long series of individual species, a policy which Myers enforced in more recent times. It gradually attained a diversity among American collections second only to the National Museum, although in numbers of specimens (between 750,000 and 1,000,000) smaller than several other large research collections. It has been especially useful for morphological work in systematics such as has been emphasized in recent years.

The herpetological collections were small when Myers took charge in 1936, consisting of fewer than 2,000 amphibians and 10,000 reptiles, mostly collected during early work in the days when John Van Denburgh was a student. Myers built these collections up judiciously until now they total about 60,000 specimens, half amphibians and half reptiles—numerous enough and diverse enough for many systematic purposes.

For curatorial work and the management of the Zoological Collections primarily as a laboratory for graduate students, Myers was greatly aided by Margaret H. Storey. She had obtained her A.M. degree with Willis Rich while Myers was at the National Museum, had stayed on as a volunteer assistant later to be appointed Assistant Curator of Zoological Collections. She supervised the paper-work and curating, helped edit *Stanford Ichthyological Bulletin* and was a tower of strength and help to all those who worked in the Zoological Museum until her untimely death in 1960.

Myers and Storey together worked out systematic methods, some of them new, for sorting, registering, bottling, labelling, arranging, installing, and finding bottled museum specimens. These methods, described chiefly in three of the Museum's mimeographed circulars, made it possible for much of the work to be done by untrained student helpers, and to handle a large research-collection operation (up to a million specimens) with less than half the staff and funds usually available for such purposes.

For all of Myers' years on the faculty, the Zoological Collections had no more than four employees besides himself—A. W. Herre, until World War II, Margaret Storey and later Warren Freihofer, as aid or associate curator, one half-time student assistant, and, after World War II, one typist-secretary who also served entomology. This staff handled large and growing research collections of fishes, amphibians, and reptiles as well as sizable collections of mammals, birds, and aquatic invertebrates. They were also responsible for the time-consuming processing of extensive loans to researchers elsewhere, running from about 500 to as many as 5,000 specimens annually. In one thing, Myers was adamant. Collections of animal groups in which he had no direct interest were also kept in good condition and order. Such curatorial conscience is rare. Moreover, collections which had strayed away from the Museum to other parts of the University and elsewhere were retrieved and set in order. Types were rigidly labelled and segregated with blue (holotypes) or red labels. Species presumed to be extinct received green labels.

The library on Systematic Ichthyology at the Museum was rich in the older literature and in reprints, all from Jordan's personal library. It was kept up by exchanges for *Stanford Ichthyological Bulletin* and by judicious buying with the small funds available. Concurrently, Myers personally purchased many ichthyological and herpetological books that were not present in the Museum, and his library books and reprints admirably supplemented the Museum's holdings. Today, since Professor Carl L. Hubbs' library has gone to Scripps Institution, Myers probably has the most extensive private fish library in the world. It is especially rich in reprints but lacks such expensive items as the great works of Bloch, Bleeker, and Agassiz.

Myers started *Stanford Ichthyological Bulletin* in 1938. It was printed cheaply by offset (the text being typed by the Museum staff), since funds for this journal were always miniscule. They began at $133.00 annually and never rose over $750.00. All sorts of schemes to get outside funds were tried, usually with only moderate success. Of the eight volumes that eventually appeared, less than half were or could be paid for from regular funds.

Myers and Miss Storey were the principal movers in two local groups. The old "Stanford Zoology Club," which originated in the 1890's and was supported by generations of Stanford students, was revived as the "Natural History Club" and survived until the 1950's. A new, informal group, the "Fishverein," composed of those at Stanford interested in fishes and the many local fishery biologists working for the Federal Fish and Wildlife Service and the California Division of Fish and Game, was formed by Myers and met fairly regularly for many years.

During his early preuniversity years (1920–24), Myers' papers reflect the growing interests and ability of an untrained young man deeply interested in the habits and taxonomy of the lower vertebrates. He published his first articles on aquarium fishes at the age of 15, in 1920. These early attempts give an inkling of the extensive boyhood observations representing dozens of families of live fishes, and also amphibians and reptiles, either in captivity or in the field in New Jersey and North Carolina. As Myers says: "By the time I was 19, I knew in a general and sometimes specific way a great deal about fish behavior that has of late been 'discovered' and formally categorized by the fish behaviorists, in the same way that the field ornithologist becomes familiar with bird behavior."

By the end of 1923, Myers had published his first really scientific papers, one on a new poeciliid from Hispaniola with J. T. Nichols and others on the nomenclature of anabantids. By the end of 1924, he had published nine taxonomic papers on fishes, and one herpetological paper. It was in 1924 that he made his first longer field trip, to Wilmington, North Carolina, where he made many observations and discovered what is now known as the common dusky shiner (*Notropis cummingsi* Myers) of the southeastern coastal plain, the description of which he published in 1925.

Although the beginning of university work in 1924 curtailed his output of papers, he continued publishing on a variety of ichthyological and herpetological subjects up to the time he finished his schooling at Stanford and went to the Smithsonian in 1933. To refer to only a few of the papers which he published during his student years at Indiana and Stanford (1924–33), there is a synopsis of Indiana amphibians and reptiles (1926), four papers on amphibians (1930–31), descriptions of many South American fishes collected by Ternetz (1927), a revision of the genera of neotropical cyprinodontids (1927), three or four important papers on Chinese fishes, and a prophetic paper on the phallostethids which foreshadowed some of the important features of Rosen's radical reclassification of the atheriniform fishes in 1964. In addition, Myers found time in 1929 to write a sizable addendum to the final volume of Eigenmann's "The American Characidae."

Myers was faced with such exceptionally time-consuming curatorial duties at the Smithsonian that his research during those years (1933–36) suffered. However, he reviewed the genera of triacanthids in 1934, published on the cyprinodonts of Hispaniola as well as the opistognathids (and owstoniids) in 1935, and revised the genera of Polynemidae in 1936. In that same year, in a report on fishes from Lake Tanganyika, he briefly pointed out for the first time some of the strange features of lake-fish evolution.

After beginning his teaching and curatorial work at Stanford in 1936, Myers' first paper was one that he had read before a meeting in New York in 1934 and which he based on observations made in the 1920's. In this short paper, he arrived independently at the same conclusions as had C. M. Breder, Jr. in regard to the evolution of oral brooding in cichlid fishes.

The most widely known and influential of Myers' papers, prepared for the 1937 Smithsonian Report (1938) was his "Fresh-water Fishes and West Indian Zoogeography." He had been highly dissatisfied with most writings on historical zoogeography, particularly the prevalence of the ideas of Matthew and others based largely on the tetrapod evidence, and especially with the use made of the evidence of fresh-water fishes. In this paper, dealing specifically with the West Indies but ranging over the fishes of all continents, Myers pointed out that what had previously been taken for true fresh-water fishes are really divisible into two physiologically different groups, one with considerable salt tolerance and the other ("primary fresh-water fishes") much more strictly confined to fresh water. The primary fresh-water fishes are much less able to spread across continents and sea gaps than are mammals and even amphibians, and thus their dispersal patterns provide a much more conservative and dependable guide to the past existence of these gaps than do those of tetrapods. Myers' zoogeographical conclusions, although stated only cautiously and tentatively, agreed with those of Matthew in regard to the absence of past continental connections of the West Indies, but disagreed with Matthew in the strong evidence provided by the primary fresh-water fishes for a past southern trans-Atlantic connection. It is notable that 20 years after publication this paper was acknowledged by P. J. Darlington in his great book "Zoogeography," as the prime reference on which he built that part of his book dealing with fishes. Myers' 1938 work combined with his later papers on salt tolerance of fresh-water fishes (1949) and East Indian zoogeography (1951), gave new direction to later studies on the historical zoogeography of continental vertebrates. Myers seemed more than half convinced of the truth of continental drift in 1938, and although he faltered in that conviction in his 1951 paper, he later reaffirmed it in 1966 and 1967, because by then the weight of his evidence favored the primary fresh-water fishes as the most significant vertebrate indicators for establishing past continental connections.

Early in 1938, Myers was able to accompany that year's expedition of the Allan Hancock Foundation's ship *Velero III* to the coasts of Mexico, Cocos Island, the Galápagos, Peru, Ecuador, and Panama. This resulted in collaborative papers with C. B. Wade on eels (1941), atherinids (1942), and other fishes (1946). In addition, a study on the zoogeography of the fishes of the Pacific Ocean appeared in 1941.

Herpetological work had been impossible in the Division of Fishes in Washington; but on Myers' return to Stanford he began a number of smaller studies on amphibians and lizards which culminated in six herpetological papers in 1942. One of these described the now well-known black toad of Deep Springs Valley (*Bufo exsul* Myers), which has perhaps the smallest range of any living amphibian.

Following the entrance of the United States into World War II, Myers was posted to the Museu Nacional in Rio de Janeiro, as part of a governmental plan to maintain good relations with Latin America in troubled times. He arrived in July, 1942, for a one-year period, which eventually lengthened to nearly 2½ years. In Rio he helped with curatorial and library methods, with setting up civil service categories for the museum staff, with exhibits and with museum administration. For the federal fish and game division and the São Paulo fish and game department, he helped by devising better methods of gathering fish-catch statistics. In addition, for a period of over a year, the Museum lent his services to the Rio office of the U.S. Coordinator of Inter-American Affairs. There was little time for research, and the wartime shortage of gasoline made travel by automobile next to impossible. Nevertheless, he managed to take many local trips, principally by tramway on weekends, to the wilder areas in the metropolitan region. These trips were mostly for frogs, in the company of Dr. Bertha Lutz and Joaquim Venancio or Antenor Carvalho. Eventually, there were longer trips with Carvalho or others by train and other conveyance, to the Rio São Francisco at Pirapora, to Santa Teresa in Espirito Santo, and southward along the coast to Rio Grande do Sul. Papers resulting from the Brazilian years were few, most of them appearing in 1944 and 1945.

On Myers' return in 1944, he hoped that the survey of Brazilian marine market fishes that he had helped to originate would result in taxonomic studies of these fishes at Stanford by Brazilian students; but the students did not appear and the project languished after 1950. The sole results have been the amassing of an excellent representation of Brazilian shore fishes in the Museu Nacional, and a smaller duplicate set at Stanford.

A trip to attend the Pacific Science Congress in New Zealand in 1949 resulted in two zoogeographical papers, one on East Indian fishes (1951 and 1954, published twice) and the other on East Indian amphibians (1954) both of which tended to firm up the concept of Wallace's Line. Myers had become editor of an aquarium magazine for two years in the early 1950's. Several of the articles published then have ichthyological interest, chief of them being "Annual Fishes" (1952), which brought together and greatly strengthened by original observations what had consisted of scattered and mostly nonscientific reports of tropical cyprinodontid fishes which exhibit a diapause when no individuals are alive except as zygotes.

At the 1958 International Congress of Zoology in London, Myers presented a paper on the endemic fishes of Lake Lanao having an important bearing on evolution. In this paper, published in 1960, he was able to show that this cyprinid fauna, now diverse enough to be alloted to several genera, almost certainly evolved very rapidly from a single ancestral species, perhaps within 10,000 years. He also pointed out similarities in the evolution of other lake faunas, and was able to establish an evolutionary sequence: 1) an increasing number of very similar species belonging to a single genus, culminating 2) in a "species swarm;" then 3) the differentiation of a few species into new endemic genera, and finally 4) considerable reduction in the total number of species. Thus the number of species of the large genus gradually diminishes while the number of distinctive endemic genera increases. Myers also pointed out the strong possibility that on a grand scale the evolution of Amazonian fishes and of deep-sea fishes might parallel that of lake fish faunas and indeed, the original evolution of the animal phyla.

In the 1960's, Myers returned to zoogeographical studies of fresh-water fishes. His paper on the North American fauna (1963) was published only in an abstract which lacked the section on continental drift; but his 1966 paper on the derivation of the fresh-water fishes of Central America directly opposed Darlington's idea that the ancestors of the South American fish groups originated in Holarctica, and suggested continental drift as an answer. In 1967 appeared his "Zoogeographical Evidence of the Age of the South Atlantic Ocean," a brief exposition of his belief that the cypriniform fishes had originated in a South Atlantic continent which split in the Triassic or Jurassic to form the South Atlantic Ocean. In 1966 was published a collaborative work by Greenwood, Rosen, Weitzman, and Myers, "Phyletic Studies of Teleostean Fishes, with a Provisional Classification of Living Forms," which broke strongly with traditional classifications of the teleosts.

Myers intended his series of apparently not directly related studies on fish zoogeography (1938, 1949, 1951, 1963, 1966, 1967), together with his two 1960 papers on lake fish evolution and the 1966 collaborative teleost study, to form an integrated whole indicating as nearly as can be done at present how and when the ostariophysan (and particularly the cypriniform) fishes evolved and dispersed. In these papers the problem is attacked from several directions on the basis of the living world fauna and the few known fossils, ecological constitution of the fishes, their probable place and time of origin from the salmoniform fishes, their dispersal and evolutionary patterns as seen against the background of paleogeography, all within the strictures imposed by the greater known fossil evidence derived from tetrapods. Considered in this way, the nine papers concerned form an impressive contribution to knowledge of the fresh-water fishes of the world.

One thing that Myers has said of his papers is that not many of them are as important, or represent as much thinking, as do a number of his reviews, mostly published since 1930 in *Copeia.* Many taxonomic and other conclusions first appeared in these reviews. Moreover, the column called by Myers "Phylax Telescopus," which he maintained for a couple of years in *Copeia* during the 1960's, contains some of the best biological criticism that has appeared anywhere. Myers has said to me that if he is remembered for anything, he would like it to be for just a few things—his graduate pupils, his critical comments and reviews, his early espousal of the need for curtailment of human population growth, his pioneer urging of the conservation of non-food and game fishes, and his integrated series of papers on the evolution and dispersal of fresh-water fishes.

Despite the number of publications listed in his bibliography (nearly 600), I doubt that he ever engaged in any research simply to increase the quantity of his publications. He has always avoided humdrum taxonomic questions unless they were of some special significance, for he is completely devoted to seeking and elucidating principles. Thanks in large measure to his scholarly creativeness, as well as to his subtle and boundless patient teaching, systematic ichthyology is alive and well today and the subject of vigorous teaching in many centers of learning where it is appreciated. It is a pity that Stanford has not appreciated the tradition it had inherited through Jordan or the treasure which he started in the Museum collection and libraries, and which Myers built up and organized. Instead, the university authorities have callously determined to give this treasure away and discontinue—*discontinue*—further teaching in this field! This is particularly tragic at a time when the natural history of the earth and its resources is the most important thing we can know.

CHRONOLOGY

1905	Born February 2, Jersey City, New Jersey, son of Harvey Derwood Myers and Lily Vale (Sprague) Myers.
1911–18	Public elementary schools, Jersey City.
1918–24	Public high schools, Jersey City.
1919–20	St. John's Military School, Ossining, New York.
1922–24	Association with American Museum of Natural History, especially G. K. Noble and J. T. Nichols.
1924	Field work during May in vicinity of Wilmington, North Carolina.
1924–26	Indiana University, with Carl H. Eigenmann. Curatorial assistant, fish collection.
1926	Married Martha Ruth Frisinger, Decatur, Indiana, September 25.
1926	Entered Stanford University, October. Beginning of association with D. S. Jordan, C. H. Gilbert, J. O. Snyder, E. C. Starks.
1926–31	Museum assistant, Stanford.
1929	Field work during April–June in western Texas and Arizona with Gregory M. Kranzthor. Rediscovery of *Elaphe bairdii.*
1930	Field work in Death Valley—Amargosa region—with Joseph H. Wales. Discovery of *Cyprinodon diabolis.*
1930	Bachelor of Arts, Stanford, June.
1931	Master of Arts, Stanford, June.
1931–32	Teaching assistant in comparative anatomy, Stanford.
1932–60	Associate editor, *The Aquarium*, Philadelphia, edited and published by William Thornton Innes, also scientific editor, 19 successive editions of Innes' "Exotic Aquarium Fishes."
1933	Appointed Assistant Curator, in charge, Division of Fishes, U.S. National Museum, Smithsonian Institution, Washington, D.C., January 1.
1933	Doctor of Philosophy, Stanford, June.
1934–36	Field work, freshwater fishes of Virginia, with E. D. Reid.
1935	Birth of first child, Thomas Sprague Myers, Washington, D.C., August 28.
1936	Awarded Silver Medal of the "Société National d'Acclimatation," Paris, for work on acclimatization, habits, and taxonomy of exotic aquarium fishes.
1936	Resignation from Smithsonian. Appointed to faculty, Department of Biological Sciences, Stanford University, as Associate Professor and Curator of Zoological Collections, September.
1937	Birth of second child, John William Myers, Palo Alto, California, December 15.
1938	Member, Hancock Pacific Expedition, aboard M. V. *Velero III*, from January–March, visiting coasts of Mexico, Guatemala, Cocos Island, Galápagos Islands, Ecuador, Peru, Chinchas Island, Gorgona Island, Colombia, Panama.

1938	Co-leader, with Rolf L. Bolin, of Crocker-Stanford Deep-sea Expedition, aboard yacht *Zaca*, off California coast in September.
1938	Initiated *Stanford Ichthyological Bulletin*. Editor to end of volume 8 in 1967.
1938	Advanced to full Professor, Stanford, September.
1939	Member, Fishery Organizing Committee, 6th Pacific Science Congress, Berkeley, California.
1940–41	Intensive extracurricular work with William Allen White's "Committee to Defend America by Aiding the Allies."
1942	Elected Corresponding Member, Zoological Society of London.
1942–44	Posted to Rio de Janeiro (State Department funds) to aid Museu Nacional and Divisão de Caca e Pesca. Lecture course on ichthyology and fishery biology in Rio. Brief visits en route to Mexico City, Guatemala, Panama, Cali, Bogota, Mariquita, Lima, Arequipa, Santa Cruz (Bolivia), Corumba. Intermittent field work near Rio, and (with Antenor Carvalho and others) to Minas Gerais, Espírito Santo, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul, and Belém do Pará.
1944	Return to Stanford, October.
1945–51	Vice-President and Council Member, California Academy of Sciences, San Francisco.
1946	Beginning of post-war upswing in graduate-student enrollment at Stanford.
1947	Bikini Scientific Resurvey, U.S. Navy, aboard U.S.S. *Chilton*. Field work on Bikini and Rongerik atolls. Plankton Survey, Bikini lagoon. Visits to Kwajalein and Honolulu, summer.
1949	Pacific Science Congress, Aukland and Christchurch, New Zealand. Some fish and reptile collecting on South Island and Aukland Harbor. Visits to Hawaii, Samoa, Noumea, Canton Island and Johnston Island en route.
1949–51	President, American Society of Ichthyologists and Herpetologists.
1950	Brief trip to Brazil during August and September, visiting Recife, Salvador (Bahia), Rio, Belém do Pará, Manáus, and Puerto Rico.
1951–53	Special taxonomic work, U.S. Fish and Wildlife Service, Washington, D.C., summers.
1952–54	Managing editor, *Aquarium Journal*, San Francisco.
1954	European trip for Fish and Wildlife Service and FAO. Paris, with stop in London, December.
1958	Field work and fish collecting during February, upper Rio Caquetá basin, vicinity of Tres Esquinas, Colombia, with General Thomas D. White. Visit to Bogotá.
1958	International Zoological Congress, London. Visits to Copenhagen and Hamburg, summer.
1958–59	Organizing Committee for First International Congress of Oceanography, held in United Nations headquarters, New York, summer of 1959.
1959	Elected honorary fellow, Zoological Society of India.
1960	Field work and fish collecting during February, upper Rio Guaviare basin, near Sierra Macarena, Colombia, with General T. D. White.
1960	Six-month study trip to Europe, visiting Hamburg, Copenhagen, Lund, Goteborg, Amsterdam, Leiden, Brussels, Frankfurt, Vienna, Lucerne, Paris, London.
1963	Field work and fish collecting during February in Nicaragua; Managua area, Lake Nicaragua, Rio San Juan, with General T. D. White.
1963	International Zoological Congress, Washington, D.C., August.
1964	International Conference on Tropical Oceanography, Miami. Arranger and convener, section of zoogeography, November.
1966	Marriage to Frances Edna Felin, Palo Alto, California.

1967	Primer Foro Internacional sobre Planificacion y Desarrollo Pesquero, Caracas, Venezuela, August. Followed by brief travel in eastern Venezuela and lower Rio Orinoco with Agustin Fernandez-Yepez. Visits to Trinidad, Panama and Puerto Rico en route.
1969–70	Vice-President, Cactus and Succulent Society of California.
1970	Statutory retirement on August 31 from faculty, Stanford, August.
1970	Appointed Henry Bryant Bigelow Visiting Professor of Ichthyology, Harvard University.

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Festschrift for George Sprague Myers

Vol. XXXVIII, No. 2, pp. 19–52. December 31, 1970

ANNOTATED CHRONOLOGICAL BIBLIOGRAPHY OF THE PUBLICATIONS OF GEORGE SPRAGUE MYERS
(to the end of 1969)

This bibliography lists all known publications by George S. Myers, scientific and other, omitting only about two dozen ephemeral items such as newspaper articles. It has been compiled almost entirely from the mimeographed bibliographies issued by Myers in 1950 and 1952 and his own card index of titles. Nearly all the bibliography and all the annotations are thus by Myers himself. The serial numbers of the papers have been used as annotations of mailed-out separata on Myers' address cards of colleagues, and have not been changed even though a few previously missing entries have now been inserted in their chronological places.

To avoid confusion, Myers almost always gave separate numbers even to subsequent reprintings or translations of original contributions and to successive installments of serially published papers. In all such cases cross references are given. The total of numbered entries is thus greater than the number of original papers, but the usefulness of this system is obvious in the annotations. The last numbered entry is 593, but with ten interpolations added, the total is 603.

Aside from formal taxonomic papers, the largest classes of publications are articles on aquarium fishes and book reviews. Myers became interested in ichthyology through aquarium fishes and retained his interest in them permanently. By 1930 he was already becoming the recognized authority on the identification and aquarium behavior of the smaller freshwater species from tropical America, Asia, and Africa. The number of Myers' publications in this field became especially large during the 26 months (June 1952–August 1954) when he acted as editor of the *Aquarium Journal.* Although many of these papers were of a popular nature, many of them contain original observations on the taxonomy or behavior of the species concerned and could not be excluded even from a bibliography of scientific publications.

In writing book reviews, Myers acted on a theory (reinforced, he says, by advice of the late Dr. Joseph Grinnell of the University of California) that carefully done, critical reviews form a powerful instrument to weed out incompetence and raise the level of any scientific discipline. Myers obviously adhered to that theory, for his reviews are usually sharply critical and often embody original ideas or taxonomic views not expressed elsewhere. He has been known to say that he puts as much thought into reviews as into more formal contributions, and that some of his best writing has gone into them. A sampling shows this to be true; his reviews, editorials, and columns-of-comment give a broader view of his thought and critical abilities than do his formal papers. Many are worth reading at any time, especially by younger workers.

There are also 49 papers dealing largely or wholly with zoological nomenclature, ranging from his early attempts to modernize the names of aquarium fishes to such nomenclatural problems as the name of *Culter* (243), the family name of the characids (335), and some Neotropical frog names (560).

Myers was asked by a former pupil if he could make a rapid analysis of his papers and came up with the following rough totals: (A) Papers of scientific interest on taxonomy, evolution, ecology, behavior, distribution, and nomenclature of fishes: 252. (B) Ditto of amphibians and reptiles: 51. (C) Historical zoogeography, chiefly of lower vertebrates: 8. (D) Formal book reviews: 104. (E) Editorials, comment, criticism: 11. (F) Taxonomic theory: 2. (G) Curatorial, collecting, preserving: 5. (H) Popular articles on fishes, of little or no scientific interest: 95. (I) Botany: 2. (J) Station records: 1. (K) History of ichthyology: 2. (L) Biographies and obituaries: 14. (M) Translations and reprints of original Myers' papers: 32. (N) Continuations of serial articles without any change of title: 6. (O) Nonfish aquarium articles: 6. (P) Verse, allegory, etc.: 3. (Q) Unimportant notes and corrections: 9. Myers says that several papers published in the aquarium literature are included under category A, but only when they contributed significantly to knowledge of the fishes concerned.

For the benefit of herpetologists, all papers of all categories that are immediately concerned with amphibians and reptiles are preceded by an asterisk (*) in the bibliography.

The form of the entries is as follows: first the serial number, followed by the full title of the paper [untitled contributions have been given a title in brackets], the journal or other vehicle of publication, the volume number and issue number, and the pagination, followed by the precise date of publication so far as Myers knew it. Annotations by Myers are in brackets, usually at the end of the entry. The dates of papers, in cases where there is not even a month given, were known only as to year. Dates of publication of *Copeia* articles are the imprinted ones of the issues concerned. All dates given for the *Stanford Ichthyological Bulletin* papers, and for articles in the *Aquarium Journal* while Myers was editor (June 1952–August 1954) are the exact dates of mailing of the issues concerned. Where the imprinted year or month of a volume or article differs from the year placement or month placement in this bibliography (as with the proceedings of different Pacific Science Congresses) the date here given is the correct one for mailing of the volumes. Joint-authorship papers have the names of the authors given, in the original order, in parentheses immediately following the title. The only year in which no paper was published was 1968.

Abbreviations of the names of journals frequently cited are as follows:

AJ = *The Aquarium Journal.* Published monthly by the San Francisco Aquarium Society, 1928–1965. [Continued 1966–1967 as *Ichthyologica, The Aquarium Journal*, published by TFH Publications, Inc., Jersey City, N. J.] Edited by G.S.M., 1952–1954.

AL = *Aquatic Life.* Published by Joseph E. Bausman and edited by W. A. Poyser in Philadelphia, 1915–1922; subsequently published and edited for many years by August M. Roth in Baltimore. Philadelphia issues usually published promptly; Baltimore issues often lagged badly.

AMN = *American Museum Novitates.* Published by The American Museum of Natural History, New York City. Separate papers numbered consecutively; numbers separately paged.

ANMG = *The Annals and Magazine of Natural History.* Published in London by Taylor and Francis, 1838–1966. Continued under the name *Journal of Natural History.*

AP = *Aquarium* (Paris). Published in Paris, 1934–at least to 1936. Many articles from TA translated into French with the original TA colored plates and other figures.

BATK = *Blätter für Aquarien- und Terrarienkunde.* Published from 1890 until about 1937, first in Magdeburg and later in Stuttgart. Many important behavioral and taxonomic papers included.

CO = *Copeia.* Journal of the American Society of Ichthyologists and Herpetologists. Published at various places in the U.S.A., 1913–present. To 1930, all issues numbered consecutively, with no volume number. Later, the year is the volume number (4 issues per year).

FC = *The Fish Culturist.* Published in Philadelphia by the Pennsylvania Fish Culturists' Association, 1921–present.

HAB = *The Home Aquarium Bulletin.* Published at first in Newark, N. J., by the Newark Aquarium Society, later by a group in East Orange, N. J., 1931–to at least March, 1936. Carl L. Hubbs and Myron Gordon were among the associated editors.

LSJ = *Lingnan Science Journal.* (Continuation of *Lingnaam Agricultural Review.*) Published by Lingnan University, Canton, China. Edited by Wm. E. Hoffman and Robert Cunningham Miller.

PBSW = *Proceedings of the Biological Society of Washington.* Washington, D. C., 1880–present.

SIB = *Stanford Ichthyological Bulletin.* Edited by G. S. M. and M. H. Storey. Published by Natural History Museum of Stanford University (later Division of Systematic Biology), Stanford, Calif., 1938–1967.

TA = *The Aquarium.* Published by Innes Publishing Co., Philadelphia, beginning in 1932. Edited by Wm. Thornton Innes. G. S. M. was an associate editor for many years.

TFH = *The Tropical Fish Hobbyist.* Published by TFH Publishing Co., Jersey City, N. J., beginning in 1952.

WATK = *Wochenschrift für Aquarien- und Terrarienkunde.* Published weekly, 1904–1950, in Braunschweig. Much important behavioral and taxonomic information included.

1920

1. *Phalloptychus januarius.* AL, vol. 5, no. 7, p. 74. July. [Misidentification; species mentioned is spotted form of *Phalloceros caudimaculatus.*]
2. The red rivulus. AL, vol. 5, no. 7, pp. 79–80. July. [Xanthic form of *Rivulus urophthalmus.*]
3. *Fundulus diaphanus.* AL, vol. 5, no. 8, p. 91. August. [The figure, supplied by the editor, is of *F. heteroclitus.*]
4. Some fish suitable for home aquaria with suggestions concerning starting and maintaining an aquarium. 8vo, 16 pp., Hudson County Aquarium Society, Jersey City, N. J. September 10. [Circular distributed at 3rd annual exhibition of H.C.A.S.; pp. 2, 4, 6, and 8 are advertisements; author's name omitted by printer. Copies in the libraries of Stanford University and the U. S. National Museum.]
5. The Mexican swordtail. AL, vol. 5, no. 11, pp. 122–123. November.

1921

6. The labyrinth fishes. I. AL, vol. 6, no. 1, pp. 1–2. January. [Continued in nos. 13 and 19.]
7. *Fundulus chrysotus.* AL, vol. 6, no. 3, p. 18, September.
8. The common sunfish. AL, vol. 6, no. 4, pp. 19–20. October–December.

1922

9. The black banded sunfish. Aquarium News, Ridgewood, N. Y., vol. 1, no. 5, p. 2. January 15.
10. *Chirodon arnoldi.* AL, vol. 6, no. 5, p. 28. January–June. [The species mentioned is actually *Astyanax mexicanus.*]
11. Planting aquaria. FC, vol. 2, no. 4, pp. 157–158. September.
12. The aquarium and its denizens, being a brief exposition of the proper arrangement and maintenance of home aquaria, with a catalog of some of the fishes suitable for aquarium culture. 8vo, 22 pp. (cover is title-page); Hudson County Aquarium Society, Jersey City, N. J. September 8. [Copies in the libraries of Stanford University, the British Museum, and the U. S. National Museum. See also no. 56.]
13. The labyrinth fishes. II. AL, vol. 6, no. 6, pp. 33–34. July–October. [Continuation of 6. See also 19.]
14. Interesting notes. FC, vol. 2, no. 6, pp. 172–173. November. [Notes on *Fundulus gularis*, *Mesogonistius chaetodon*, and *Pterophyllum scalare*; article includes six lines on p. 173, not well differentiated from other notes below.]

15. Hudson County exhibition. AL, vol. 6, no. 7, p. 46. November.
16. A true fish story. Swastika, Jersey City, vol. 1, no. 7, pp. 4–5. December 10. [Concerns the climbing perch. See 18 for note.]
17. A recently described aquarium fish. CO, no. 113, p. 89. December 20.
*18. The largest frog—the smallest frog. Swastika, Jersey City, vol. 1, no. 8, p. 5. December 25. [A brief note on the size of *Rana goliath* and newly hatched *Eleutherodactylus*. The Swastika was a student publication of the city high schools in Jersey City. Edited by Meyer Levin.]

1923

19. The labyrinth fishes. III. AL, vol. 6, no. 9, pp. 63–64. January. [Continuation of 6 and 13. Never concluded.]
20. The characins. FC, vol. 2, no. 8, pp. 186–187. January.
21. A note on the fighting fish. FC, vol. 2, no. 10, pp. 202–203. March. [Note on the identification of aquarium examples of *Betta*; in the third paragraph, line four, the word "small" was transferred by printer's error from before "lake" in preceding line.]
22. Correct names. FC, vol. 2, no. 11, pp. 210–212. April. [An attempt to modernize the scientific names of aquarium fishes. See also 24.]
23. *Aplocheilus chaperi.* AL, vol. 7, no. 1, pp. 1–2, 12. May.
24. Correct names. AL, vol. 7, no. 1, pp. 3–6. May. [A reprint of 22, with the addition of some name meanings.]
25. Notes on the nomenclature of certain anabantid fishes and a new generic name proposed. CO, no. 118, pp. 62–63. May 20.
26. *Ctenobrycon spilurus.* FC, vol. 2, no. 13, p. 226. June.
27. On the subject of scavengers in the aquarium. FC, vol. 2, no. 12, pp. 228–229. June.
28. A new limia from San Domingo. (John Treadwell Nichols and G. S. Myers.) AMN, no. 79, 2 pp. June 12.
29. *Hyphessobrycon anisitsi*, a new fish for the aquarist. FC, vol. 3, no. 3, pp. 250–251. November. [Identification erroneous; species mentioned is *Hemigrammus caudovittatus.*]
30. Further notes on anabantids. CO, no. 124, pp. 111–113. November 20.

1924

31. The labyrinth fishes. FC, vol. 3, no. 7, pp. 282–284. March. [Not part of the series: 6, 13, and 19.]
32. New genera of African poeciliid fishes. CO, no. 129, pp. 41–45. May 20.
33. A new rivulus from Rio de Janeiro. ANMG, ser. 9, vol. 13, pp. 588–590. June. [*R. dorni*; holotype in British Museum. This species is a synonym of *R. brasiliensis* Valenciennes, according to G. S. M.]
34. A new poeciliid fish from the Congo, with remarks on funduline genera. AMN, no. 116, 9 pp. June 6.
35. A new poeciliid fish of the genus *Micropanchax* from Ubangi. AMN, no. 112, 3 pp. June 24.
*36. Amphibians and reptiles from Wilmington, N. C. CO, no. 131, pp. 59–62. June 30.
37. On the existence of the Japanese killifish, *Fundulichthys virescens.* ANMG, ser. 9, vol. 14, pp. 253–254. August.
38. Mutanda ichthyologica. *Neoborus* Boulenger and *Barbus rubripinnis* Nichols and

Griscom. Revue Zoologie Africaine, Tervuren, Belgium, vol. 12, no. 3, p. 397. August 1.

39. *Lucania ommata* in the aquarium. FC, vol. 4, no. 1, p. 314. September.
40. A new poeciliid fish of the genus *Rivulus* from British Guiana. AMN, no. 129, 2 pp. September 23.
41. A new characin fish from Rio de Janeiro. FC, vol. 4, no. 3, pp. 330–331. November. [The legend for the figure was omitted by the printer; it is given correctly in 295. The two cotypes (syntypes) are now in the U. S. National Museum. See also 48.]
42. On a small collection of fishes from Upper Burma. AMN, no. 150, 7 pp. November 13.
43. The largest rivulus. CO, no. 135, p. 96. November 18.

1925

44. Concerning melanodimorphism in killifishes. CO, no. 137, pp. 105–107. January 15. [The specimens of *Platypoecilus couchianus* mentioned were misidentified in the Field Museum collection; they were *Mollienisia sphenops*.]
45. Description of a new catfish from Abyssinia. CO, no. 139, pp. 12–13. February 15. [See 520 for corrections.]

45a. [Description of *Rivulus rogoaguae*.] (Nathan Everett Pearson and G. S. Myers.) *In*: Pearson, N. E., Fishes of the Rio Beni Basin (Indiana University Studies, "1924," vol. 11, no. 64), p. 51. February.

46. Results of some recent studies on the American killifishes. FC, vol. 4, no. 8, pp. 370–371. April. [Contains original diagnosis of *Trigonectes strigabundus*, n. gen. and n. sp. from the Rio Tocantins. Reprinted as 234.]
47. Introduction of the European bitterling (*Rhodeus*) in New York and of the rudd (*Scardinius*) in New Jersey. CO, no. 140, pp. 20–21. April 14.
48. Ein neuer Characinide von Rio de Janeiro. BATK, Jahrg. 36, no. 4, pp. 98–99, 1 colored plate. April 15. [Translation of 41, omitting the original figure, but accompanied by a colored plate by Curt Bessiger and by an article on breeding and care in aquaria, by Wilhelm Schreitmüller.]
49. *Notropis cummingsi*, a new minnow from Wilmington, North Carolina. AMN, no. 168, 4 pp. April 23. [Although named for a woman, Mrs. J. H. Cummings, the ending of cummingsi was intentional, the rationale being that Cummings was the name of her husband.]
50. Concerning mollienisias. AL, vol. 9, no. 1, pp. 3–4, 13–14. May.
51. *Astyanax fasciatus* in the aquarium. AL, vol. 9, no. 3, p. 40. July.
52. Description of a new cheirodontine characin from Rio de Janeiro. Annals of the Carnegie Museum, Pittsburgh, vol. 16, pp. 143–144, pl. 10. July 31. [*Spintherobolus broccae*, n. sp. = *Phoxinopsis typicus* Regan.]
53. Fishes changing sex. AL, vol. 9, no. 4, pp. 56–57. August.
54. The blue characin, *Coelurichthys microlepis*. Aquarium Bulletin, St. Louis, vol. 2, no. 3, pp. 3–4. September 1. [Reprinted as 95.]
55. Labyrinth fishes for the aquarist. Aquarium Bulletin, St. Louis, vol. 2, no. 4, pp. 3, 6. October.
56. The aquarium and its denizens, being a brief exposition of the proper arrangement and maintenance of home aquaria, with a catalog of some of the fishes suitable for aquarium culture. Second edition, revised and enlarged; 12mo, 45 pp., August M. Roth, Publisher, Baltimore. November. [A revised edition of 12.]
57. *Tridentopsis pearsoni*, a new pygidiid catfish from Bolivia. CO, no. 148, pp. 83–86. November 25.

58. Fishes and human disease. FC, vol. 5, no. 4, pp. 27–29. December. [An account of the part played by fishes in malaria and yellow fever control. The reference to *Astroblepus* (*Arges*) is a lapsus; the genus intended is *Pygidium.*]

1926

59. Notes on anabantids. III. CO, no. 150, pp. 97–100. January 25.
60. On the correct names of the tetra from Buenos Aires, the haplochilus from Madras, and the mouthbreeder. FC, vol. 5, no. 8, p. 61. April.
61. Two new genera of African characin fishes. Revue Zoologie Africaine, Tervuren, Belgium, vol. 13, nos. 3–4, pp. 174–175. April 1.
62. Die Nomenklatur der Labyrinthfische. BATK, Jahrg. 37, no. 8, pp. 190–193. April 30.
63. Descriptions of a new characin fish and a new pygidiid catfish from the Amazon basin. CO, no. 156, pp. 150–152. July 20. [Proof not seen by author; there are several bad typographical errors which are corrected in 71.]

*64. A synopsis for the identification of the amphibians and reptiles of Indiana. Proceedings of the Indiana Academy of Science, vol. 35 (1925), pp. 277–294. [Published in summer, 1926.]

65. A cichlid fish that hangs its young on aquatic plants. AL, vol. 10, no. 4, pp. 60–61. August.
66. Eine neue südamerikanische Characinidenart der Gattung *Pyrrhulina*. BATK, Jahrg. 37, no. 18, pp. 441–442. September 30. [The type locality, left indefinite in this paper, was later found to be Rosario, Argentina; syntypes now in U. S. National Museum.]
68. Alphabetical list of aquarium fishes, their breeding habits, care, etc. *In*: Innes, W. T., Goldfish varieties and tropical aquarium fishes, 9th ed., Philadelphia, pp. 264–283. October. [All of this chapter, save the introduction (pp. 264–265) and the concluding remarks (pp. 283–284), is by G. S. Myers. This same list appeared in the later, cheaper edition of this book, called "The Complete Aquarium Book," published by Halcyon House, N. Y., in 1936.]
69. Eine neue Characinidengattung der Unterfamilie Cheirodontinae aus Rio de Janeiro, Brasilien. BATK, Jahrg. 37, no. 24, pp. 566–567. December 30. [Syntypes of *Rachoviscus crassiceps* now in U. S. National Museum. This fish was probably not from the Baixada Flumenense but from farther inland. Perhaps equals *Oligobrycon?*]

1927

70. An analysis of the genera of neotropical killifishes allied to *Rivulus*. ANMG, ser. 9, vol. 19, pp. 115–129. January.
71. Note [correcting typographical errors in no. 63.] CO, no. 158, pp. 167–168. January.

*72. *Rana areolata* at Bloomington, Indiana. (Herman P. Wright and G. S. Myers.) CO, no. 159, pp. 173–175. January 11. [First description of eggs.]

73. On the identity of the killifish *Fundulus meeki* Evermann with *Fundulus lima* Vaillant. CO, no. 160, p. 178. January 12.
74. *Puntis streeteri*, a new cyprinoid fish from Borneo, and *Cobitophis*, a new genus of Bornean Cobitidae. AMN, no. 265, 4 pp. April 20.
75. The status of the darter *Richiella brevispina* (Coker). CO, no. 163, pp. 39–43. June.

*76. The differential characters of *Bufo americanus* and *Bufo fowleri*. CO, no. 163, pp. 50–53. June.

77. Descriptions of new South American fresh-water fishes collected by Dr. Carl Ternetz. Bulletin of the Museum of Comparative Zoology, Harvard, vol. 68, no. 3, pp. 107–135.

July. [Types of *Otothyris canaliferus* now in U. S. National Museum, Paris, and London; paratypes of *Bunocephalus salathei* in Washington. See also 163 for corrections.]

78. A new genus of Brazilian characin fishes allied to *Bivibranchia*. (Carl H. Eigenmann and G. S. Myers.) Proc. National Academy of Sciences, Washington, vol. 13, no. 8, pp. 565–566. August.

*79. Notes on Indiana amphibians and reptiles. Proceedings of the Indiana Academy of Science, vol. 36 (1926), pp. 337–340. September.

80. *Rasboras*. FC, vol. 7, no. 2, pp. 175–177. October.

1928

81. Carl H. Eigenmann—Ichthyologist. Natural History, New York, vol. 28, no. 1, pp. 98–101, portrait.

82. The systematic position of the phallostethid fishes, with diagnosis of a new genus from Siam. AMN, no. 295, 12 pp. February 1.

83. The species of *Piabucina* inhabiting Colombia. CO, no. 166, pp. 4–5. March 23.

84. Two new genera of fishes. CO, no. 166, pp. 7–8. March 23.

85. *Haplochilus cameronensis*. AL, vol. 11, no. 12, p. 204. April. [A short note written in 1923 and published without author's knowledge in 1928. See 89.]

86. The existence of cichlid fishes in Santo Domingo. CO, no. 167, pp. 33–36. June 28.

87. The urostyle in larval characin fishes. CO, no. 167, pp. 36–37, June 28.

88. New fresh-water fishes from Peru, Venezuela, and Brazil. ANMG, ser. 10, vol. 2, pp. 83–90. July. [Two of the species are described by C. H. Eigenmann, and one jointly by Eigenmann and Myers.]

89. "*Haplochilus cameronensis*." AL, vol. 12, no. 5, p. 94. September. [Correcting 85, above.]

90. The characins. AL, vol. 12, no. 7, pp. 119–120, 122, 134–135. November.

91. The characins. AL, vol. 12, no. 8, p. 152. December. [Continuation of 90.]

1929

92. The happy family tank. FC, vol. 8, no. 5, pp. 51–52. January. [On "community aquaria."]

93. The history of the veiltail fighting fish. AL, vol. 12, no. 10, pp. 195–199. February. [History of the original introduction of long tailed cultivated *Betta splendens* into the United States.]

94. Cranial differences in the African characin fishes of the genera *Alestes* and *Brycinus*, with notes on the arrangement of related genera. AMN, no. 342, 7 pp. March 2.

95. The blue characin, *Mimagoniates microlepis*. FC, vol. 8, no. 8, pp. 92–93. April. [A reprint of 54, above, with emendations.]

96. Mutanda icthyologica. II. *Heringia* vs. *Rhinosardinia* (Clupeidae), *Medipellona* vs. *Chirocentrodon* (Clupeidae), and *Entonanthias* vs. *Mirolabrichthys* (Anthiidae). CO, no. 170, pp. 1–2. April 30.

97. A note on the Formosan homalopterid fish, *Crossostoma lacustre* Steindachner. CO, no. 170, p. 2. April 30.

*98. Notes on the names of the spring peeper, the carpenter frog, and *Aneides aeneus*. CO, no. 170, pp. 22–23. April 30. [See 121 for correction.]

99. On curimatid characin fishes having an incomplete lateral line, with a note on the peculiar sexual dimorphism of *Curimatopsis macrolepis*. ANMG, ser. 10, vol. 3, pp. 618–621. June.

100. Notes on soles related to *Achirus*. CO, no. 171, pp. 36–38. June 28.
101. The American Characidae. [Part 5] (Carl H. Eigenmann and G. S. Myers.) Memoirs of the Museum of Comparative Zoology, Harvard, vol. 43, part 5, pp. 429–558, 11 pls. September. [The supplement, pp. 516–550, is nearly all by G.S.M; the rest of the text is nearly all by Eigenmann.]
102. Our aquarium fishes. I. The mouthbreeder. AJ, vol. 2, no. 8, p. 31. October 3.

1930

*103. Amphibians and reptiles observed in the Palisades Interstate Park, New York and New Jersey. CO, no. 173, pp. 99–103. January 16.
*104. Notes on some amphibians in western North America. PBSW, vol. 43, pp. 55–64. March 12.
105. Fishes from the upper Rio Meta basin, Colombia. PBSW, vol. 43, pp. 65–71. March 12.
*106. The status of the southern California toad, *Bufo californicus* (Camp). PBSW, vol. 43, pp. 73–77. March 12.
107. On the occurrence and habits of ocean sunfish (*Mola mola*) in Monterey Bay, California. (G. S. Myers and Joseph Howe Wales.) CO, 1930, no. 1, pp. 11–12. April 30.
108. The killifish of San Ignacio and the stickleback of San Ramon, Lower California. Proceedings of the California Academy of Sciences, ser. 4, vol. 19, no. 9, pp. 95–104. July 15.
109. *Ptychidio jordani*, an unusual new cyprinoid fish from Formosa. CO, 1930, no. 4, pp. 110–113. December 31. [Type later found to represent a chance introduction in Formosa, originating from the pondfish-fry export industry centering at Wuchow. Genus and species are endemic to the Si Kiang (West River) system, near to and above Wuchow, Kwangsi, China.]
110. [Review of] Publications of the University of Oklahoma Biological Survey, vol. 1. By A. Richards, C. L. Hubbs, and A. I. Ortenburger. CO, no. 4, pp. 159–160. December 31.
111. [Review, with critical comments, of] Hall, H. M., and Clements, F. E., The phylogenetic method in taxonomy. Micropaleontology Bulletin, Stanford University, vol. 2, no. 3, pp. 55–58. December 31.

1931

112. Eigenmann, Carl H. *In*: Dictionary of American Biography, vol. 6, pp. 62–63. Charles Scribner's Sons, New York.
113. Killifishes in Hispaniola. FC, vol. 10, no. 6, pp. 103–104. February.
114. Ichthyological reminiscences of a trip east. AJ, vol. 4, no. 2, p. 9. February.
115. Ichthyological reminiscences of a trip east (continued). AJ, vol. 4, no. 3, pp. 14–15. March 5.
116. Ichthyological reminiscences of a trip east (concluded). AJ, vol. 4, no. 4, pp. 20–21. April 2.
117. The primary groups of oviparous cyprinodont fishes. Stanford University Publications, University Series, Biological Sciences, vol. 6, no. 3, pp. 241–254. [Copies first mailed April 7.]
*118. *Ascaphus truei* in Humboldt County, California, with a note on the habits of the tadpole. CO, 1931, no. 2, pp. 56–57. July 20.
119. Fishes from southeastern China and Hainan. (Albert W. Herre and G. S. Myers.) LSJ, vol. 10, no. 2–3, pp. 233–254. August. [Key to Asiatic genera of Clupeidae by G.S.M. alone. See 126 for correction.]

120. On the fishes described by Koller from Hainan in 1926 and 1927. LSJ, vol. 10, nos. 2–3, pp. 255–262. August.

*121. The original descriptions of *Bufo fowleri* and *Bufo americanus*. CO, 1931, no. 3, pp. 94–96. October 30.

122. Poeciliid fishes of the genus *Mollienisia* in Hispaniola, with notice of a new limia from the Samaná Peninsula. AMN, no. 503, 2 pp. November 9.

123. On the identity of *Ophicephalus and Channa*, two genera of labyrinth fishes. (G. S. Myers and Leo Shapovalov.) Peking Nat. Hist. Bull., Peiping, China, vol. 6 (1931–32), pt. 2, pp. 33–37. November. [Vol. 6, part 2 has usually been considered to have been published in 1932. Copies of vol. 6, part 2 reached regular subscribers in California in December 1931, and publication in China must have been in November or earlier.]

1932

124. Gambusias in the aquarium. HAB, vol. 2, no. 1, pp. 2–5. March. [See also 150.]

125. The osteoglossid fish *Scleropages* in the Malay Peninsula. CO, 1932, no. 1, p. 30. April 12.

126. *Nealosa* Herre and Myers equals *Konosirus* Jordan and Snyder. CO, 1932, no. 1, p. 30. April 12.

127. A new name for a Melanesian pseudochromid fish confused with *Nesiotes purpurascens* de Vis. CO, 1932, no. 1, p. 30. April 30.

*128. A neglected description of a Mexican garter-snake, *Thamnophis stejnegeri* McLain. CO, 1932, no. 1, p. 35. April 12.

129. [Review of] Osborn, H. F. Cope: Master Naturalist, and Biographical memoir of Edward Drinker Cope. CO, 1932, no. 1, pp. 39–41. April 12.

130. *Danio analipunctatus* identified as *Brachydanio nigrofasciatus*. TA, vol. 1, no. 2, p. 54. June. [Boulenger's holographic description of *Danio analipunctatus*, which he sent to J. P. Arnold and which was published by Arnold in BATK, was sent to G.S.M. by Arnold, and is now in Library of U. S. National Museum.]

131. A note on the two Chinese paradise fishes. HAB, vol. 2, no. 5, p. 9. July. [Preliminary synopsis of 137.]

132. Some new aquarium fishes from Panama. TA, vol. 1, no. 3, pp. 68–69, 82. July.

133. Some notes on the characin, *Astyanax mexicanus*, in Texas. AL, vol. 16, no. 3, pp. 97–98. July.

134. A new gonostomatid fish, *Neophos nexilis*, from the Philippines. CO, 1932, no. 2, pp. 61–62. July 1.

135. A new whitefish, *Prosopium snyderi*, from Crescent Lake, Washington. CO, 1932, no. 2, pp. 62–64. July 1.

136. *Fundulus chrysotus*, geschechte Abart. WATK, Jahrg. 29, no. 29, pp. 450–451. July 19. [Notes on black-spotted, melanic or melanodimorphic specimens of *Fundulus*, *Gambusia*, and *Mollienisia*. See also 44.]

137. The two Chinese labyrinth fishes of the genus *Macropodus*. LSJ, vol. 11, no. 3, pp. 385–403, pls. 6–7. July 22. [A taxonomic revision of the genus. Proof not seen by author; many typographical and editorial errors, especially in explanation of plates. See also 131; see 576 for additional information and another synonym.]

138. A rare deep-sea scombrid fish, *Xenogramma carinatum* Waite, on the coast of southern California. Trans. San Diego Society of Natural History, vol. 7, no. 11, pp. 111–117,

pl. 7. July 28. [First American record. First synonymization of several nominal species. Species later known as *Lepidocybium flavobrunneum* (A. Smith) 1849.]

139. Dangers in identifications. TA, vol. 1, no. 4, pp. 94–97, 110. August.

140. *Pterophyllum*, king of aquarium fishes. TA, vol. 1, no. 5, pp. 115–118, 140–141. September. [A systematic review of the 3 species.]

141. A new genus of funduline cyprinodont fishes from the Orinoco Basin, Venezuela. PBSW, vol. 45, pp. 159–162. September 27.

142. Recent importations—*Stethaprion innesi* and *Mylossoma aurem* from the Amazon. TA, vol. 1, no. 6, pp. 149–150, 171. October. [This will probably have to stand as the original description of *S. innesi*, which was formally described in 148. Reprinted as 262.]

143. A native fish, *Notropis lutrensis*, in the aquarium. AJ, vol. 5, no. 8, pp. 45–46. October 6.

144. Notes on Colombian fresh-water fishes, with description of a new astroblepus. CO, 1932, no. 3, pp. 137–138. October 7.

1933

145. *Pachypanchax*, a new genus of cyprinodont fishes from the Seychelles Islands and Madagascar. AMN, no. 592, 1 p. January 23.

146. A new genus of Chinese fresh-water serranid fishes. Hong Kong Naturalist, vol. 4, no. 1, p. 76. April. [Proposing the new genus *Acroperca*, which was antedated by *Coreosiniperca* Fang and Chong 1932. The difference in date was about three months.]

*147. Two records of the leatherback turtle on the California coast. CO, 1933, no. 1, p. 44. April 3.

148. Description of a new characid fish of the genus *Stethaprion* from the Lower Amazon. ANMG, ser. 10, vol. 11, pp. 604–605. May. [See 142.]

149. *Stevardia albipinnis?* HAB, vol. 3, no. 4, p. 11. June.

150. Gambusen im Aquarium. WATK, Jahrg. 30, no. 26, pp. 401–403. June 27. [Translation of 124.]

151. [Review of] Hora, S. L., Classification, bionomics and evolution of homalopterid fishes. CO, 1933, no. 2, p. 109. July 20.

152. The classification of the African cyprinodont fishes with a discussion of the geographical distribution of the Cyprinodontidae of the world. Stanford Univ. Bull., ser. 5, no. 158 (Abstracts of dissertations, vol. 8, 1932–33), pp. 10–12. July 31. [Brief abstract of doctorate thesis, which was more usefully abstracted as 157 and 214.]

153. Anent Mr. Schoenfeld on scientific names. HAB, vol. 3, no. 6, pp. 6–11. August.

154. New importations—"Jack Dempsey" unmasked. Aquarium, Philadelphia, vol. 2, no. 6, pp. 141–142. October. [Reidentifies fish previously known to aquarists as *Cichlasoma nigrofasciatum*—the "Jack Dempsey"—as *C. biocellatum*.]

155. Note on the breeding habits of *Corynopoma*. FC, vol. 13, no. 3, p. 61. November.

156. New importations.—Leopard Corydoras. TA, vol. 2, no. 8, pp. 188–189. December. [Contains first diagnosis of *Corydoras leopardus*, which is compared to *C. julii* and *C. trilineatus*. The species is formally described in 178. Translated as 166.]

157. The genera of Indo-Malayan and African cyprinodont fishes related to *Panchax* and *Nothobranchius*. CO, 1933, no. 4, pp. 180–185. December 27. [See also 180.]

1934

158. The identification of aquarium fishes related to *Metynnis* and *Serrasalmus*. FC, vol. 13, no. 5, pp. 120–122. January. [Generic identification of live specimens.]
159. New importations—The black-winged flying characin. (*Carnegiella marthae* Myers.) TA, vol. 2, no. 9, pp. 217–218. January. [First account of life colors and habits, first record from Amazon basin, and first photograph of living specimens. See also 186 and 289, and comments in 345.]
160. [Radio interview on fish work in the National Museum.] AL, vol. 17, no. 9, pp. 239–240. January.
161. [Review of] Coates, W., Tropical fishes for a private aquarium. FC, vol. 13, no. 6, p. 154. February.
162. Reports on the collections obtained by the first Johnson-Smithsonian Deep-sea Expedition to the Puerto Rican Deep. Three new deep-water fishes from the West Indies. Smithsonian Miscellaneous Collections, vol. 91, no. 9, 12 pp., 1 pl. April 2.
163. Corrections of the type localities of *Metzia mesembrina*, a Formosan cyprinid, and of *Othonocheirodus eigenmanni*, a Peruvian characin. CO, 1934, no. 1, p. 43. April 24.
164. A new name for the Alaskan cottoid fish *Ulca marmorata* (Bean). CO, 1934, no. 1, p. 44. April 24.
165. [Review of] Regan, C. T., and Trewavas, E., Deep-sea angler fishes (Ceratioidea). CO, 1934, no. 1, pp. 54–55. April 24.
166. Le Corydoras Léopard. AP, no. 5, p. 77. May. [A re-edited translation of 156.]
167. *Barbus partipentazona* Fowler. TA, vol. 3, no. 4, p. 83. August. [See also 182.]
168. Our downtrodden helper, the snail. AL, vol. 18, no. 4, p. 74–76, 93. August. [Snails in aquaria.]
169. Judging fish shows. TA, vol. 3, no. 5, pp. 103–106. September.
170. *Gnathocharax steindachneri*, a new characin for the aquarium. HAB, vol. 4, no. 7, pp. 5, 29–30. September. [Records species from the Orinoco (Caicara) and from British Guiana (Rockstone) for the first time; also records *Monocirrhus polyacanthus* from Rockstone, British Guiana.]
171. Correct nomenclature. AL, vol. 18, no. 6, pp. 139–141. October. [Nomenclature of aquarium fishes.]
172. [Review of] Lederer, N., Tropical fish and their care. CO, 1934, no. 3, p. 143. October 31.
173. Ueber den Namen des Zwergdrachenflossers, *Corynopoma riisei* Gill (=*Stevardia albipinnis* Gill). WATK, Jahrg. 31, no. 48, pp. 755–756. November 27.
174. [Review of] Herre, A. W. C. T., Notes on fishes in the zoological museum of Stanford University, 1: The fishes of the Herre Philippine Expedition of 1931. CO, 1934, no. 4, pp. 196–197. December 31.

1935

175. *Cichlasoma biocellatum*. TA, vol. 3, no. 9, p. 196. January.
176. The mouth-breeding fighting fish, *Betta brederi*. TA, vol. 3, no. 9, p. 210. January. [This must stand as the original description of *B. brederi*, which is formally described in 179. Translated as 181 and 191.]
177. A new phallostethid fish from Palawan. PBSW, vol. 48, pp. 5–6. February. [Proposes new suborder Phallostethoidea.]

178. Four new fresh-water fishes from Brazil, Venezuela and Paraguay. PBSW, vol. 48, pp. 7–13. February 6. [One new species, *Corydoras leopardus*, was first diagnosed in 156.]

179. A new anabantid fish of the genus *Betta* from Johore. PBSW, vol. 48, pp. 25–26. February 6. [First diagnosed in 176.]

180. The genera of Indo-Malayan and African cyprinodont fishes allied to *Panchax* and *Nothobranchius*. Canadian Aquaria, London, Ontario, vol. 3, no. 3, pp. 42–45. March. [Unauthorized reprint of part of 157.]

181. Der maulbrutende Kampffisch *Betta brederi*. WATK, Jahrg. 32, no. 20, p. 307. May 14. [Translation of no. 176. See also 191.]

182. *Barbus partipentazona*, Fowler. AP, no. 19, p. 111. July. [Translation of 167.]

183. [Review of] Schreitmüller, W., Leitfaden zur Pflege und Zucht von einheimischen und fremländischen Zierfischen, Seetieren, Schnecken und Wasserpflanzen nebst einem Anhang über Trocken- und Kunstfischfutterarten; 3rd edition. CO, 1935, no. 2, p. 107. July 18.

184. [Review of] Holly, M.; Meinken, H.; and Rachow, A., Die Aquarienfische in Wort und Bild. CO, 1935, no. 2, p. 107. July 16.

185. Fishes of the upper Potomac. *In*: Shosteck, Robert, The Potomac trail book (128 pp., 12mo; published by the Washington Post, Washington, D. C.), pp. 90–95. [Fish chapter edited by Shosteck and proof not seen by G.S.M. before publication. Paragraphs on the eel and the goldfish on pp. 94–95 were added by Shosteck. The term "upper Potomac" was insisted on by Shosteck; the paper concerns the fishes of the region above the estuary but below Great Falls. The book was published (placed on sale) on October 6. Copies in libraries of U.S. National Museum, Carl L. Hubbs, and G.S.M.]

186. *Carnegiella marthae* Myers. AP, no. 23, pp. 173–174. November. [Translation of 159. See also 289.]

187. An annotated list of the cyprinodont fishes of Hispaniola, with descriptions of two new species. Zoologica, New York, vol. 10, no. 3, pp. 301–316. November 29.

188. Reports on the collections obtained by the first Johnson-Smithsonian Deep-sea Expedition to the Puerto-Rican Deep. A new genus of opisthognathid fishes. Smithsonian Miscellaneous Collections, vol. 91, no. 23, 5 pp. December 24. [Contains notes on Owstoniidae, *Macrurocyttus*, etc.]

189. [Review of] Two new state ichthyological papers [Greene, C. W., the distribution of Wisconsin fishes, and O'Donnell, D. J., Annotated list of the fishes of Illinois]. CO, 1935, no. 4, pp. 196–197. December 31. [In this was attempted the only published history and evaluation of the unfortunate check-list of North American fishes by Jordan, Evermann, and Clark.]

1936

190. [The use of fishes in mosquito control.] *In*: Sweetman, H. L., the biological control of insects (Comstock Publishing Co., Ithaca, N. Y.), pp. 318–325. [This chapter, although not credited to G.S.M. as author, was written by him and is printed from the MS. he supplied to Sweetman, with the change of only a very few words. Most of the bibliography and references given in the MS., however, were omitted by Sweetman.]

191. Le *Betta brederi*. AP, no. 25, p. 15. January. [A translation of 176, with additional notes on habits and breeding. See also 181.]

192. Note on *Rhamphichthys cingulatus* Brind. Aquarium News, Rochester, N. Y., vol. 3, no. 5, p. 68. January.
193. On the Indo-Australian fishes of the genus *Scatophagus*, with description of a new genus, *Selenotoca*. PBSW, vol. 49, pp. 83–85. July 3.
194. A new characid fish of the genus *Hyphessobrycon* from the Peruvian Amazon. PBSW, vol. 49, pp. 97–98. July 3.
195. A third record of the albulid fish *Dixonina nemoptera* Fowler, with notes on an albulid from the Eocene of Maryland. CO, 1936, no. 2, pp. 83–85. July 31.
196. A note on the stephanoberycid fishes. CO, 1936, no. 2, p. 118. July 31. [Resuscitates *Acanthochaenus luetkenii* Gill = *Stephanoberyx gilii*.]
197. [Review of] Herre, A. W. C. T., The fishes of the Crane Pacific Expedition. CO, 1936, no. 2, pp. 128–129. July 31. [Notes that *Disparichthys* is probably not a genus of eels and may be near the blennies, and that *Alepideleotris* equals *Eleotrica*.]
198. A new genus of gymnotid eels from the Peruvian Amazon. PBSW, vol. 49, pp. 115–116. August 22. [*Oedemognathus exodon*; also synonymizes *Tateichthys duidae* LaMonte with *Steatogenys elegans* (Steindachner).]
199. A new polynemid fish collected in the Sadong River, Sarawak, by Dr. William T. Hornaday, with notes on the genera of Polynemidae. Journal of the Washington Academy of Science, vol. 26, no. 9, pp. 376–382. September 15. [Revision of genera of Polynemidae.]
200. Report on the fishes collected by H. C. Raven in Lake Tanganyika in 1920. Proceedings of the United States National Museum, vol. 84, no. 2998, pp. 1–15, pl. 1. September 24.
201. Description of a new blennioid fish of the genus *Acanthemblemaria* from the Pacific coast of Panama. (G. S. Myers and Earl D. Reid.) Allan Hancock Pacific Expeditions, vol. 2, no. 2, pp. 7–10. December.
202. [Note on the identity of the dead fish in the Tidal Basin at Washington, D. C.] PBSW, vol. 49, p. viii. [Oral communication; no title. It concerned thousands of adults of *Opisthonema oglinum* floating dead in the Tidal Basin after thawing of the heavy ice in spring, 1936. This section of the Proceedings was published at the end of the year.]

1937

203. Notes on phallostethid fishes. Proceedings of the United States National Museum, vol. 84, no. 3007, pp. 134–143. January 6.
204. The deep-sea zeomorph fishes of the family Grammicolepidae. Proceedings of the United States National Museum, vol. 84, no. 3008, pp. 145–156, 3 pls. January 18.
205. [A] possible method of evolution of oral brooding habits in the cichlid fishes. AJ, vol. 10, no. 4, pp. 4–6. April. [Printer omitted the "A" in the title. Reprinted in facsimile, except for title, as 218. See also 223.]
206. A contribution to the ichthyology of the Malay Peninsula, Part II. Fresh-water fishes. (Albert W. C. T. Herre and George S. Myers.) Bull. Raffles Mus., Singapore, no. 13, pp. 53–75, pls. 5–7. August. [The first part of this paper, on marine fishes, and the general introduction, are by Herre alone, although the title page would lead one to think otherwise.]
207. [Review of] Monographs on the fishes of the Iberian Peninsula and Madeira. [Buen, F. de, Catálogo de los peces Ibéricos; Lozano Rey, L., Los peces fluviales de España; Nobre, A., Fauna marinha de Portugal, I, Vertebrados; Noronha, A. C. de,

and Sarmento, A. A., Os peixes dos mares do Madeira.] CO, 1937, no. 4, pp. 239–240. December 31.

208. [Review of] Three new Asiatic check lists [Suvatti, C., Index to fishes of Siam; Roxas, H. A., and Martin, C., A check list of Philippine fishes; Mori, T., and Uchida, K., A revised catalogue of the fishes of Korea]. CO, 1937, no. 4, pp. 241–242. December 31.

1938

209. [Review of] Hubbs, C. L., and Trautman, M. B., A revision of the lamprey genus *Ichthyomyzon*. CO, 1938, no. 1, p. 51. March 31.
210. Foreword. SIB, vol. 1, no. 1, pp. 1–2. June 22. [Explains editorial policy and aims of the Bulletin.]

*211. *Hydromantes platycephalus* in Sonora Pass, California. CO, 1938, no. 2, p. 91, June 30.

212. Notes on *Ansorgia*, *Clarisilurus*, *Wallago*, and *Ceratoglanis*, four genera of African and Indo-Malayan catfishes. CO, 1938, no. 2, p. 98. June 30. [See 322 for correction.]
213. Fresh-water fishes and West Indian zoogeography. Annual Report Smithsonian Institution for 1937, publication 3465, pp. 339–364, 3 pls. [volume appeared late in the summer of 1938.]
214. Studies on the genera of cyprinodont fishes. XIV. *Aplocheilichthys* and its relatives in Africa. CO, 1938, no. 3, pp. 136–143. September 24. [Numbers 32, 34, 37, 46, 70, 84, 117, 141, 145, 157, 178, 187, and 200 are taken to be the first 13 papers in this series.]
215. [Review of] Wells, L. A., Tropical aquariums, plants and fishes. CO, 1938, no. 3, p. 152. September 24.
216. Harvest of the sea. Stanford Illustrated Review, vol. 40, no. 2, pp. 20–21, 25–26. October. [Originally given as a radio address.]
217. [Review of] Costen, H. E. T., Beneath the surface, the cycle of river life. CO, 1938, no. 4, p. 208. December 10.

1939

218. A possible method of evolution of oral brooding habits in cichlid fishes. SIB, vol. 1, no. 3, pp. 85–87. February 3. [A reprint, in photographic facsimile except for the title, of 205. See also 223.]
219. Notes on the labrid genus *Lienardella*. SIB, vol. 1, no. 3, pp. 87–88. February 3.
220. On the Brazilian characid fish *Notropocharax difficilis* Marini, Nichols and La Monte. SIB, vol. 1, no. 3, p. 8. February 3.
221. [Review of] Norman, J. R., Discovery reports, coast fishes. CO, 1939, no. 1, p. 61. March 9.
222. A new owstoniid fish from deep water off the Philippines. PBSW, vol. 52, pp. 19–20. March 11.
223. Mouthbreeding in cichlid fishes. Aquarist and Pond-keeper, London, vol. 9, no. 3, pp. 90–91, 94. May. [Reprint of 205. See also 218.]
224. *Hesperomyrus fryi*, a new genus and species of echelid eels from California. (G. S. Myers and Margaret Hamilton Storey.) SIB, vol. 1, no. 4, pp. 156–159. May 24.
225. The possible identity of the Congo fish *Teleogramma* with the cichlid genus *Leptolamprologus*. SIB, vol. 1, no. 4, p. 160. May 24.

226. A living coelacanth fish. CO, 1939, no. 2, p. 124. July 12. [A note on the discovery of *Latimeria chalumnae* in South Africa, with references to accounts in popular magazines.]
227. [Review of] Watson, D. M. S., The acanthodian fishes. CO, 1939, no. 3, p. 178. September 9.
228. [Review of] Tchernavin, V., Changes in the salmon skull. CO, 1939, no. 3, p. 178. September 9.
229. [Obituary of Alipio de Miranda-Ribeiro, 1874–1939.] CO, 1939, no. 3, p. 184. September 9. [See also 535.]
230. [Review of] Moy-Thomas, J. A., Palaeozoic fishes. CO, 1939, no. 4, p. 239. December 26.
231. [Review of] Clements, F. E., and Shelford, V. E., Bio-ecology. (Lionel Albert Walford and G. S. Myers.) CO, 1939, no. 4, p. 240. December 26.

1940

232. Suppression of *Acaropsis* and *Chalcinus*, two preoccupied names of South American fresh-water fishes. SIB, vol. 1, no. 5, p. 170. February 7.
233. On the use of the generic name *Barbus* in ichthyology and ornithology. SIB, vol. 1, no. 5, p. 170. February 7. [Shows that "Barbus" of Cuvier is a plural vernacular term for a bird group, and does not preoccupy the fish name *Barbus*.]
234. Results of some recent studies on the American killifishes. SIB, vol. 1, no. 5, pp. 171–172. February 7. [A photographic facsimile of 46.]
235. Zoological nomenclature. Nature, London, vol. 145, no. 3668, pp. 264–265. February 17. [The word "many" in the MS. was misprinted "any" in fourth from last line of the last paragraph.]
236. [Review of] Neave, S. A., Nomenclator zoologicus. CO, 1939, no. 1, p. 56. March 30.
237. [Review of] Kuhne, E. R., A guide to the fishes of Tennessee and the mid-south. CO, 1939, no. 1, p. 58. March 30.
238. [Remarks on resolution regarding dams and migratory fishes.] SIB, vol. 1, no. 6, p. 209. May 3.
239. Cope as an ichthyologist. CO, 1940, no. 2, pp. 76–78, 1 pl. July 28. [In Edward Drinker Cope Centenary Number.]
240. A note on *Monognathus*. CO, 1940, no. 2, p. 141. July 28. [Selects a type species for *Monognathus* and proposes new genus *Phasmatostoma* for other species.]
241. The probable identity of *Sphyraena chrysotaenia* from the Red Sea and Arabia with *S. aureoflamma* from the Philippines, with notes on *Naso vomer* and *N. lopezi*. CO, 1940, no. 2, p. 143. July 28.
242. [Review of] Cutright, P. R., The great naturalists explore South America. CO, 1940, no. 2, p. 145. July 28.
243. The nomenclatural status of the Asiatic fish genus *Culter*. CO, 1940, no. 3, pp. 199–201. November 14. [See 516.]
244. A note on the status of the generic name *Corydoras*. SIB, vol. 2, no. 1, pp. 11–12. December 23. [Inserted as part of paper by William Gosline on the Callichthyidae.]
245. Suppression of some preoccupied generic names of fishes (*Kessleria*, *Entomolepis*, *Pterodiscus*, and *Nesiotes*), with a note on *Pterophyllum*. SIB, vol. 2, no. 1, pp. 33–36. December 23. [The cichlid generic name *Pterophyllum* is not preoccupied.]
246. An American cyprinodont fish, *Jordanella floridae*, reported from Borneo, with notes on the possible widespread introduction of foreign aquarium fishes. CO, 1940, no. 4,

pp. 267–268. December 27. [First warning of the now worldwide introductions of tropical freshwater aquarium fishes in warmer regions.]

247. The neotropical anchovies of the genus *Amplova*. Proceedings of the California Academy of Sciences, 4th ser., vol. 23, no. 29, pp. 437–442. December 31. [This paper, written in 1926, follows Eigenmann's system of giving total lengths (including caudal) of the specimens, but the length of the holotype of *Amplova alleni*, as given, is the standard length. The holotype was selected by Hildebrand from among what G.S.M. had intended to be syntypes of the species.]

1941

248. Suppression of *Lissochilus* in favor of *Acrossocheilus* for a genus of Asiatic cyprinid fishes, with notes on its classification. CO, 1941, no. 1, pp. 42–44. March 25.
249. [Review of] Huxley, J., The new systematics. CO, 1941, no. 1, p. 61. March 25.
250. The fish fauna of the Pacific Ocean, with especial reference to zoogeographical regions and distribution as they affect the international aspects of the fisheries. Proceedings, Sixth Pacific Science Congress, vol. 3, pp. 201–210. [Vol. 3 was issued in April 1941.]
251. The work and program of the Natural History Museum of Stanford University in fisheries and general ichthyology. Proceedings, Sixth Pacific Science Congress, vol. 3, pp. 413–415. April. [See note under 250.]
252. Four new genera and ten new species of eels from the Pacific coast of tropical America. (G. S. Myers and Charles Barkley Wade.) Allan Hancock Pacific Expeditions, vol. 9, no. 4, pp. 65–111, pls. 7–16. June 25.
253. [Review of] Schuchert, C., and Le Vene, C. M., O. C. Marsh, pioneer in paleontology. CO, 1941, no. 2, p. 121. July 8.
254. [Review of] Sherborn, C. D., Where is the———collection? An account of the various natural history collections which have come under the notice of the compiler. CO, 1941, no. 2, p. 122. July 8.

*255. [Review of] Fitch, H. S., A biogeographical study of the *ordinoides* Artenkreis of garter snakes (genus *Thamnophis*). CO, 1941, no. 2, pp. 122–123. July 8.

256. [Review of] Phillips, W. J., The fishes of New Zealand. CO, 1941, no. 3, p. 187. September 30.
257. [Review of] Berg, L. S., Classification of fishes, both recent and fossil. CO, 1941, no. 4, pp. 274–275. November 21.
258. [Review of] Hubbs, C. L., and Lagler, K. F., Guide to the fishes of the Great Lakes and tributary waters. CO, 1941, no. 4, p. 275. November 21.
259. [Review of] Parker, T. J., and Haswell, W. A., A text-book of zoology, 6th edition. CO, 1941, no. 4, pp. 275–276. November 21. [Comments on the decline of morphological zoology.]
260. [Review of] Norris, H. W., The plagiostome hypophysis, general morphology and types of structure. CO, 1941, no. 4, p. 277. November 21.
261. A new name for *Taenionema*, a genus of Amazonian siluroid fishes. SIB, vol. 2, no. 3, p. 88. November 27.

1942

262. *Stethaprion innesi* and *Mylossoma aureum*. TA, vol. 10, no. 11, pp. 185–186. March. [A slightly altered reprint of no. 142.]
263. [Review of] Longley, W. H., Systematic catalogue of the fishes of Tortugas, Florida,

with observations on color, habits, and local distribution. CO, 1942, no. 1, pp. 57–58. March 24. [Gives a history of Dr. Longley's submarine ichthyological researches.]

264. [Review of] Child, C. M., Patterns and problems of development. CO, 1942, no. 1, p. 58. March 24.

265. The Pacific American atherinid fishes of the genera *Eurystole*, *Nectarges*, *Coleotropis*, and *Melanorhinus*. (G. S. Myers and Charles Barkley Wade.) Allan Hancock Pacific Expeditions, vol. 9, no. 5, pp. 113–149, pls. 17–19. March 30.

*266. A new frog from the Anamallai Hills, with notes on other frogs and some snakes from South India. PBSW, vol. 55, pp. 49–55. June 25.

*267. A new frog of the genus *Micrixalus* from Travancore. PBSW, vol. 55, pp. 71–74. June 25.

*268. Notes on Pacific Coast *Triturus*. CO, 1942, no. 2, pp. 77–82. July 10.

269. [Review of] Beebe, W., Book of bays. CO, 1942, no. 2, p. 130. July 10.

269a. [Description of *Pimelodella peruana*.] (Carl H. Eigenmann and G. S. Myers.) *In*: Eigenmann, C. H., and Allen, W. R., Fishes of western South America (University of Kentucky, Lexington), p. 101, pl. 3. Summer of 1942.

270. Studies on South-American fresh-water fishes. I. SIB, vol. 2, no. 4, pp. 89–114. August 24.

271. The "lungs" of *Bothriolepis*. SIB, vol. 2, no. 4, pp. 134–136. August 24. [Virtually predicts existence of such an agnathan genus as *Jamoytius*.]

*272. The black toad of Deep Springs Valley, Inyo County, California. Occ. Pap. Mus. Zool. Univ. Michigan, no. 460, 13 pp., 3 pls. September 16.

*273. Neotropical lizards in the collection of the Natural History Museum of Stanford University. (Charles E. Burt and G. S. Myers.) Stanford Univ. Publ., Univ. Ser., Biol. Sci., vol. 8, no. 2, pp. 273–324, portrait. October 6.

*274. Notes on some frogs from Peru and Ecuador. PBSW, vol. 55, pp. 151–155. October 17.

275. [Review of] Marcgrave, J., Historia natural do Brasil. CO, 1942, no. 4, p. 269. December 28. [Portugese translation of Marcgrave.]

1943

276. The Myers Expedition. TA, vol. 11, no. 9, pp. 160–162. January. [Extracts from letter from G.S.M. to W. T. Innes on fishes of the Rio Japuhyba, near Angra dos Reis, State of Rio de Janeiro, Brazil. Figures are of aquarium fishes, supplied by editor.]

277. The influence of Louis Agassiz on the ichthyology of Brazil. Revista Brasileira de Biología, vol. 3, no. 1, pp. 127–133. March.

278. [Review of] Eigenmann, C. H., and Allen, W. R., Fishes of western South America. CO, 1943, no. 1, pp. 60–61. March 31. [Includes comments on the Gregory and Conrad classification of Characidae.]

*279. [Review of] Santos, E., Anfíbios e Répteis do Brasil. CO, 1943, no. 1, p. 60. March 31.

*280. Notes on *Rhyacotriton olympicus* and *Ascaphus truei* in Humboldt County, California. CO, 1943, no. 2, pp. 125–126. June 30.

281. George S. Myers reports. TA, vol. 12, no. 6, pp. 104–106. October. [Extracts from letter from G.S.M. to W. T. Innes on fishes in Minas Gerais, Brazil.]

*282. Rediscovery of the Philippine discoglossid frog, *Barbourula busuangensis*. CO, 1943, no. 3, pp. 148–150. October 15.

*283. The lizard names *Platyurus* and *Cosymbotus*. CO, 1943, no. 3, p. 192. October 15.

283a. Sistemática gerál de peixes e biología da pesca. Rio de Janeiro. 84 pp. [This is a compiled set of notes taken by several students during a course of lectures given by G.S.M. at the Museu Nacional in Rio de Janeiro, of which a large number of mimeographed copies were issued. The notes were not corrected by G.S.M. before mimeographing, and many errors are present.]

1944

284. Field notes on fishes of the vicinity of Rio de Janeiro. TA, Philadelphia, vol. 12, no. 11, pp. 185–186. March. [Figure supplied by editor.]
285. Field notes on fishes of the vicinity of Rio de Janeiro (concluded). TA, vol. 12, no. 12, pp. 204–206. April. [Figure supplied by editor.]
286. A new species of carangid fish from the northeastern Pacific. (Lionel Albert Walford and G. S. Myers.) CO, 1944, no. 1, pp. 44–47. April 21. [Equals *Trachurus symmetricus* (Ayres), large adults.]
*287. California records of the western spade-foot toad. CO, 1944, no. 1, p. 58. April 21.
288. *Rhinobrycon negrensis*, a new genus and species of characid fishes from the Rio Negro, Brazil. Proceedings of the California Academy of Sciences, ser. 4, vol. 23, no. 39, pp. 587–590. August 22.
289. The black-winged flying characin (*Carnegiella marthae* Myers). TA, vol. 13, no. 7, pp. 105–106. November. [A reprint of 159. See also 186.]
290. Two extraordinary new blind nematognath fishes from the Rio Negro, representing a new subfamily of the Pygidiidae, with a rearrangement of the genera of the family, and illustrations of some previously described genera and species from Venezuela and Brazil. Proceedings of the California Academy of Sciences, ser. 4, vol. 23, no. 40, pp. 591–602, pls. 52–56. November 7.
*291. Brazilian books of interest to ichthyologists and herpetologists. CO, 1944, no. 4, pp. 262–263. December 26.

1945

292. A new gurnard (*Prionotus alipionis*) from the coast of Brazil. (Gerard Warden Teague and G. S. Myers.) Boletim do Museu Nacional, Rio de Janeiro, n. s., zool., no. 31, 19 pp. January 24. [Teague wanted to describe this fish although G.S.M. was doubtful.]
293. A remarkable new genus of sexually dimorphic characid fishes from the Rio Paraguay Basin in Matto Grosso. (G. S. Myers and Paulo de Miranda-Ribeiro.) Boletim do Museu Nacional, Rio de Janeiro, n. s., zool., no. 32, 8 pp. January 25.
*294. Possible introduction of Argentine toads into Florida. CO, 1945, no. 1, p. 44. March 31.
295. The habitat of *Hyphessobrycon flammeus* Myers. FC, vol. 24, no. 10, pp. 73–75. June.
*296. A natural habitat of the house gecko (*Hemidactylus mabouia*) in Brazil. CO, 1945, no. 2, p. 120. June 30.
*297. Notes on some new or little-known Brazilian amphibians, with an examination of the history of the Plata salamander, *Ensatina platensis*. (G. S. Myers and Antenor Leitão de Carvalho.) Boletim do Museu Nacional, Rio de Janeiro, n. s., zool., no. 35, 39 pp. August 25. [Original printed date of issue not correct.]
*298. A third record of the Sonoran box turtle. CO, 1945, no. 3, p. 172. October 15.
*299. A strange new leaf-nosed lizard of the genus *Anolis* from Amazonia. (G. S. Myers and Antenor Leitão de Carvalho.) Boletim do Museu Nacional, Rio de Janeiro, n. s., zool., no. 43, 22 pp. October 20.
*300. Nocturnal observations on sea-snakes in Bahia Honda, Panama. Herpetologica, vol. 3, no. 1, pp. 22–23. November 23.

1946

*301. Lista provisória dos anfíbios do Distrito Federál, Brasil. Boletim do Museu Nacional, Rio de Janeiro, n. s., zool., no. 55, 36 pp. February 14. [Written in August 1944. Text in both Portugese and English.]

302. The introduction of the guppy (*Lebistes*) as an aquarium fish, and something on the origin of its name. TA, vol. 15, no. 3, pp. 46–48. March.

303. On a recently proposed new family of deep-sea fishes (Barbourisiidae, Parr, 1945). CO, 1946, no. 1, pp. 41–42. April 30. [This and 290 both discuss absence of pelvic fins as a taxonomic character.]

304. Occurrence of uranoscopid fishes of the western Pacific genus *Gnathagnus* in the American Atlantic fauna. CO, 1946, no. 1, p. 42. April 30.

305. [Review of] Honig, P., and Verdoorn, F., editors, Science and scientists in the Netherlands Indies. CO, 1946, no. 1, p. 52. April 30.

306. New fishes of the families Dactyloscopidae, Microdesmidae, and Antennariidae from the west coast of Mexico and the Galapagos Islands with a brief account of the use of rotenone fish poisons in ichthyological collecting. (G. S. Myers and Charles Barkley Wade.) Allan Hancock Pacific Expeditions, vol. 9, no. 6, pp. 151–179 (pls. 20–23 included). December 16.

1947

307. The Amazon and its fishes. Part 1. The river. AJ, vol. 18, no. 3, pp. 4–9. March 3.

*308. Murray's Reptiles of Sind, with a note on three forgotten descriptions of Indian sea-snakes, published therein. Herpetologica, vol. 3, no. 5, pp. 167–168. [The book mentioned is not Murray's Vertebrate Zoology of Sind.]

309. The Amazon and its fishes. Part 2. The fishes. AJ, vol. 18, no. 4, pp. 13–20. April 1.

310. [Review of] Smith, H. M., The fresh-water fishes of Siam, or Thailand. CO, 1947, no. 1, p. 69. April 20.

311. [Review of] Hildebrand, S. F., A descriptive catalog of the shore fishes of Peru. CO, 1947, no. 1, p. 69. April 20.

312. [Review of] Romer, A. S., Vertebrate paleontology. CO, 1947, no. 1, p. 70. April 20.

313. [Review of] Woods, R. S., The naturalist's lexicon. CO, 1947, no. 1, pp. 70–71. April 20.

314. The Amazon and its fishes. Part 3. Amazonian aquarium fishes. AJ, vol. 18, no. 5, pp. 6–13, 32. May 1.

315. The varieties of the Siamese fighting fish. AJ, vol. 18, no. 6, pp. 19–21. June 2.

316. The Amazon and its fishes. Part 4. The fish in its environment. AJ, vol. 18, no. 7, pp. 8–19, 34. July.

317. [Review of] Seale, A., Quest for the golden cloak. CO, 1947, no. 3, p. 213. September 12.

318. Foreign introduction of North American fishes—Inadvisability of recommending North American fishes without careful appraisal of foreign fishes and ecology. Progressive Fish Culturist, Washington, D.C., vol. 9, no. 4, pp. 177–180. October.

1948

319. The ramirezi cichlid identified. (G. S. Myers and Robert Rees Harry, Jr.) TA, vol. 17, no. 4, p. 7. April. [This constitutes the original diagnosis of *Apistogramma ramirezi*; this species probably belongs to *Geophagus*.]

320. [Review of] Hubbs, C. L., and Lagler, K. F., Fishes of the Great Lakes Region. CO, 1948, no. 2, p. 150. June 30.

321. *Apistogramma ramirezi*, a cichlid fish from Venezuela. (G. S. Myers and R. R. Harry, Jr.) Proceedings of the California Zoological Club, vol. 1, no. 1, pp. 1–8. August. [See 319.]

322. Notes on two generic names of Indo-Malayan silurid fishes, *Wallago* and *Wallagonia*. Proceedings of the California Zoological Club, vol. 1, no. 4, pp. 19–20. August. [Correction of 212.]

*323. The California plethodont salamander, *Aneides flavipunctatus* (Strauch), with description of a new subspecies and notes on other western aneides. (G. S. Myers and Thomas Paul Maslin.) PBSW, vol. 61, pp. 127–135. September 3.

*324. Proposed reprinting of Boulenger's British Museum herpetological catalogues. Herpetologica, vol. 4, part 5, p. 180. September 13. [See also 325 and 352.]

*325. Proposed reprinting of Boulenger's British Museum herpetological catalogues. CO, 1948, no. 3, p. 229. [See also 324 and 352.]

326. A list of common and scientific names of the better known fishes of the United States and Canada. (W. H. Chute, R. M. Bailey, W. A. Clemens, J. R. Dymond, S. F. Hildebrand, G. S. Myers and L. P. Schultz.) American Fisheries Society, Special Publication no. 1, 45 pp.

327. [*Fundulus* in the West Indies.] *In*: Rivas, L. R., Cyprinodont fishes of the genus *Fundulus* in the West Indies (Proceedings of the United States National Museum, vol. 98, no. 3229, pp. 215–222), pp. 216–217. October 19. [Letter from G.S.M.]

1949

328. The Amazon and its fishes. Part 5. A monograph on the piranha [first part]. AJ, vol. 20, no. 2, pp. 52–61. February. [See 331.]

*329. Geographic variation in the ribbed frog, *Ascaphus truei*. (M. B. Mittleman and G. S. Myers.) PBSW, vol. 62, pp. 57–66. April 27. [Little save introduction is by G.S.M.]

*330. A new frog of the genus *Cornufer* from the Solomon Islands, with notes on the endemic nature of the Fijian frog fauna. (Walter Creighton Brown and G. S. Myers.) AMN, no. 1418, 10 pp. May 9.

331. The Amazon and its fishes. Part 5. A monograph on the piranha (concluded). AJ, vol. 20, no. 3, pp. 76–85. [Published May 31, although issue is for March; see 328.]

332. Cichlid fishes in salt water. AJ, vol. 20, no. 6, pp. 147–149, 163. June.

333. Usage of anadromous, catadromous, and allied terms for migratory fishes. CO, 1949, no. 2, pp. 89–97. June 30.

334. Salt-tolerance of fresh-water fish groups in relation to zoogeographical problems. Bijdragen tot de Dierkunde, vol. 28, pp. 315–322. August. [*In* Festschrift for L. L. de Beaufort.]

335. The family name of the characid fishes. CO, 1949, no. 3, pp. 195–204. September 15.

336. Initial steps in the conservation of fresh-water fisheries in tropical South America, with remarks on fishery resources in general. Inter-American Conference on Conservation of Renewable Natural Resources, held at Denver, Colorado, Sept. 7–20, 1948, pp. 501–506. October. [Proof not seen by author; references confused by editors. Published by the Department of State, Washington, D. C., October 1949.]

*337. A new frog of the genus *Batrachylodes* from the Solomon Islands. (Walter Creighton Brown and G. S. Myers.) Journal of the Washington Academy of Sciences, vol. 39, no. 11, pp. 379–380. November 15.

*338. Status of the generic name *Lioheterodon* applied to Madagascan serpents. Herpetologica, vol. 5, part 6, p. 146. December 15. [Text confused by printer; proof not seen by author; correctly reprinted as 341.]

1950

339. Systematic notes on some Amazonian clupeid fishes of the genus *Ilisha*. CO, 1950, no. 1, pp. 63–64. March 30.

340. On the characid fishes called *Hydrocynus* and *Hydrocyon* by Cuvier. Proceedings of the California Zoological Club, vol. 1, no. 9, pp. 45–47. May 1.

*341. Status of the generic name *Lioheterodon* applied to Madagascan serpents. Herpetologica, vol. 6, part 2, p. 52. June 5. [No. 338, corrected.]

*342. Manual of tropical herpetological collecting. 12 pp., mimeographed. Natural History Museum, Stanford University. June 15.

343. Bibliography of the published papers of George Sprague Myers from 1920 to 1949 inclusive. 18 pp., mimeographed. June 15.

344. Identity of the stromateid fish *Centrolophus californicus* with *Icichthys lockingtoni*. SIB, vol. 3, no. 4, p. 181. August 21.

345. Supplementary notes on the flying characid fishes, especially *Carnegiella*. SIB, vol. 3, no. 4, pp. 182–183. August 21.

346. Studies on South American fresh-water fishes. II. The genera of anostomine characids. SIB, vol. 3, no. 4, pp. 184–198. August 21.

347. A new lump-sucker of the genus *Eumicrotremus* from the northwestern Atlantic. (G. S. Myers and James Erwin Böhlke.) SIB, vol. 3, no. 4, pp. 199–202. August 21.

348. Station records of the Crocker-Stanford Deep-sea Expedition, Coast of California, September 1938. (Rolf Ling Bolin and G. S. Myers.) SIB, vol. 3, no. 4, pp. 203–214. August 21.

349. The "imitator catfish" which mimics a corydoras. (William Thornton Innes and G. S. Myers.) TA, vol. 19, no. 9, pp. 222–223. September 1. [See 366.]

*350. The systematic status of *Hyla septentrionalis*, the large tree frog of the Florida Keys, the Bahamas and Cuba. CO, 1950, no. 3, pp. 203–214. September 5. [See also 447b.]

*351. [Review of] Bourret, R., Les batraciens de l'Indochine. CO, 1950, no. 3, pp. 243–244. September 5.

*352. Proposed reprinting of Boulenger's herpetological catalogues. CO, 1950, no. 3, p. 244. September 5. [See also 324 and 325.]

353. A new genus of poeciliid fishes from Hispaniola, with notes on genera allied to *Poecilia* and *Mollienisia*. (Luis Rene Rivas and George S. Myers.) CO, 1950, no. 4, pp. 288–294. I plate. December 22.

354. Flying of the halfbeak, euleptorhamphus. CO, 1950, no. 4, p. 320. December 22.

*355. [Review of] Liu, C. C., Amphibians of western China. CO, 1950, no. 4, p. 325. December 22.

356. [Statement regarding A.S.I.H. Committee on Fish Classification.] CO, 1950, no. 4, p. 327. December 22.

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*357. Notes on salamander voices. CO, 1951, no. 1, p. 76. March 21.

358. [Review of] Hatch, M. H., editor, Studies honoring Trevor Kincaid. CO, 1951, no. 1, pp. 104–105. March 21.

359. [Review of] Tortonese, E., Gli animali superiori nella loro struttura e nella loro vita. CO, 1951, no. 1, p. 106. March 21.
360. Study of fishes was the work David Starr Jordan loved best. Stanford Alumni Review, vol. 52, no. 7, pp. 13–15. March 27.
361. The Amazonian mottled knife-fish, *Steatogenys elegans*, and its strange vermiform organ. TA, vol. 20, no. 4, pp. 85–86. April 10.
362. The Amazonian checkerboard cichlid (*Crenicara maculata*). TA, vol. 20, no. 5, pp. 109–110. May 1. [See 367.]
363. Notas sobre la distribución de los peces Sudamericanos del grupo Bivibranchia. Memórias Sociedad de Ciéncias Naturales La Salle, Caracas, tomo 10, no. 27 (for Sept.–Dec. 1950), pp. 193–194. [Published in late Spring, 1951.]
*364. The most widely heard amphibian voice. CO, 1951, no. 2, p. 179. June 8. [Voice of *Hyla regilla* in Hollywood sound-cinema.]
*365. Asiatic giant salamander caught in the Sacramento River, and an exotic skink near San Francisco. CO, 1951, no. 2, pp. 179–180. June 8.
366. The "imitator catfish" which mimics a corydoras. (William Thornton Innes and G. S. Myers.) *In*: Innes, W. T. (editor), Aquarium Highlights, consisting of reprints of the most popular articles from the monthly magazine, the *Aquarium*, since 1932 (Innes Publishing Co., Philadelphia, 519 pp.), pp. 117–118. October. [Reprint of 349.]
367. Amazon dwarf checkerboard cichlid. *In*: Innes, W. T. (editor), Aquarium Highlights (see 366 for full reference), pp. 120–121. October. [Reprint of 362.]
368. Dangers in identifications. *In*: Innes, W. T. (editor), Aquarium Highlights (see 366 for full reference), pp. 366–371. October. [Reprint of 139.]
369. Judging fish shows. *In*: Innes, W. T. (editor), Aquarium Highlights (see 366 for full reference), pp. 410–413. October. [Reprint of 169.]
370. David Starr Jordan, ichthyologist, 1851–1931. SIB, vol. 4, no. 1, pp. 2–6. December 27.
371. Fresh-water fishes and East Indian zoogeography. SIB, vol. 4, no. 1, pp. 11–21. December 27. [See 483.]
372. Some forgotten but available names for Indian fishes. SIB, vol. 4, no. 1, p. 26. December 27.
*373. A new giant toad from Southwestern Colombia. (G. S. Myers and John W. Funkhouser.) Zoologica, New York, vol. 36, pt. 4, pp. 279–281, 1 pl. December 28. [*Bufo blombergi*, n. sp.]

1952

374. Tower of Babel. [Editorial.] CO, 1952, no. 1, pp. 57–58. June 2.
375. [Obituary of] William G. Holbein. AJ, vol. 23, no. 6, pp. 118–119. June 12.
376. *Danio* or *Brachydanio*, *Barbus* or *Puntius*? AJ, vol. 23, no. 6, pp. 121–122. June 12. [Vol. number erroneously given as 24 on the issue.]
377. [Review of] Axelrod, H. R., Tropical fish as a hobby. CO, 1952, no. 2, pp. 120–121. June 26.
378. [Review of] Ladiges, W., Der Fisch in der Landschaft. CO, 1952, no. 2, p. 121. June 26.
379. [Review of] Steward, J. H., Handbook of South American Indians. Vol. 6. CO, 1952, no. 2, pp. 121–122. June 26.
380. [Review of] Carter, G. S., Animal evolution, a study of recent views on its causes. CO, 1952, no. 2, p. 122. June 26.

381. [Review of] Kuenen, P. K., Marine geology. CO, 1952, no. 2, p. 122. June 26.

382. [Review of] Suwatti, C., Fauna of Thailand. CO, 1952, no. 2, pp. 122–123. June 26.

383. [Review of] Primer Congresso Nacionál de Pesquerías Marítimas y Indústrias Derivadas. CO, 1952, no. 2, p. 123. June 26.

384. [Review of] Soljan, T., Fauna et Flora Adriatica, vol. 1, Pisces. CO, 1952, no. 2, p. 123. June 26.

*385. [Review of] Stebbins, R. C., Amphibians of Western North America. CO, 1952, no. 2, pp. 123–124. June 26.

386. [Obituary of] Chloe Leslie Starks. CO, 1952, no. 2, pp. 124–125. June 26. [America's most able fish illustrator.]

*387. A new dwarf toad from southeastern Brazil. (G. S. Myers and Antenor Leitão de Carvalho.) Zoologica, New York, vol. 37, no. 1, pp. 1–3. June 30. [*Bufo pygmaeus*, n. sp.]

388. Annual fishes. AJ, vol. 23, no. 7, pp. 125–141. July 11.

389. [Obituary of] Louis L. Mowbray. AJ, vol. 23, no. 7, p. 141. July 11.

389a. On the problem of the status of names published by Scopoli in 1777 in his "Introductio ad Historiam Naturalem." Bulletin of Zoological Nomenclature, vol. 6, pt. 8, p. 255. July 23. [Reprinted in: Opinions and Declarations, vol. 9, pt. 23, p. 316.]

390. Bibliography of the published papers of George Sprague Myers from 1920 to 1951, inclusive. 20 pp., mimeographed. [Dated May 1951; issued during July 1952.]

391. [Review of] Gohm, D., Tropical fish in the home. AJ, vol. 23, no. 8, pp. 152–153. August 7.

*392. [Review of] Carr, A., Handbook of turtles. AJ, vol. 23, no. 8, p. 153. August 7.

393. Hints to fish importers, no. 1. AJ, vol. 23, no. 8, pp. 156–157. August 7.

394. [Obituary of] Johann Paul Arnold, 1868–1952. AJ, vol. 23, no. 9, pp. 169–170. August 20.

395. Hints to fish importers, no. 2. AJ, vol. 23, no. 9, pp. 171–173. August 28. [Lake Tanganyika; helped initiate the reports of Tanganyikan aquarium fishes.]

396. A note on the feathertail, an African characin (*Phenacogrammus*). AJ, vol. 23, no. 9, p. 173. August 28.

397. [Review of] Hervey, G. F., and Hems, J., Freshwater tropical aquarium fishes. AJ, vol. 23, no. 9, pp. 174–177. August 23.

398. The nature of systematic biology and of a species description. Systematic Zoology, vol. 1, pp. 106–111. September.

399. Easiest of all to spawn and raise, the medaka. AJ, vol. 23, no. 10, pp. 189–194. September 30. [Care, spawning, and raising *Oryzias latipes*.]

400. Varieties of the three-spot gourami, *Trichogaster trichopterus*. AJ, vol. 23, no. 10, pp. 198–200. September 30.

401. [Review of] Beck, P., Traité complét de la vie des animaux en aquarium. AJ, vol. 23, no. 10, p. 200. September 30.

402. Amazonian tetras of the genus *Thayeria*. AJ, vol. 23, no. 10, pp. 206–207. September 30. [Species here called T. sanctae-mariae later described as *T. boehlkei* Weitzman. See also 429.]

403. How the shooting apparatus of the archer fish was discovered. AJ, vol. 23, no. 10, pp. 210–214. September 30.

404. Hints to fish importers, no. 3. AJ, vol. 23, no. 10, pp. 215–216. September 30. [Burmese fishes.]

405. A new Amazonian catfish for the aquarist. AJ, vol. 23, no. 11, pp. 224–225. October 31. [*Corydoras elegans*.]

406. Color schemes in your fishes. AJ, vol. 23, no. 11, pp. 228–230. October 31.
407. Hints to fish importers, no. 4. AJ, vol. 23, no. 11, pp. 237–238. October 31. [Hispaniola.]
408. [Review of] Ladiges, W., Der Fisch in der Landschaft. AJ, vol. 23, no. 11, p. 239. October 31.
409. [Review of] Tropical Fish Hobbyist. AJ, vol. 23, no. 11, pp. 239–240. October 31.
410. *Corydoras elegans.* TA, Philadelphia, vol. 21, no. 11, pp. 300–301. November.
411. [Review of] L'Aquarium Exotique. AJ, vol. 23, no. 12, pp. 254–255. December 1.
412. [Review of] Wendt, A., Die Aquarienpflanzen in Wort und Bild. AJ, vol. 23, no. 12, p. 255. December 1.
413. [Review of] Holly, M., Meinken, H., and Rachow, A., Die Aquarienfische in Wort und Bild. AJ, vol. 23, no. 12, p. 255. December 1.
414. [Review of] Lorenz, K., King Solomon's ring. AJ, vol. 23, no. 12, p. 256. December 1.
415. Hints to fish importers, no. 5. AJ, vol. 23, no. 12, p. 256. December 1. [*Fundulus stellifer.*]
416. [Obituary of] Dr. Ernst Bade. AJ, vol. 23, no. 12, p. 264. December 1.
417. [Review of] Innes, W. T., Exotic aquarium fishes, 15th edition. AJ, vol. 24, no. 1, p. 9. December 19.
418. The miniature fish aquarium. AJ, vol. 24, no. 1, pp. 11–12. December 19.
419. Hints to fish importers, no. 6. AJ, vol. 24, no. 1, p. 20. December 19. [Sierra Leone; *Epiplatys annulatus.*]
420. Sharks and sawfishes in the Amazon. CO, 1952, no. 4, pp. 268–269. December 26.
421. [Review of] Deraniyagala, P. E. P., A colored atlas of some vertebrates from Ceylon. CO, 1952, no. 4, p. 286. December 26.

1953

422. Spawning behavior of *Polycentrus.* AJ, vol. 24, no. 2, pp. 31–33. January 28.
423. Hints to fish importers, no. 7. AJ, vol. 24, no. 2, pp. 33–34. January 28. [*Chologaster.*]
*424. [Review of] Knight, M., Keeping reptiles and fishes. AJ, vol. 24, no. 2, p. 46. January 28.
425. [Review of] Whitney, L. F., All about guppies. AJ, vol. 24, no. 3, p. 55. February.
426. [Aquarium water-testers, filters, oil traps, and thermostatic heaters.] AJ, vol. 24, no. 3, pp. 60–61. February 23.
427. Hints to fish importers, no. 8. Two beautiful little characins (*Nematobrycon*) from western Colombia and their peculiar distribution. AJ, vol. 24, no. 3, pp. 64–65. February 23. [This initiated importation of the "Emperor tetra" as an aquarium fish.]
428. The living-fossil coelacanth fishes. AJ, vol. 24, no. 3, pp. 66–68. February 23.
429. Vinkeltetrornas vetenskapliga nanm. Akvariet (Organ för Sveriges Akvarieföreningar), Argang 27, no. 3, pp. 42–44. March. [See also 402.]
430. Queens of the water. AJ, vol. 24, no. 4, pp. 75–78. March 30. [An essay on water-lilies: *Nuphar*, *Nelumbo*, *Nymphaea*, *Victoria*, and *Euryale.*]
431. Pets. [Verse.] AJ, vol. 24, p. 78. March 30.
432. Hints to fish importers, no. 9. AJ, vol. 24, no. 5, p. 112. April 29. [*Moenkhausia costae.*]
433. [Review of] Whitney, L. F., The complete book of home pet care. AJ, vol. 24, no. 5, p. 119. April 29.
434. [Review of] Knowles, F. G. W., Freshwater and saltwater aquaria. AJ, vol. 24, no. 5, p. 119. April 29.

435. [Review of] Ladiges, W., Zierfisch Bilderbuch. AJ, vol. 24, no. 5, p. 119. April 29.
436. [Review of] Kramer, K., and Weise, H., Aquarienkunde. AJ, vol. 24, no. 5, pp. 119–120. April 29.
437. The coelacanth fishes—living fossils. TA, vol. 22, no. 5, pp. 145–146. May. [Figure erroneously labeled.]
438. Aquarium difficulties with black mollienesias. AJ, vol. 24, no. 6, pp. 125–129. May 29. [This paper was later reprinted at least twice in the same journal, but references are not at hand.]
439. Hints to fish importers, no. 10. A strange glandulocaudine characin from the Rio das Velhas (*Hysteronotus*). AJ, vol. 24, no. 6, p. 137. May 29.
*440. [Review of] Leutscher, A., Vivarium life. AJ, vol. 24, no. 6, p. 141–142. May 29.
441. [Review of] Evans, A., Aquariums. AJ, vol. 24, no. 6, p. 142. May 29.
442. [Review of] Ichthys. AJ, vol. 24, no. 7, p. 157. June 29.
443. [Review of] Tropical fish handbook-catalog. AJ, vol. 24, no. 7, pp. 157–158. June 29.
444. [Review of] Taschenkalender für Aquarien und Terrarienfreunde, 1953. AJ, vol. 24, no. 7, p. 158. June 29.
445. [Review of] Rounsefell, G. A., and Everhart, W. H., Fishery science; its methods and applications. AJ, vol. 24, no. 7, p. 158. June 29.
446. [Review of] New Zealand Aquatic World. AJ, vol. 24, no. 7, p. 158. June 29.
447. Hints to fish importers, no. 11. Glass catfishes. AJ, vol. 24, no. 7, pp. 161–162. June 29. [*Kryptopterus*, *Ailiichthys*, *Parailia*, *Physailia*, *Pseudepapterus*. Evolutionary convergence in 3 families of catfishes.]
447a. [Quotation from letter regarding retention of original spellings of zoological names.] Bulletin of Zoological Nomenclature, vol. 10, pt. 7, p. 216. July 14.
*447b. [On the acceptance of certain names originally published in synonymy, especially *Eleutherodactylus* and *Hyla septentrionalis*.] Bulletin of Zoological Nomenclature, vol. 10, pts. 10–11, p. 312. July 24.
448. *Piabucus* in the aquarium. AJ, vol. 24, no. 8, pp. 172–174. July 28. [Identification of live examples of *Piabucus* and similar genera.]
449. Unbanded color variety of the Malayan "coolie" loach, *Acanthophthalmus semicinctus*. AJ, vol. 24, no. 8, p. 174. July 28.
450. The Florida pigmy topminnow, *Leptolucania ommata*, its history, and a record of the first California breeding. AJ, vol. 24, no. 8, pp. 184–187. July 28.
451. On aquarium magazines. [Editorial.] AJ, vol. 24, no. 8, pp. 188–189. July 29.
452. The Cuban green glass fish, *Atherina evermanni*. AJ, vol. 24, no. 9, pp. 195–197. September. [For correction of name to *Alepidomus evermanni*, see same journal, vol. 24, no. 11, p. 170.]
453. Why show standards for most tropical fishes are unwise. AJ, vol. 24, no. 9, pp. 200–202. September.
454. Publication dates of the Aquarium Journal. [In 1952–1953.] AJ, vol. 24, no. 9, p. 202. September.
455. Hints to fish importers, no. 12. *Rivulus ornatus*. AJ, vol. 24, no. 9, p. 208. September.
456. Neon tetra. AJ, vol. 24, no. 9, pp. 210–211. September.
457. [Obituary of] Floyd S. Young. AJ, vol. 24, no. 9, pp. 211–212. September.
458. What's wrong with aquarists? Tropical Fish Tales, Springfield, Mass., vol. 2, no. 4, pp. 6–7. September.
459. Zebra danio. AJ, vol. 24, no. 10, pp. 230–231. October. [*Brachydanio rerio*.]

460. Classification of the danios. AJ, vol. 24, no. 10, pp. 235–238. October. [Critical taxonomic evaluation of four genera, *Danio*, *Daniops*, *Allodanio*, *Brachydanio*. See also 513a.]
461. Where, oh where do the pictures come from? [Editorial.] AJ, vol. 24, no. 10, pp. 242–243. October.
462. Hints to fish importers, no. 13. *Rivulus zygonectes*. AJ, vol. 24, no. 10, p. 244. October.
463. Notes on selecting an aquarium. AJ, vol. 24, no. 11, pp. 254–256. November.
464. [Review of] Innes, W. T., Exotic aquarium fishes, 16th Edition. AJ, vol. 24, no. 11, p. 258. November.
465. Serpa tetra. AJ, vol. 24, no. 11, pp. 264–265. November. [*Hyphessobrycon callistus.*]
466. Hints to fish importers, no. 14. *Garmanella pulchra*. AJ, vol. 24, no. 11, p. 266. November.
467. A note on the habits and classification of *Corydoras hastatus*. AJ, vol. 24, no. 11, pp. 268–270. November. [Subgenus *Microcorydoras.*]
468. The Christmas-tree fish. [Fantasy.] AJ, vol. 24, no. 12, p. 280. December.
469. The secrets of the German fish breeders. [Editorial.] AJ, vol. 24, no. 12, pp. 287–288. December.
470. Hints to fish importers, no. 15. *Barbus candens*. AJ, vol. 24, no. 12, p. 296. December.
471. Habits of the spotted knife-fish (*Steatogenys elegans*) in the aquarium. AJ, vol. 24, no. 12, pp. 297–298. December.

1954

472. Hints to fish importers, no. 16. A fish that hasn't been discovered yet. AJ, vol. 25, no. 1, p. 5. January. [Predicts the occurrence of a relative of *Cubanichthys* and *Chriopeopoides* in Hispaniola.]
473. [Review of] Todd, R., The tropical fish book. AJ, vol. 25, no. 1, p. 7. January.
474. Siamese fighting fish. AJ, vol. 25, no. 2, pp. 27–29. February.
475. The fighting fish and its history. AJ, vol. 25, no. 2, pp. 30–33. February. [*Betta splendens.*]
476. Hints to fish importers, no. 17. AJ, vol. 25, no. 2, p. 39. February. [Wild stock of *Betta splendens.*]
477. [Review of] Emmens, C. W., Keeping and breeding aquarium fishes. AJ, vol. 25, no. 2, pp. 45–46. February.
478. Fifty years of devotion to the aquarium hobby. TA, vol. 23, no. 2, pp. 35–39. February. [Tribute to William Thornton Innes, on his 80th birthday.]
479. Protective coloration in the leaf fish and *Thayeria*. AJ, vol. 25, no. 3, pp. 62–63. March.
480. [Review of] Roberts, J. B., Jr., The pet shop manual. AJ, vol. 25, no. 3, pp. 77–78. March.
481. [Review of] The Tropical Fish Magazine. AJ, vol. 25, no. 3, p. 78. March.
*482. Ability of amphibians to cross sea barriers, with especial reference to Pacific zoogeography. Proceedings 7th Pacific Science Congress [New Zealand, February 1949], vol. 4 (zoology), pp. 19–27. [Dated 1953; published March 1954.]
483. Paleogeographical significance of fresh-water fish distribution in the Pacific. Proceedings 7th Pacific Science Congress [New Zealand, February 1949], vol. 4 (zoology), pp. 38–48. [When printing of the Proceedings had already been delayed for nearly three years, the present paper was printed in the United States as 371. Vol. 4 of the Proceedings finally was published (dated 1953) in March 1954.]
484. The protection of rare and vanishing fishes. Proceedings 7th Pacific Science Congress

[New Zealand, February 1949], vol. 4 (zoology), pp. 691–694. [Dated 1953; published March 1954. Aside from the Australian lungfish, this represents the first plea for the conservation of non-food, non-game fishes.]

485. Blue gularis [*Aphyosemion caeruleum.*] AJ, vol. 25, no. 4, pp. 87–88. April.

486. How to preserve fish specimens for study. AJ, vol. 25, no. 4, pp. 89–90. April.

487. Another new corydoras from Brazil. (G. S. Myers and Stanley Howard Weitzman.) AJ, vol. 25, no. 4, pp. 93–94. April. [*Corydoras cochui*, n. sp.]

488. Hints to fish importers, no. 18. AJ, vol. 25, no. 4, p. 102. April. [*Poecilocharax bovallii.*]

489. A new corydoras. (G. S. Myers and William Thornton Innes.) TA, vol. 23, no. 4, p. 105. April. [*Corydoras cochui* Myers and Weitzman. See 487 for original description.]

489a. [Supplementary note.] Opinions and Declarations rendered by the International Commission on Zoological Nomenclature, vol. 4, pt. 15, p. 167. April 21. [Concerns *Raphistoma versus* Belone.]

490. Hints to fish importers, no. 19. An unknown characin from the Cerro Duida, Venezuela. AJ, vol. 25, no. 5, pp. 111–112. May. [A lost and still undescribed relative of *Poecilocharax.*]

491. The Amazon longfin, *Pterolebias longipinnis.* (Fritz Mayer and G. S. Myers.) AJ, vol. 25, no. 5, pp. 113–115. May.

492. [Review of] Fisher, E. L., Marine tropicals. AJ, vol. 25, no. 5, pp. 126–128. May.

493. [Review of] La vita nell 'acquario. Manuale catalogo dell 'Acquario di Bologna. AJ, vol. 25, no. 5, p. 128. May.

494. The black-banded sunfish. AJ, vol. 25, no. 6, pp. 133–134. June. [*Mesogonistius chaetodon.*]

495. The name of the Indian glassfish (*Chanda lala*). AJ, vol. 25, no. 6, pp. 149–150. June.

496. The kissing gourami. AJ, vol. 25, no. 7, pp. 155–156. July. [*Helostoma temminckii.*]

497. A new cyprinodont fish from the Peruvian Amazon. AJ, vol. 25, no. 8, pp. 175–177. July 28. [*Pterolebias peruensis*, n. sp.]

498. [Review of] Nachstedt, J., and Tusche, H., Breeding aquarium fishes. AJ, vol. 25, no. 8, p. 183. July 28.

499. A beautiful new cyprinodont fish from the Amazon. TA, vol. 23, no. 8, pp. 236–237. August. [*Pterolebias peruensis*; see 497 for original description.]

500. The life and times of *Polycentrus* and the leaf-fish tribe. Tropical Fish Magazine, Springfield, Mass., vol. 4, no. 2, pp. 6–7. October. [Suggests possible relationship between Nandidae, *Datnioides*, and *Lobotes.*]

501. What fish is that? Tropical Fish Magazine, Springfield, Mass., vol. 4, no. 3, pp. 8–9. November.

1955

501a. Notes on the freshwater fish fauna of middle Central America, with especial reference to pond culture of Tilapia. Fish Papers, FAO, Rome, no. 2. 1955. [Pagination and exact date lacking; warns of dangers in Tilapia introductions.]

501b. [Limericks] *In*: Martin, H. R. (editor), The little limerick book (Peter Pauper Press, Mt. Vernon, N. Y., 62 pp.). 1955.

502. Notes on the classification and names of cyprinodont fishes. Tropical Fish Magazine, Springfield, Mass., vol. 4, no. 7, p. 7. March 1. [Includes diagnoses of *Pantanodon podoxys* Myers, n. g., n. sp., and *Potamophylax pygmaeus* Myers and Carvalho, n. gen., n. sp. Proof not seen by author. There are a few editorial and printer's errors.]

503. English names of aquarium cichlids. Tropical Fish Magazine, Springfield, Mass., vol. 4, no. 7, pp. 8–9. March 1. [On p. 9, two columns of print are transposed.]

504. The wonderful world under the sea. Part 1. Tropical Fish Magazine, Springfield, Mass., vol. 4, no. 8, pp. 8–9. April.

505. Gambusinos—a new term proposed for "live-bearing toothcarps." TA, vol. 24, no. 5, pp. 149–152. May.

506. The wonderful world under the sea. Part 2. Tropical Fish Magazine, Springfield, Mass., vol. 4, no. 9, pp. 11, 14. May.

1956

*507. Manual of tropical herpetological collecting. Ed. 2. Natural History Museum of Stanford University, Circular no. 4, 13 pp. [Mimeographed; very limited edition; second edition of 342.]

*508. Brief directions for preserving and shipping specimens of fishes, amphibians and reptiles. Natural History Museum of Stanford University, Circular no. 5, 3 pp. [Mimeographed; very limited edition.]

509. [Comments on Axelrod, H., and Schultz, L. P., Handbook of tropical fishes.] TA, vol. 25, no. 2, pp. 60–61. February. [Quotes from letter from G. S. Myers.]

510. Two new Brazilian fresh-water fishes. (G. S. Myers and Stanley Howard Weitzman.) SIB, vol. 7, no. 1, pp. 1–4. February 21. [*Hyphessobrycon cardinalis* and *Hassar praelongus*. *H. cardinalis* was also described by Schultz as *Cheirodon axelrodi*, in a publication bearing the printed date February 20.]

511. The name of the South American clupeid fish, *Pristigaster*. CO, 1956, no. 1, pp. 63–64. February 29.

*512. [Review of] Cochran, D. M., Frogs of southeastern Brazil. CO, 1956, no. 1, p. 69. February 29.

*513. Zoological results of the California Himalayan Expedition to Makalu, Eastern Nepal. I. Amphibians and Reptiles. (Alan E. Leviton, G. S. Myers, and Lawrence W. Swan.) Occasional Papers of the Natural History Museum of Stanford University, no. 1, 18 pp. March 9.

513a. Classification des danios. L'Aquarium et les Poissons, Paris, 6me Année, no. 4, pp. 5–8. April. [Translation of 460.]

514. Note on guppies in Mexico. TA, vol. 25, no. 4, p. 123. April

515. Studies on the fishes of the family Characidae. No. 11. A new genus and species of hemiodontins from the Rio Orinoco in Venezuela. (James Erwin Böhlke and G. S. Myers.) Notulae Naturae, Philadelphia, no. 286, 6 pp. May 23.

516. Request for a ruling as to the species to be accepted as the type species of the genera Culter and Nasus Basilewsky, 1855 (class Pisces). Bulletin of Zoological Nomenclature, vol. 12, pp. 136–138. July. [Francis Hemming, Secretary of the I.C.Z.N., reworded 243, added certain requests to it, and published it under the name of G. S. Myers. Reprinted in: Opinions and Declarations, 1958, vol. 18, pt. 17, pp. 294–297.]

517. The Xenurobryconini, a group of minute South American characid fishes with teeth outside the mouth. (G. S. Myers and James Erwin Böhlke.) SIB, vol. 7, no. 2, pp. 6–12. August 30.

518. *Copella*, a new genus of pyrrhulinin characid fishes. SIB, vol. 7, no. 2, pp. 12–13. August 30.

519. *Esomus rehi*, an Indo-Malayan cyprinid fish. SIB, vol. 7, no. 2, pp. 13–14. August 30. [*Pogonocharax rehi* Regan, described as from "Argentina."]

520. A note on an Abyssinian catfish, *Clarias depressus* Myers. SIB, vol. 7, no. 2, p. 14. August 30. [See 45.]

521. Curatorial practices in zoological research collections. 2. System followed in filing specimens of Recent fishes in the Natural History Museum of Stanford University. (G. S. Myers and Margaret Hamilton Storey.) Natural History Museum of Stanford University, Circular no. 6, 44 pp. October. [Mimeographed; very small edition.]

1957

522. Exotic aquarium fishes—a work of general reference. By William Thornton Innes. 19th Edition, revised, enlarged, and edited by G. S. Myers. Innes Publishing Company, Philadelphia; 541 pp., colored frontispiece, 90 colored figs., 366 black and white figs., 7 maps, 2 maps on linings. [All previous 18 editions of this book were also revised by G.S.M. before publication, but only in this edition was editorial responsibility formally assumed. Previous editions are not listed in this bibliography.]

1958

523. [Four world maps, showing extent of reef coral, current knowledge of species occurrence of marine fishes, current knowledge of habits of marine food fishes, and the species composition of marine food-fish faunas.] *In*: Walford, L. A., Living resources of the sea—opportunities for research and expansion (New York, Ronald Press Co., xvi + 231 pp.), figs. 16–19, with discussions on pp. 246, 248, and 250. [Original maps and discussions by G.S.M. Other research for this book was also done by G.S.M.]

524. Trends in the evolution of teleostean fishes. SIB, vol. 7, no. 3, pp. 27–30. July 31. [Paper presented before Society for the Study of Evolution, August 1957.]

525. Nomenclator of certain terms used for higher categories of fishes. SIB, vol. 7, no. 3, pp. 31–40. July 31.

526. The priacanthid fish genus *Pristigenys*. SIB, vol. 7, no. 3, pp. 40–42. July 31.

1959

527. The endemic fish-fauna of Lake Lanao and the evolution of higher categories. Proceedings XVth International Congress of Zoology (London, 1958), pp. 151–152. [Abstract of 537.]

528. A remarkable new genus of anostomin characid fishes from the upper Rio Xingú in central Brazil. (G. S. Myers and Antenor Leitão de Carvalho.) CO, 1959, no. 2, pp. 148–152. July 24. [*Sartor respectus*, n. gen., n. sp.]

529. A Caribbean chaetodont fish, *Chaetodon eques* Steindachner, now referred to *Chaetodon aya* Jordan. CO, 1959, no. 2, p. 158. July 24.

530. [Review of] Simpson, G. G., and Roe, A., Behavior and evolution. CO, 1959, no. 3, pp. 270–271. October 9.

1960

531. Restriction of the croakers (Sciaenidae) and anchovies (Engraulidae) to continental waters. CO, 1960, no. 1, pp. 67–68. March 25.

*532. Phylax telescopus. CO, 1960, no. 1, pp. 75–78. March 25. [A column of comment, criticism, and review dealing not only with ichthyology and herpetology but also broader subjects.]

533. [Review of] Whitley, P. G., and Allen, J., The sea-horse and its relatives. CO, 1960, p. 78. March 25.

534. [Review of] Poll, M., Les genres des poissons d'eau douce de l'Afrique. CO, 1960, no. 1, pp. 78–79. March 25.

*535. Phylax telescopus, II. CO, 1960, no. 2, pp. 157–159. June 29. [Darwin; ideas versus data; the eel problem; Alipio de Miranda-Ribeiro, etc. In footnote, for Freund read Freud.]

536. [Review of] McInerny, D., and Girard, G., All about tropical fish. CO, 1960, no. 2, p. 162. June 29.

537. The endemic fish fauna of Lake Lanao, and the evolution of higher taxonomic categories. Evolution, vol. 14, no. 3, pp. 323–333. September. [Proof not seen by author; p. 328, paragraph 2, for biotypes read biotopes; p. 330, delete entire sentence containing word "Triglopsis." See also 527 for abstract; also 591 for reprintings.]

538. Fish evolution in Lake Nyasa. Evolution, vol. 14, no. 3, pp. 394–396. September. [Diversity of freshwater fish faunas of the world, etc.]

539. Some reflections on phylogenetic and typological taxonomy. Systematic Zoology, vol. 9, no. 1, pp. 37–41. [March 1960; published September 1960.]

*540. Phylax telescopus, III. CO, 1960, no. 3, pp. 263–266. September 26. [On borrowing specimens; electric fishes; frog phylogeny, etc.]

541. [Review of] Poll, M., Expedition océanographique Belge . . . l'Atlantic sud. Poissons. CO, 1960, no. 3, pp. 267–268. September 26.

542. [Review of] Parr, A. E., Mostly about museums. CO, 1960, no. 3, p. 268. September 26.

543. [Obituary of] Margaret Hamilton Storey (1900–1960). SIB, vol. 7, no. 4, p. 62a. October 27. [See 557 for another obituary of M.H.S.]

544. A new zeomorph fish of the family Oreosomatidae from the coast of California, with notes on the family. SIB, vol. 7, no. 4, pp. 89–98. October 27.

545. Two new fishes collected by General Thomas D. White in eastern Colombia. (G. S. Myers and Stanley Howard Weitzman.) SIB, vol. 7, no. 4, pp. 98–109. October 27.

546. The mormyrid genera *Hippopotamyrus* and *Cyphomyrus*. SIB, vol. 7, no. 4, pp. 123–125. October 27.

547. The genera and ecological geography of the South American banjo catfishes, family Aspredinidae. SIB, vol. 7, no. 4, pp. 132–139. October 27.

548. A Brazilian pike-characid, *Boulengerella lateristriga*, rediscovered in the Rio Negro. (G. S. Myers and Stanley Howard Weitzman.) SIB, vol. 7, no. 4, pp. 201–205. October 27.

549. The South American characid genera *Exodon*, *Gnathoplax*, and *Roeboexodon*, with notes on the ecology and taxonomy of characid fishes. SIB, vol. 7, no. 4, pp. 206–211. October 27.

550. Preface to any future classification of the cyprinid fishes of the genus *Barbus*. SIB, vol. 7, no. 4, pp. 212–215. October 27.

551. A forgotten account of a fresh-water belonid fish from northern India. SIB, vol. 7, no. 4, pp. 345–346. October 27.

552. The names of the South American catfish genera *Conorhynchos* and *Diplomystes*. SIB, vol. 7, no. 4, pp. 246–248. October 27. [See errata on p. 62b of same issue. *Conorhynchos* misspelled in three places on p. 247.]

*553. Phylax telescopus, IV. CO, 1960, no. 4, pp. 373–377. December 30. [Oceanography and the neglect of biological collecting; European centers; *Denticeps*, etc.]

1961

*554. Phylax telescopus, V. CO, 1961, no. 1, pp. 117–120. March 17. [Conservationists neglect fishes; a new living perch from Europe; etc.]

*555. The South American hylid frog names *Sphaenorhynchus*, *Dryomelictes*, and *Sphoenohyla*. (G. S. Myers and Alan Edward Leviton.) Herpetologica, vol. 17, pp. 61–62. April 15.

*556. Phylax telescopus, VI. CO, 1961, no. 2, pp. 244–247. June 19. [Fishery biology and management; European museums, etc. Proof not seen by author; for Wandsee read Wansee.]

557. [Obituary of] Margaret Hamilton Storey (1900–1960). CO, 1961, no. 2, pp. 261–263. June 19. [Not the same as 543.]

*558. Generic type species citation in taxonomic zoology. A guide for students. Natural History Museum of Stanford University, Circular no. 8, 7 pp. August. [Mimeographed, very small edition. Also reproduced later by U.S. Bureau of Commercial Fisheries Ichthyological Laboratory, U.S. National Museum, Washington, D.C.]

*559. The New Zealand lizard names *Naultinus* and *Hoplodactylus*. Herpetologica, vol. 17, no. 3, pp. 169–172. October 9.

1962

*560. The American leptodactylid frog genera *Eleutherodactylus*, *Hylodes* (= *Elosia*), and *Caudiverbera* (= *Calyptocephalus*). CO, 1962, no. 1, pp. 195–202. April 11. [Suako 447b.]

561. Statement regarding the argument of W. I. Follett and Daniel M. Cohen concerning the type species of the genus *Bathylagus*. Bulletin of Zoological Nomenclature, vol. 19, pp. 130–131. May 28. [Dealing principally with the type designations of Jordan and Evermann.]

*562. The Hong Kong newt described as a new species. (G. S. Myers and Alan Edward Leviton.) Occasional Papers, Division of Systematic Biology [formerly Natural History Museum], Stanford University, no. 10, 4 pp. June 15.

*563. Generic classification of the high-altitude pelobatid toads of Asia (*Scutiger*, *Aelurophryne*, and *Oreolalax*). (G. S. Myers and Alan Edward Leviton.) CO, 1962, no. 2, pp. 287–291. July 20.

1963

564. Killifish identification. American Killifish Association, Killie Notes, Vol. 2, no. 2, pp. 7–10. March.

565. Fresh-water fishes. Pacific Discovery, San Francisco, vol. 16, no. 4, pp. 36–39. July. [Freshwater fishes of the world, general facts, diversity, sizes, distribution, conservation.]

566. Comments on the proposed rejection of the type designations of Jordan and Evermann 1896–1900 and 1896. Bulletin of Zoological Nomenclature, vol. 20, part 4, p. 259. July 12. [See also 561.]

567. The fresh-water fauna of North America. Proceedings, XVI International Congress of Zoology, vol. 4, pp. 15–20. August. [Only abstracts were published in this volume.

The paper as delivered at the Congress was much longer and argued in favor of continental drift.]

568. Foreward. *In*: Jordan, D. S., The genera of fishes and a classification of fishes (reprint; Stanford University Press; xvi + 800 pp.), pp. vii – xvi. December 30. [Sets these two important works in perspective, gives considerable historical information on zoological nomenclature and fish classification, and warns against misuse of the Jordan papers.]

1964

*569. An electrophoretic survey of rattlesnake venoms. (Alan E. Leviton, G. S. Myers, and B. W. Grunbaum.) *In*: Leone, C. A. (editor), Taxonomic biochemistry and serology (New York; Ronald Press: x + 728 pp.), pp. 667–671. [On the basis of the venoms of 10 species, relations similar to those shown by morphology were found.]

570. A brief sketch of the history of ichthyology in America to the year 1850. CO, 1964, no. 1, pp. 33–40. March 26.

571. Foreward. *In*: Albert W. Herre (1868–1962): a brief autobiography (Division of Systematic Biology, Stanford University, Circular no. 10, 20 pp.), pp. 1–2. March.

572. Bumblebee catfishes (*Plotosus*). TFH, vol. 13, no. 3, pp. 5–7, 75. November. [They are black-and-yellow, they buzz, they swarm, and they sting.]

1965

573. *Gambusia*, the fish destroyer. TFH, vol. 13, no. 5, pp. 31–32, 53–54. January. [First indictment of *Gambusia affinis*, the mosquitofish, as a serious danger to other fishes, small and large, wherever introduced. See also 575.]

574. The body-wag, an innate behavioral characteristic of bony fishes. TFH, vol. 13, no. 9, pp. 21, 24–25. May.

575. *Gambusia*, the fish destroyer. Australian Zoologist, vol. 13, no. 2, p. 102. August. [Partial reprint of 573, with editorial note about Australian introductions.]

576. Races of the Chinese paradise fish (*Macropodus*). TFH, vol. 14, no. 1, pp. 48–49. [Continuation of taxonomic revision begun in 137. Southernmost race in Indochina is *M. opercularis concolor* Ahl. Adds *Polyacanthus yangye* Dabry 1872 to synonymy of *M. chinensis*.]

1966

577. Foreword [to first issue]. Ichthyologica, the Aquarium Journal [continuation of AJ], vol. 37, no. 1, pp. 3–5. January. [G.S.M. resigned as editor after this issue appeared.]

578. How to become an ichthyologist. Part 1. TFH, vol. 14, no. 8, pp. 47, 50–51. April. [See 580, 581, 583. Advice for young prospective ichthyologists.]

579. Phyletic studies of teleostean fishes, with a provisional classification of living forms. (P. Humphry Greenwood, Donn Eric Rosen, Stanley Howard Weitzman, and G. S. Myers.) Bulletin of the American Museum of Natural History, vol. 131, art. 4, pp. 339–446, pls. 21–23. April 18.

580. How to become an ichthyologist. Part 2. TFH, vol. 14, no. 9, pp. 47, 50–51. May. [See also 578, 581, 583.]

581. How to become an ichthyologist. Part 3. TFH, vol. 14, no. 10, pp. 28–30. June. [See also 578, 580, 583.]

582. Two remarkable new trichomycterid catfishes from the Amazon basin in Brazil and Colombia. (G. S. Myers and Stanley Howard Weitzman.) Journal of Zoology [continuation of the Proceedings of the Zoological Society of London], vol. 149, pp. 277–287. July.
583. How to become an ichthyologist. Part 4. TFH, vol. 14, no. 2, pp. 29–31. August. [See also 578, 580, 581.]
584. Megalomycteridae, a previously unrecognized family of deep-sea cetomimiform fishes based on two new genera from the North Atlantic. (G. S. Myers and Warren Curtis Freihofer.) SIB, vol. 8, no. 3, pp. 193–206. October 7.
585. Derivation of the freshwater fish fauna of Central America. CO, 1966, no. 4, pp. 766–773. December 23. [Paper read before the American Society of Ichthyologists and Herpetologists in June 1964.]

1967

586. [Review of] Breder, C. M., and Rosen, D. E., Modes of reproduction in fishes. Natural History, N.Y., vol. 76, no. 2, pp. 66–67. February. [Suggests possibly primitive nature of nesting and parental care in bony fishes and notes its widespread occurrence.]
587. Note on the name of a Guatemalan cactus, *Mammillaria voburnensis* Scheer. Cactus and Succulent Journal of America, vol. 39, no. 4, p. 153. July.
588. Zoogeographical evidence of the age of the South Atlantic Ocean. Studies in Tropical Oceanography, no. 5 (Miami, xx + 847 pp.), pp. 614–621. October 1. [Paper read at International Conference on Tropical Oceanography, Miami, two years previously.]
589. Named main divisions of teleostean fishes. (P. Humphry Greenwood, G. S. Myers, Donn Eric Rosen, and Stanley Howard Weitzman.) PBSW, vol. 80, pp. 227–228. December 1.
590. Note on the dentition of *Creagrudite maxillaris*, a characid fish from the upper Orinoco-upper Rio Negro system. (G. S. Myers and Tyson Royal Roberts.) SIB, vol. 8, no. 4, pp. 248–249. December 5.

1969

591. The endemic fish fauna of Lake Lanao, and the evolution of higher taxonomic categories. *In*: Ehrlich, P. R., Holm, R. W., and Raven, P. H. (editors), Papers on evolution (Boston, Little Brown and Co., xii + 564 pp.), pp. 247–261. [Reprint of 537, with corrections.]
592. [Review of] Harden Jones, F. R., Fish migration. CO, 1969, no. 2, pp. 409–411. June 3.
593. Peace! It's wonderful! [Allegory.] Palo Alto Times, Thursday, November 27, 1969, p. 26. [Based on a true story.]
594. The endemic fish fauna of Lake Lanao, and the evolution of higher taxonomic categories. *In*: Laetsch, Watson M., the biological perspective (Boston; Little, Brown and Co., xii + 574 pp.), pp. 351–365. [There were two reprints of this paper during 1969, this being the second. See also 591. Both are reprints of 537.]

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A NEW SPECIES OF THE DORADID CATFISH GENUS *LEPTODORAS*, WITH COMMENTS ON RELATED FORMS

By

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Abstract: *Leptodoras myersi* is described from a trawl haul made in Rio Amazonas near Iquitos, Peru. *Leptodoras juruensis*, previously known only from the holotype taken in Rio Jurua, Brasil, is recorded from the same haul.

It was originally intended that this be a revision of the genus *Leptodoras* but at the last moment it became apparent that the species *L. linnelli* is a composite that will require further study. Also, in Eigenmann's (1925) review of the Doradidae, the related genera *Opsodoras*, *Hassar*, and *Leptodoras* are perhaps the least well defined and thus require more attention. At present, I describe as new a well-marked species and comment on its relatives.

The newly recorded specimens of *Leptodoras myersi* and *L. juruensis* were collected on the 1955 Catherwood Foundation Peruvian-Amazon Expedition by Charles C. G. Chaplin and Ruth Patrick of the Academy's staff. They were taken with an otter trawl from the Amazonas (Marañon) between Isla Iquitos and Isla Lapuna. Only one downstream haul was made, because of the swiftness of the current and the many snags in the bottom, but this caught a fascinating group of mostly new and rare catfishes plus one specimen of *Rhytiodus microlepis* Kner. This suggests that more bottom sampling should be attempted in the large South American rivers.

For the loan of important specimens, I thank P. H. Greenwood of the British Museum (Natural History) and W. I. Follett of the California Academy of Sciences.

METHODS

The *standard length* measurement was made with some difficulty but, by flexing the caudal fin and using reflected light, I believe fairly good accuracy was achieved. The *head length* includes the fleshy opercular flap. The *eye* and *snout* measurements involve the eyeball proper. The *predorsal* measurement, *length of dorsal spine*, and *depth at dorsal-fin origin* all have as one terminus the anterior groove of the small bony element at the base of the spine. The anterior end of the adipose dorsal-fin base is somewhat difficult to define, but measurements involving it are more easily duplicated in this species than in *L. acipenserinus* for example. The *greatest width of the peduncle* is at the posterior end of the anal-fin base and includes the lateral spines that jut out from the body. The *length of the pectoral spine* is measured basally from the notch, where a needle-point fits in snugly, and not from the extreme base of the spine. *Ventral-fin length* is the greatest length of the fin, not of an individual ray. The *greatest head width* is of the bony portion and not of the rather indifferent fleshy portion posteriorly. The *greatest scute depth* is a vertical measurement of the area covered by scutes, rather than the diagonal measurement of an individual scute.

The *anal-ray* counts are separated into anterior unbranched, small roman numerals, and posterior branched, arabic numerals; the last anal ray sometimes is simple, sometimes consists of two rays united at their bases, but in either case is counted as one. The *lateral scutes* are all of those in the main lateral series, including the ones on the caudal-fin base but not the small ones in the humeral region, the tympanum.

Leptodoras myersi Böhlke, new species.

Diagnosis. This is an elongate, long-snouted species like *L. acipenserinus*, *L. linnelli*, and *L. juruensis*. Its dark color markings, particularly the broad nuchal band, are distinctive. Lateral scutes few, 36 or 37, each scute bearing few points. Total anal-fin rays few, 13 or 14 (except see discussion of *L. linnelli* below). Lacking extremely elongate first dorsal spine of *L. juruensis*. While anterior base of adipose dorsal fin is not sharply defined, it does not extend far forward as a fleshy ridge. Dorsal and pectoral spines with small hooks or spines along their anterior and posterior margins, these weakest on the dorsal spine and strongest on the posterior margins of the pectoral spines. Nuchal foramen

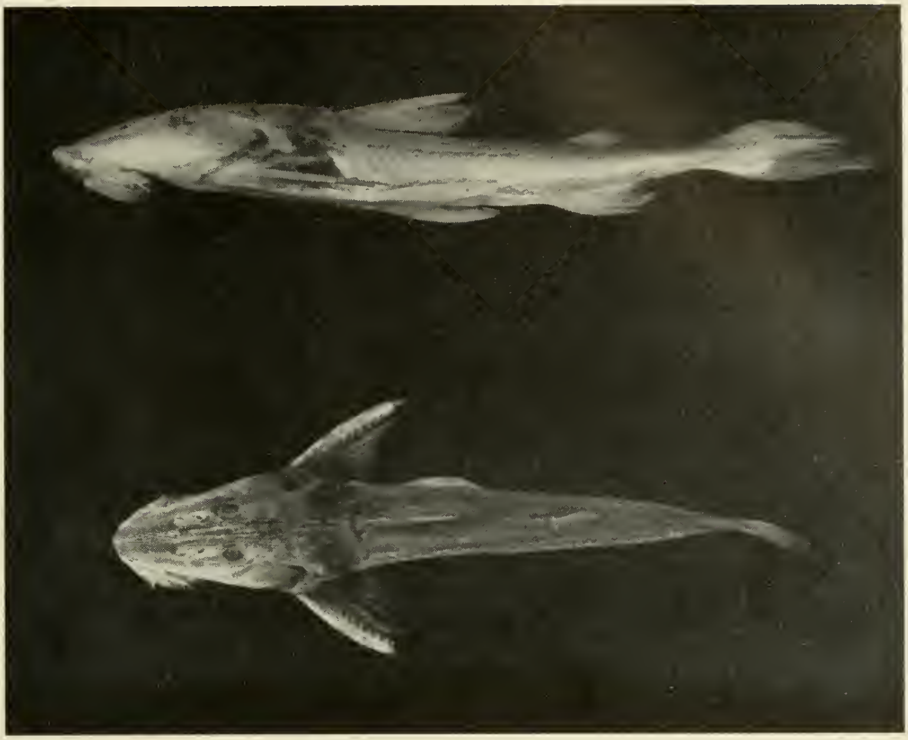

Figure 1. *Leptodoras myersi*: Holotype, 74.6 mm. standard length, ANSP 112318.

present. Head covered by small, elongate, pale fleshy ridges, arranged in a pattern (see fig. 1).

Description. The body shape and dark color markings are shown on the photographs (fig. 1). Selected measurements and counts made on a series of 10 specimens appear in table 1.

Dorsal rays I, 6. Total anal rays 13 or 14, nearly always 14. Pectoral rays I, 9 or I, 10, usually I, 10. Ventral rays i, 6/i, 6. Principal caudal rays i, 15, i, the ventral unbranched ray counted not extending back to the tip of the lobe as does the dorsal one. Number of lateral scutes 36 or 37 in equal numbers. Anterior dorsal serrae 7 to 12, posterior dorsal serrae 6 to 11, anterior pectoral serrae 19 to 23, and posterior pectoral serrae 12 to 15; the numbers of serrae apparently are not related to the length of the fish, at least within the limited size range examined.

No teeth present. Nostrils both with raised margins, that of the rear nostril lowest posteroventrally. Anterior nostril nearer eye than tip of snout. Distance between the two nostrils on one side equal to that between posterior nostril and

Table 1. Leptodoras myersi: *Measurements in percent of standard length and several counts of the holotype (*) and nine paratypes.*

Standard length (mm.)	60.7	67.3	68.5	68.5	68.8	69.4	74.6*	74.8	76.6	77.6
Head length	35.2	34.5	34.2	34.7	35.6	34.6	33.9	33.3	33.4	34.9
Snout length	19.8	18.9	19.4	19.6	20.3	19.3	19.3	18.8	18.5	19.8
Eye width	04.6	04.6	04.2	04.4	04.1	04.2	04.0	04.3	04.3	04.2
Eye height	03.0	03.0	02.9	03.1	02.8	02.9	02.8	02.8	02.9	03.0
Bony interorbital	04.1	04.2	04.2	04.2	04.2	04.0	04.2	03.9	03.8	04.2
Predorsal distance	41.8	40.9	40.5	41.0	41.7	40.9	40.3	39.4	39.9	40.8
Dorsal fin to adipose origin	22.6	23.2	22.6	22.5	24.4	22.5	21.4	22.7	22.6	23.8
Greatest peduncle width	08.1	07.4	07.6	07.9	08.3	07.5	08.2	07.6	08.1	07.7
Least peduncle depth	03.9	03.7	03.8	03.9	03.9	03.6	03.6	03.6	03.6	03.6
Dorsal spine length	18.0	19.5	19.8	16.8	19.2	19.2	19.0	19.0	17.2	20.0
Pectoral spine length	22.4	21.5	23.1	21.9	23.4	21.3	21.6	22.9	21.4	21.8
Ventral-fin length	20.1	19.5	19.4	18.8	18.7	17.9	18.0	19.1	18.7	17.6
Greatest head width	19.1	18.3	18.8	17.4	18.0	18.4	18.2	18.0	17.4	19.1
Preventral-fin distance	46.1	45.3	45.4	45.8	46.1	45.5	45.8	44.8	45.2	45.2
Preanal-fin distance	69.8	68.6	69.9	70.2	69.3	69.6	70.4	69.0	68.1	67.8
Depth at dorsal-fin origin	13.2	13.2	13.3	13.1	13.7	12.7	12.5	12.6	12.9	13.5
Greatest scute band depth	04.6	04.4	04.2	04.2	04.5	04.6	04.7	04.4	04.6	04.5
Anal-fin rays	v,8[1]	v,9[2]	v,9[2]	vi,8[2]	v,9[2]	v,9[2]	v,9[2]	vi,8[1]	v,9[2]	v,9[1]
Pectoral-fin rays	I,10/I,10	I,10/I,10	I,10/I,10	I,10/I,9	I,10/I,10	I,9/I,9	I,10/I,10	I,10/I,10	I,10/I,10	I,10/I,10
Lateral scutes	36	36	37	37	36	37	37	37	36	36

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[1] Last ray consisting of two elements united at their bases.

[2] Last ray simple.

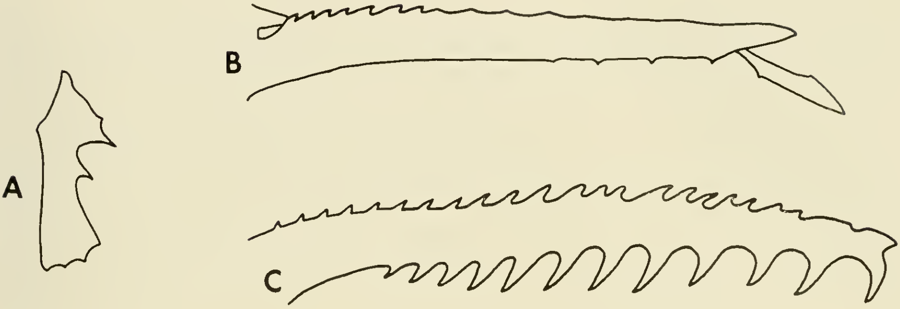

Figure 2. *Leptodoras myersi*: Paratype, 63.3 mm. standard length, ANSP 112320. A, outline of sixth lateral scute on left side of fish (central ridge not indicated), 3.1 mm. in longest dimension; B, dorsal spine with break-away tip, main spine 11.5 mm.; C, right pectoral spine, 14.2 mm.

eye. Eyes distinctly horizontally elongate. Horizontal width of eye equal to least width of bony interorbit, or nearly so.

The middorsal fontanel is long and narrow, extending from just behind a line drawn between the rear margins of the posterior nostrils to one drawn between the rear margins of the eyes. A middorsal groove extends in front of the fontanel on the snout and posteriorly from the fontanel to the dorsal-fin origin. Gill membranes connected to isthmus ventrally, the ventral ends of the two gill openings separated by a space of slightly more than the least interorbital width. Gill rakers low fleshy bumps. Two maxillary and 4 mental barbels present, all interconnected to form a hood of considerable size when spread. Each maxillary barbel is divided, its outer portion with barblets along its outer margin; these barblets are in two series, the upper ones short and numerous, the lower ones long and fewer in number. The outer portion of the maxillary barbel usually fails to reach the ventral end of the gill opening but may just attain that level. The inner portion of the maxillary barbel forms the lateral margin of an extensive fleshy lobe that connects the maxillary with the outer mental barbel; this lobe has short barblets around its margin. The mental barbels are studded with short barblets all around. The maxillary is ossified to the extent of about one-third the length of the outer division of the barbel. Branchiostegal rays 7. Upper end of gill opening just behind lower end of upper third of dark opercular spot shown on figure 1.

On the dorsal spine, the anterior serrae are longer than the posterior; the anterior ones are crowded and overlapping, especially basally, are directed toward the spine tip, and are distributed along less than the basal half of the spine. The posterior serrae are short, widely spaced, their tips directed perpendicular to the main axis of the spine or slightly inclined either basally or distally; when their tips are angled, the outer serrae are tilted basally and the lower serrae are tilted distally. On one individual the uppermost serration is directed distally. The posterior serrae extend along the distal one-half to three-quarters of the spine. There is a distinct ossified break-away tip on the spine when intact, this tip fitting into a median groove in the spine proper; the dorsal spine outlined in figure 2 shows this tip nearly completely disengaged.

On the pectoral spines the anterior serrae are shorter than the posterior, are directed toward the spine tips, and the distalmost one counted forms the tip of each spine (not the case in several related species in which the spine tips are rounded or blunt and without projections). The posterior serrations are strong hooks, their tips directed toward the bases of the spines. There are pointed fleshy extensions beyond the ossified spine tips, indicating that there probably are no ossified break-away segments as on the dorsal spine of this species and the pectoral spines of *L. juruensis* (the latter will be discussed and figured in a subsequent paper when the status of *L. linnelli* also will be treated). Pectoral spines, when depressed, extending back well beyond the ventral-fin bases. A single pectoral pore present on each side.

Tips of ventral fins rounded, not extending back to the anal-fin origin. Anal and genital papillae placed between the ventral fins, at or slightly before mid-fin. Adipose dorsal fin well developed, short-based, its origin above points varying between the base of the sixth to the interspace between the seventh and eighth anal rays. Caudal fin distinctly forked, the lower lobe the longer. On the single stained individual there are 18 procurrent caudal rays above and 17 below the principal rays.

In the humeral region there is a sharp spine on the posterior margin of the supraclavicle followed, across the center of the tympanum, by 3 narrow, elongate, mostly embedded ossifications. The first of the three is longest and has a rise in the middle that appears as a low hump externally; the second is completely embedded or with only a minute portion exposed; the third is shortest and bears a sharp projecting spine at its posterior end. The pointed coracoid processes extend posteriorly beyond the base of the last pectoral ray, but not as far back as do the humeral processes; the last-mentioned are shallowly convex dorsally and terminate in a narrowly rounded tip. There is a horizontally elongate nuchal foramen on each side.

The lateral series of scutes begins behind the tip of the humeral process and continues out onto the caudal fin basally. The scute outlined in figure 2 is much like those just before and after it (the outline does not indicate the median longitudinal ridge and the sharp outward angulation of the median spine itself); proceeding posteriorly the scutes become increasingly wider, less deep, less angular, and more overlapping. The terminal ossification in the series is a narrow, elongate, tubular element that lacks a spine and usually is overlooked on unstained specimens. This was not included in the counts of scutes recorded in this paper; apparently it also was not counted by Eigenmann (1925: 358), for I obtained the same count as he did on the same specimen of *L. acipenserinus*, omitting this element.

The pattern of coloration in alcohol is shown in figure 1; however, the broad nuchal band is more definitely continuous across the dorsum than is suggested on the dorsal view, and the dark opercular margin frequently is more intense and continues farther ventrally. A faint dusky stripe is present on the upper half of the lower caudal-fin lobe, and sometimes there is an even fainter one on the lower half of the upper lobe. The dorsum is dusky between the dorsal fin and caudal-fin base. The top of the head is dusky before the nostrils and in a roughly circular middorsal patch immediately behind the eyes. The basal half or more of the pectoral fin exclusive of the spine (except sometimes the membrane encasing the posterior serrae) usually is distinctly dark, sometimes only dusky and the extent of the dusky area variously more reduced than shown in the figure.

Relationships. The elongate, long-snouted species *L. acipenserinus, L. linnelli* (both types if they represent more than one species) and *L. juruensis* are most closely related to *L. myersi. Leptodoras juruensis* is the most distinctive and most spectacular looking member of this group, with its extremely elongate anterior dorsal-fin element and distinctive black color markings (see fig. 3); it also has more lateral scutes than the others: 44 to 46 in *L. juruensis*, 42 in *L. acipenserinus*, 38 or 39 in the *L. linnelli* complex, and 36 or 37 in *L. myersi. Leptodoras juruensis* is distinctive in certain proportions, but these will be treated later. *Leptodoras myersi* has a lower anal-fin ray count than other species of *Leptodoras* excepting, evidently, the Guianan (typical) population of the *L. linnelli* complex. Eigenmann (1912: 192), in his original description of *L. linnelli,* gave an anal-ray count of 12 to 14; the specimen (ANSP 39734) from Rio Rupununi recorded by Fowler (1914: 264) has 12 rays. *Leptodoras myersi* has 13 or 14 rays, *L. acipenserinus* has 17 rays (16 recorded for the holotype by Günther 1868: 230), *L. juruensis* has 16 or 17 rays, and the Peruvian specimens nearest *L. linnelli* have 15 to 17 rays.

In the size range represented by the Peruvian material, the shapes of the lateral scutes are most similar in *L. myersi* and *L. juruensis*, those of *L. acipenserinus* and nominal *L. linnelli* having more teeth above and below the median spine.

While differing in numerous relative proportions (to be discussed further when the *L. linnelli* question is resolved), *L. myersi* has a distinctly smaller eye than *L. linnelli* (four or five percent of standard length versus seven or eight percent). *Leptodoras linnelli* has no color pattern except for a faint dusky stripe that extends out each caudal lobe, while *L. myersi* has the distinctive pattern described above. *Leptodoras acipenserinus* is described as devoid of a color

Figure 3. *Leptodoras juruensis*: 125.8 mm. standard length, ANSP 112321.

pattern (Günther 1868: 230) and IUM 15878 (Eigenmann 1925: 358) shows no trace of one. This color difference, coupled with the differences listed above between the elongate *L. acipenserinus* and *L. myersi*, plus numerous proportional differences that will be outlined in a subsequent paper, indicate how different are the two species. *Leptodoras myersi* has elongate, pale, raised ridges on the head, *L. acipenserinus* has pale low papillae, while *L. linnelli* has nothing of the sort.

Name. For my professor and good friend, George S. Myers.

Material examined. *Holotype*: ANSP 112318 (74.6 mm. standard length, photographed), Peru: vicinity of Iquitos, Rio Amazonas (Marañon) between Isla Iquitos and Isla Lapuna, near Isla Lapuna shore; to 12 ft. (3.66 meters); trawl; 9 October 1955; C.C.G. Chaplin, R. Patrick.

Paratypes: ANSP 112319 (9; 54.9–77.6), ANSP 112320 (1; 63.3, cleared and stained) and USNM 203816 (2; 68.5–74.8), taken with the holotype.

Leptodoras juruensis Boulenger.

Leptodoras juruensis Boulenger 1898, p. 478 (Type locality: Rio Jurua, Brasil). Eigenmann 1925, pp. 357, 358 (diagnosis based on type).

Previously known only from the holotype from Rio Jurua, this species now is recorded from the same trawl haul that collected the type material of *L. myersi*. A fine Peruvian example is illustrated in figure 3. Peruvian specimens have been compared with the much larger holotype of the species and the results of this comparison will be forthcoming.

Material examined. British Museum (Natural History) 1898–10–11–25 (223 mm. standard length, holotype), Brasil: Rio Jurua; Goeldi. ANSP 112321 (1; 125.8, photographed), ANSP 112322 (6; 71.4–96.7) and USNM 203817 (1; 92.6), taken with the holotype of *L. myersi*.

NOTE

While this manuscript was in proof, a paper on Venezuelan doradids was received from Fernández Yépez (1968, Boletin del Instituto Oceanographico, Universidad de Oriente, Cumana, Venezuela, vol. 7, no. 1, pp. 7–72). In it, he includes the species "*leporhinus*," "*linnelli*," and "*notospilus*" in the genus *Opsodoras*, whereas "*linnelli*" previously was in *Leptodoras* and "*notospilus*" was in *Hassar*. Subsequent correspondence with that author revealed that his rationale for making these and other nomenclatural changes is in a manuscript still in press. The new species, "*myersi*," is closest to "*linnelli*" and "*acipenserinus*," which were placed by Eigenmann (1925: 357) in *Leptodoras*, so the name combination *Leptodoras myersi* is here published, with the realization that the species may later be transferred to a different genus.

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SYSTEMATICS OF THE GENUS *HEMITRIAKIS* (SELACHII: CARCHARHINIDAE), AND RELATED GENERA

By

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Division of Systematic Biology, Stanford University

INTRODUCTION

Herre (1923) described *Hemitriakis leucoperiptera*, a new genus and species of shark from the Philippine Islands. *Hemitriakis* was thought to differ from *Triakis* Müller and Henle in its dentition, snout, nasal valves, body, and caudal fin. However, Fowler (1941), Bigelow and Schroeder (1948), Garrick (1954), and Kato (1968) considered *Hemitriakis* a junior synonym of *Triakis*.

Present data shows that *Hemitriakis* is a well defined genus with two species: *H. leucoperiptera* Herre, 1923; and *H. japanica* (Müller and Henle, 1841). This account is a review of the systematics of *Hemitriakis* and related genera in the family Carcharhinidae.

ACKNOWLEDGMENTS

Reeve M. Bailey (University of Michigan Museum of Zoology), Myvanwy M. Dick (Museum of Comparative Zoology, Harvard University), W. I. Follett, William D. Eschmeyer, Lillian J. Dempster (Department of Ichthyology, California Academy of Sciences), and Stanley H. Weitzman (Division of Fishes, U. S. National Museum) loaned or gave specimens to me and provided working facilities at their institutions. C. G. Alexander (Department of Biology, San

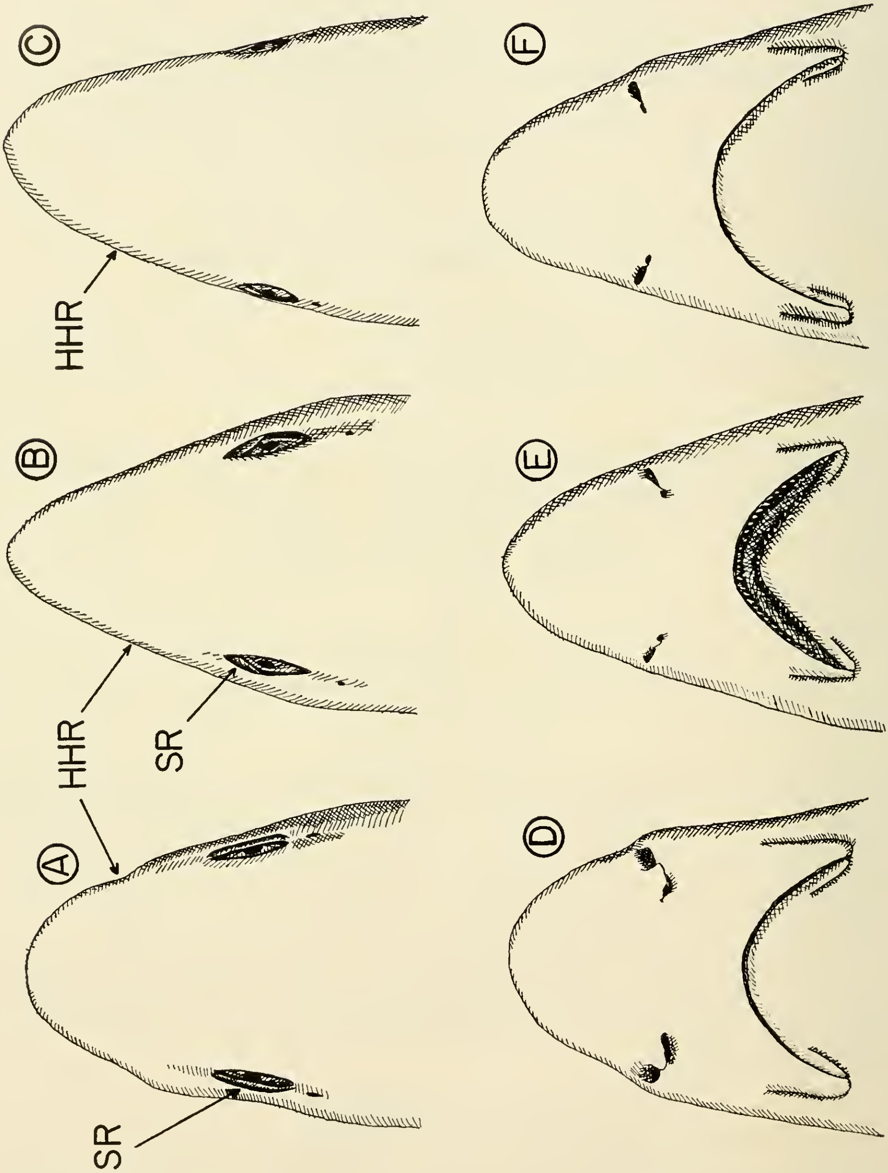


Figure 1. A, dorsal view, and D, ventral view, of head of *Hemitriakis japanica* (SU-12677). B, dorsal view of head of *Hypogaleus hyugaensis*, adopted from Miyosi (1939). C, dorsal view, and F, ventral view, of head of *Galeorhinus zyopterus* (LJVC-0238; 847 mm. female.). E, ventral view of head of *Hypogaleus zanzibariensis*, adopted from Smith (1957b). Abbreviations: HHR, horizontal head rim; SR, subocular ridge.

Francisco State College), Robert P. Dempster (Steinhart Aquarium, California Academy of Sciences), and Louis Garibaldi (American Broadcasting Company Marine World, Redwood City, California) supplied many fresh and frozen carcharhinids for anatomical preparations. The late J. L. B. Smith (Department of Ichthyology, Rhodes University, Grahamstown, South Africa) sent specimens of *Eridacnis sinuans* and *Scylliogaleus quecketti*; Leslie W. Knapp (Smithsonian Oceanographic Sorting Center, Washington, D. C.), C. Richard Robins, and Phillip C. Heemstra (Institute of Marine Sciences, University of Miami) loaned other carcharhinids. In addition to providing numerous specimens and research facilities, Shelton P. Applegate (Division of Vertebrate Palaentology, Los Angeles County Museum of Natural History), Susumu Kato (Bureau of Commercial Fisheries Fishery-Oceanography Center, La Jolla, California), and Stewart Springer (Bureau of Commercial Fisheries Systematics Laboratory, U. S. National Museum) have discussed various aspects of carcharhinid taxonomy covered in this paper with me. J. A. F. Garrick (Department of Zoology, Victoria University of Wellington, New Zealand) sent comments on several systematic problems concerning carcharhinid genera and species. George S. Myers critically reviewed the first draft of the manuscript, and Warren C. Freihofer (Division of Systematic Biology, Stanford University) offered useful suggestions. I am most grateful for the help offered by all of these people, without which this account could not have been written.

STUDY MATERIAL

Specimens mentioned in the text and figures are from the collections of the George Vanderbilt Foundation at the California Academy of Sciences (GVF); Division of Systematic Biology, Stanford University (SU); University of Michigan Museum of Zoology (UMMZ); U. S. National Museum (USNM); and of the writer (LJVC).

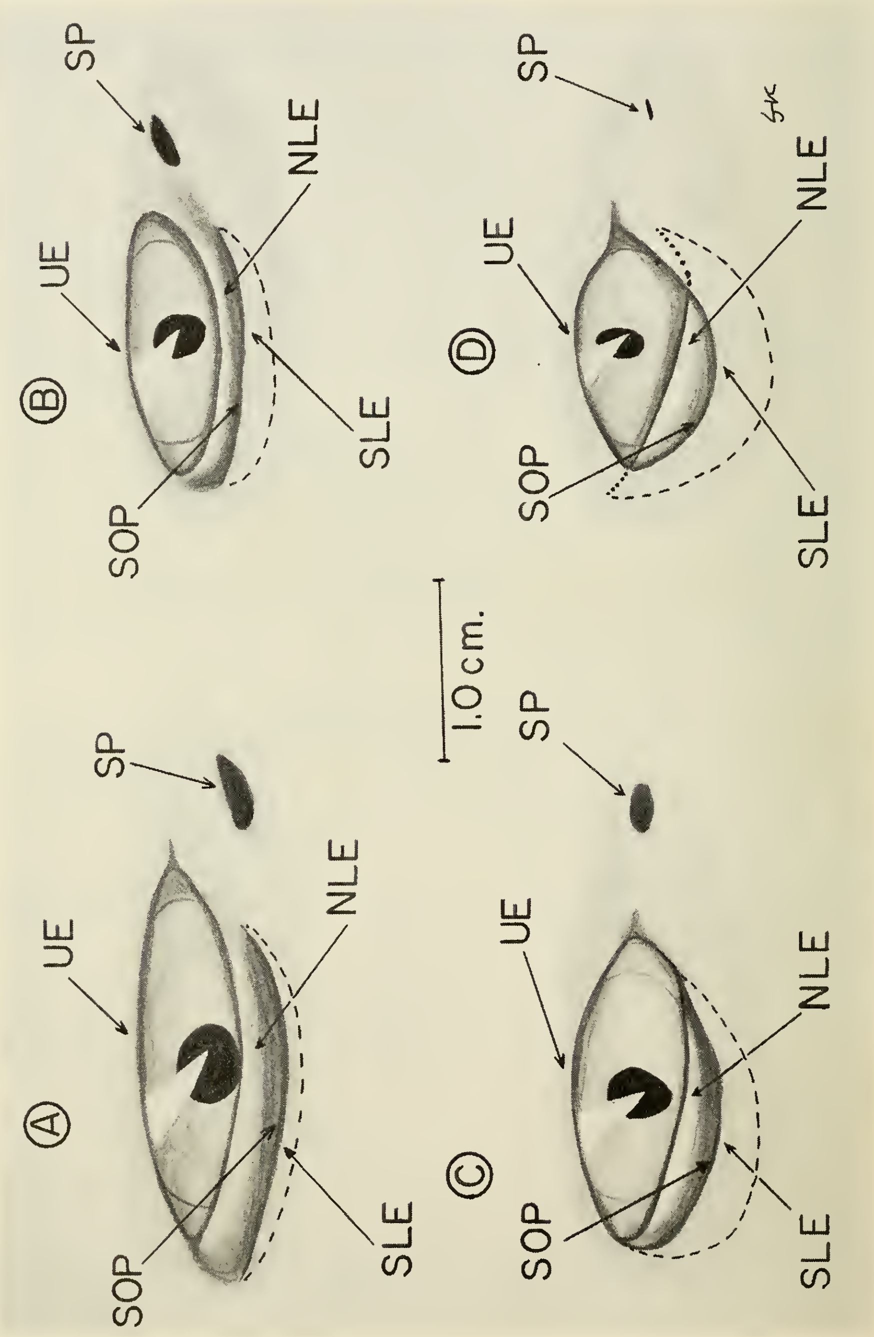
Hemitriakis specimens examined are listed below, with number of specimens and total lengths in parentheses.

Hemitriakis japanica: SU–12677, Nagasaki, Japan (1; 682 mm.); UMMZ–179060, Auraji (Osaki Market, Osaki), Japan (1; 650 mm.); UMMZ–179061, Ainoshima (Fukuoka Market, Fukuoka), Japan (1; 560 mm.); UMMZ–179062, Ezumi (Ezumi Market), Japan (1; 505 mm.); USNM–191193, Taipeihsien, Taiwan (3; 651–685 mm.).

Hemitriakis leucoperiptera: SU–27118, Dumaguete, Oriental Negros, Philippine Islands (2; 169–170 mm.).

Hemitriakis species: SU–40097, Dumaguete, Oriental Negros, Philippine Islands (4; 161–180 mm.).

Comparative material including most carcharhinid genera and species was examined. As the number of specimens in this sample is enormous, they are not listed here but will be given in a forthcoming revision of carcharhinid genera.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1.0 cm.

Instead, the genera and species examined are listed. *Carcharhinus* species nomenclature is modified from Garrick (1967); that for *Scoliodon, Rhizoprionodon,* and *Loxodon* is from V. Springer (1964).

Aprionodon isodon, Carcharhinus acronotus, C. albimarginatus, C. altimus, C. amblyrhynchus, C. borneensis, C. cauta, C. falciformis, C. galapagensis, C. leucas, C. limbatus, C. longimanus, C. maculipinnis, C. melanopterus, C. menisorrah, C. milberti, C. obscurus, C. pleurotaenia, C. porosus, C. remotus, C. sorrah, C. springeri, C. tjutjot, C. velox, Eridacnis barbouri, E. radcliffei, E. sinuans, Galeocerdo cuvier, Galeorhinus australis, G. chilensis, G. galeus, "G." omanensis, G. zyopterus, Hemigaleus balfouri, H. macrostoma, H. microstoma, H. pectoralis, H. tengi, Hemipristis elongatus, Hypoprion hemiodon, H. macloti, H. signata, Isogomphodon oxyrhynchus, Lamiopsis temmincki, Leptocharias smithii, Loxodon macrorhinus, Mustelus antarcticus, M. asterias, M. californicus, M. canis, M. dorsalis, M. fasciatus, M. griseus, M. henlei, M. higmani, M. kanekonis, M. lenticulatus, M. lunulatus, M. manazo, M. mento, M. mustelus, M. norrisi, M. schmitti, Negaprion acutidens, N. brevirostris, N. forsteri, N. fronto, Prionace glauca, Proscyllium habereri, Rhizoprionodon acutus, R. lalandei, R. longurio, R. oligolinx, R. porosus, R. terraenovae, Scoliodon laticaudus, Scylliogaleus quecketti, Triaenodon obesus, Triakis acutipinna, "T." fehlmanni, T. maculata, T. scyllia, T. semifasciata.

TERMINOLOGY

For descriptive purposes the morphological terminology of the head, eyes, dentition, vertebral column, and fins of carcharhinid sharks is discussed and elaborated here.

Head Morphology. The horizontal head rim (fig. 1) is the head margin in dorsal or ventral view. The subocular ridge is a ventrolateral expansion of the horizontal head rim beneath the eye. In *Hemitriakis, Triakis, Mustelus, Furgaleus,* and other carcharhinid genera with well developed subocular ridges, the eyes appear medial to the horizontal head rim in dorsal view. A subocular ridge obscures the eyes in ventral view.

Nictitating Lower Eyelid (fig. 2). Form and terminology of the carcharhinoid ocular structures variously termed nictitating membranes, nictitating

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Figure 2. Lateral views of carcharhinid eyes, showing nictitating lower eyelid types. A. *Proscyllium habereri* (UMMZ-179064; 535 mm. female), with rudimentary NLE. B. *Mustelus canis* (USNM-197676; 337 mm. female), with external NLE. C. *Galeorhinus australis* (USNM-176995; 385 mm. male), with transitional NLE. D. *Leptocharias smithii* (USNM-202677; 570 mm. male), with internal NLE. Abbreviations: NLE, nictitating lower eyelid; SLE, secondary lower eyelid; SOP, subocular pouch; SP, spiracle; UE, upper eyelid. Dashed line is bottom of subocular pouch; dotted line in *Leptocharias* is edge of NLE inside palpebral aperture.

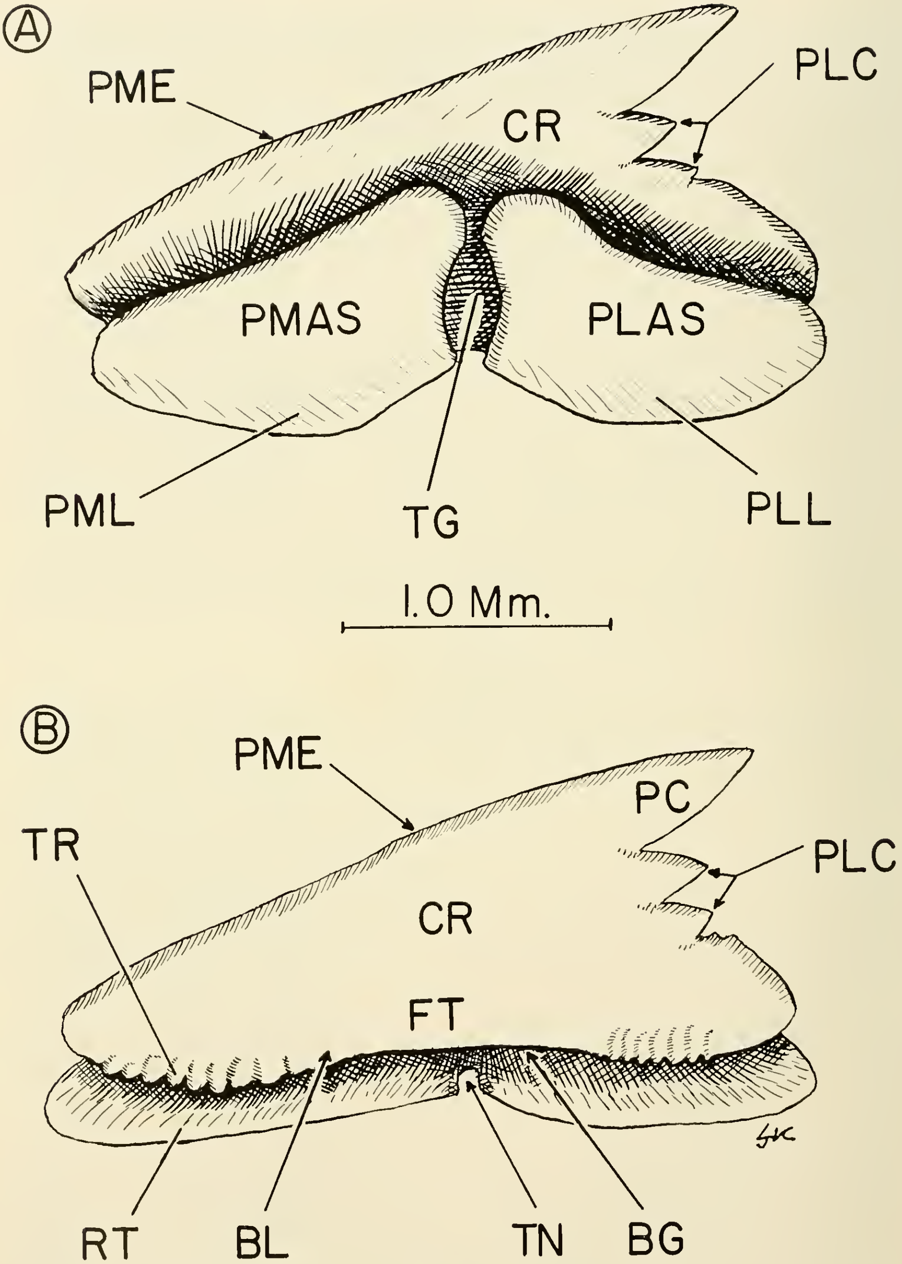

FIGURE 3. Anteroposterior teeth of *Hemitriakis japanica* (SU-12677). A. Inner face of right lower tooth. B. Outer face of left lower tooth. Abbreviations: BG, basal groove; BL, basal ledge; CR, crown; FT, crown foot; PC, primary cusp; PLAS and PMAS,

folds, subocular folds, movable lower eyelids, and nictitans were reviewed by Gilbert (1963) and by Gilbert and Oren (1964). They used the term "nictitans" to cover all variations of the mobile eyelid of scyliorhinids and carcharhinids, but this term is not adopted here as the selachian structure is morphologically and developmentally unlike the true nictitans or nictitating membrane of tetrapods and in many cases is merely a little-modified movable lower eyelid. Instead, the term nictitating lower eyelid (NLE) is introduced to avoid some of the connotations of nictitans and to recognize the probable derivation of the structure from the original lower eyelid of precarcharhinoid sharks.

The exterior fold formed by the groove below the NLE is termed the secondary lower eyelid (SLE). The groove itself is the subocular pouch.

Four nictitating lower eyelid types can be distinguished among carcharhinids if subdivisions are made in the morphological gradient seen in this structure. The rudimentary type is the least specialized. In it the NLE forms the ventral edge of the palpebral aperture and connects anteriorly and posteriorly with the upper eyelid. The SLE is a weak ridge below the NLE and does not connect with either the upper eyelid or the NLE. The upper edge of the SLE is not defined and the subocular pouch is a very shallow, external groove. The external type differs from the rudimentary in that the SLE is a strong flap with a well defined edge. The subocular pouch, although relatively shallow, is strongly differentiated. The internal type is the most advanced, with the NLE ends entirely internal to the palpebral aperture and not connected to the upper eyelid. The SLE replaces the NLE in contacting the anterior and posterior ends of the upper eyelid and forms the ventral edge of the palpebral aperture. The subocular pouch is entirely within the palpebral aperture and varies from moderately shallow (*Leptocharias*) to very deep (*Carcharhinus*). The transitional type covers intermediates between internal and external types. These often have the SLE attached by one of its ends (posterior or anterior) to the upper eyelid, while the NLE has its opposite end also attached to the upper eyelid.

Dentition (figs. 3–4). Tooth topography of selachians was discussed briefly by Applegate (1967). He divides the tooth into two external regions, the crown and the root. The crown is the enamel-covered region of the tooth distal to its attachment with the jaw. The proximal root lacks the enamel covering and has its component osteodentine exposed to the surface. The region of the crown proximal to the root is termed the foot. As used by Bigelow and Schroeder (1948), the term base includes both the root and the crown foot.

The crown and root are both compressed in a plane with its horizontal sides

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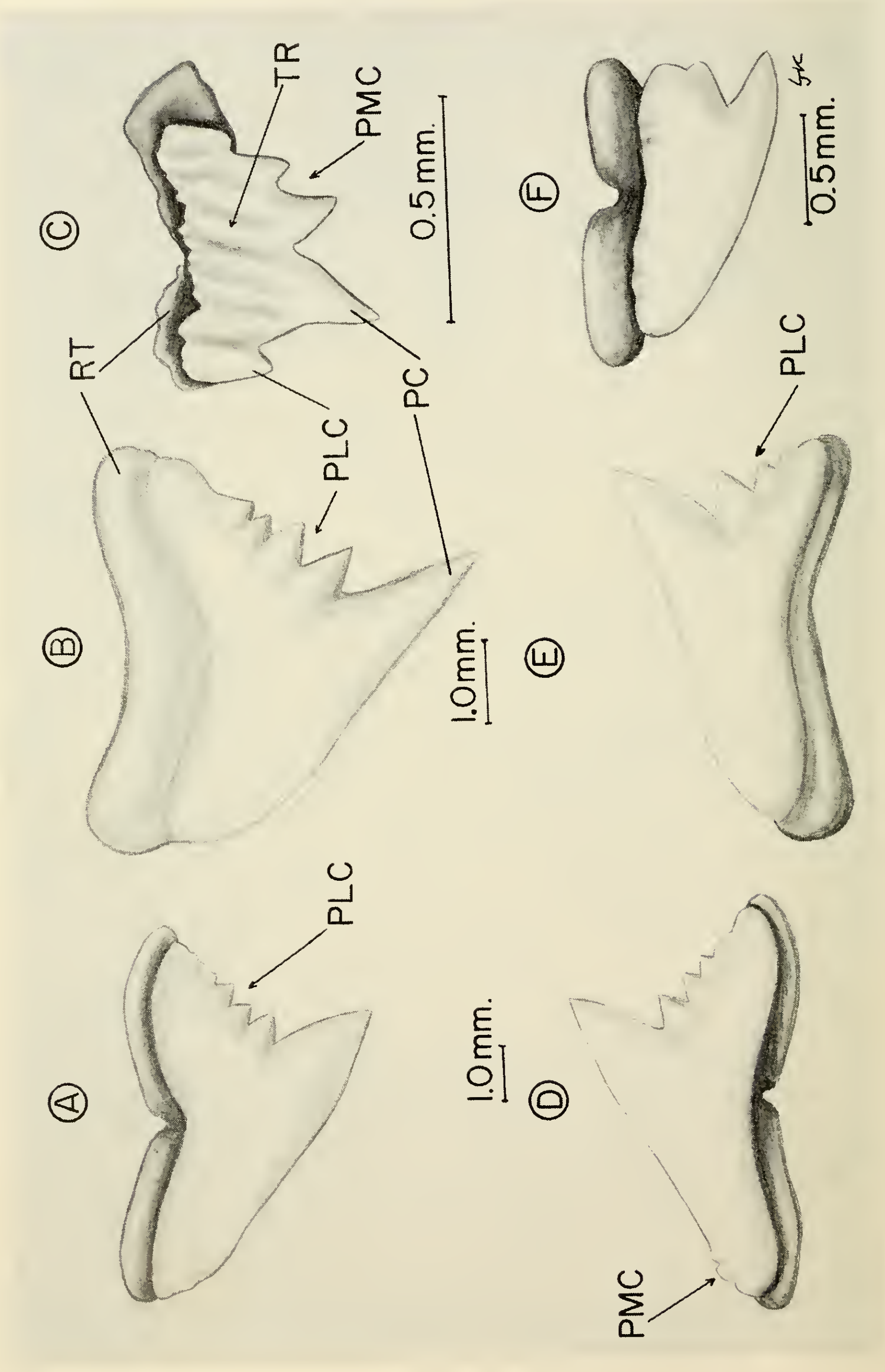
postlateral and premedial parts of attachment surface; PLC, postlateral cusplets; PLL, postlateral lobe of root; PME, premedial edge of crown; PML, premedial lobe of root; RT, root; TG, transverse groove; TN, transverse notch; TR, transverse ridges.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parallel to the jaw axis and its vertical sides perpendicular to it. Teeth in upright functional positions at the edge of the jaw have outer and inner faces on their planes of compression. The orientations of these faces are reversed when the teeth are in replacement position but as a convention the functional orientation is used here for any tooth.

The root has its inner face partially formed into a flattened attachment surface that seats in the dental membrane against the jaw surface. The root has a vertical transverse groove that superficially divides the attachment surface into two lobes and may extend over the extreme rim of the root to form a transverse notch. The outer face of the root may have a strong basal groove extending horizontally across it that is overlapped by a strong basal ledge of the crown foot. A series of vertical transverse ridges may be present on the basal ledge and often extend distally on the outer face of the crown. In many species of *Mustelus* the crown inner face has a rounded protuberance or peg. The peg of one tooth extends into the basal groove of the next tooth in succession in the same row, an arrangement that may serve to interlock the teeth in the pavement dentitions of these forms.

The distal part of the crown, as opposed to the foot, may have its margin in the plane of its compression formed into a sharp cutting edge, with or without serrations. Pointed projections from the crown edge are termed cusps or cusplets according to their size relative to each other. In carcharhinids a median primary cusp is commonly present and is usually larger than other projections of the crown edge (when such are present). The primary cusp may have its axis perpendicular or oblique to the tooth base. Its proximal origin may occupy all or only part of the foot. When a primary cusp origin is restricted, the adjacent crown edges may be formed into other cusps or cusplets, sharp-edged blades, or rounded shoulders.

The planes of compression in the teeth of carcharhinid sharks have their horizontal sides parallel to the jaw axis, but this axis changes from nearly perpendicular to the body axis at the symphysis to nearly parallel with the body axis at either end of the dental arcade. The horizontal sides of the planes of compression for tooth roots and crowns are therefore oriented in an anteromedial-to-posterolateral direction relative to the anterior-to-posterior horizontal body axis along

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Figure 4. Outer views of carcharhinid teeth. All teeth except C from left half of dental band. A, upper 8th tooth, and D, lower 10th tooth, of *Galeorhinus zyopterus* (LJVC-0114; 1670 mm. male). B, upper 10th tooth, and E, lower 9th tooth, of *Hypogaleus zanzibariensis* (1220 mm. male; modified from Smith, 1957b). C. Upper tooth of third row from end of dental band, *Proscyllium habereri* (GVF-Hong Kong-88; 523 mm. female). F. Same of *Triakis semifasciata* (LJVC-0137; 1097 mm. male). Abbreviations as in Figure 3, except for: PMC, premedial cusplets.

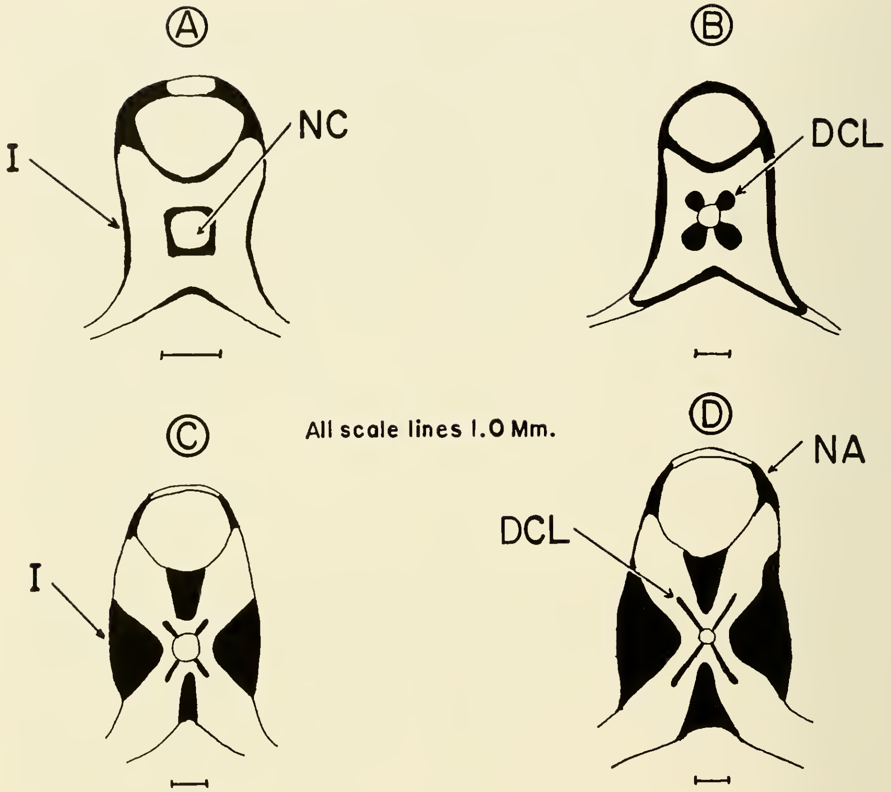

Figure 5. Transverse views of carcharhinid vertebral calcification patterns, with calcified areas indicated in black. A. *Eridacnis barbouri* ("Silver Bay" 3514; 258 mm. female). B. *Proscyllium habereri* (UMMZ-179065; 565 mm. male). C. *Mustelus henlei* (LJVC-0020; 630 mm. female). D. *Hemitriakis japanica* (SU-12667). Abbreviations: DCL, diagonal calcified lamellae; I, intermedialia; NA, neural arch; NC, notochordal canal.

most of the jaw, with the angle between the sides and the body axis decreasing from symphysis to rictus. It is possible with these orientations to distinguish anteromedial and posterolateral edges on the crowns and anteromedial and posterolateral lobes on the roots of most teeth. Exceptions occur at the symphysis, where teeth may have medial-to-lateral orientation, and at the ends of the dental arcade, where teeth can have anterior-to-posterior orientation. As a convention the anteromedial-to-posterolateral relations are used for all teeth. For brevity, structures having an anteromedial orientation on the tooth are termed premedial, whereas posterolateral structures are postlateral. Thus, carcharhinid teeth can have premedial and postlateral cusp edges, cusplets, serrations, blades, etc.

The terms row and series were used almost interchangeably by Bigelow and

Schroeder (1948), but Applegate's (1965) usage is followed here. A row is a single replicating file of teeth approximately transverse to the jaw axis that includes both functional teeth and their replacements in various stages of development. The row represents an entire family of teeth derived from one germinal area on the jaw. The term "series" is used for a line of teeth along the jaws which is parallel to the jaw axis and includes teeth from all rows present. In some carcharhinids, especially those with pavement dentitions and very numerous teeth, the concept of series may be meaningless as all teeth are closely adpressed in quincunx formation and do not form distinct transverse lines.

As indicated by Applegate (1965), there are two primary types of heterodonty, or differentiation between teeth in various positions on the jaws, that can be demonstrated in sharks. The first, here termed dignathic heterodonty, involves differences in morphology between teeth in opposition or approximate opposition in the upper and lower jaws. Dignathic heterodonty can apply to all opposing teeth in both jaws or to only some of them. The second type, monognathic heterodonty, involves differences between teeth in different positions on the same jaw series. Monognathic heterodonty is not restricted to situations in which adjacent teeth differ strongly in morphology, but also applies when a tooth in one position is different from that in another position on the same series but has a gradient of intermediate teeth between itself and the second tooth. The first condition can be called disjunct monognathic heterodonty; the second, gradient monognathic heterodonty.

Applegate (1965) used a row-group terminology for implied disjunct monognathic heterodonty in the dentitions of *Odontaspis taurus* (Odontaspidae) and other sharks. The terms symphysials, alternates, and medials were used for different tooth types in the region of the symphysis. Remaining teeth were grouped into anteriors, intermediates, laterals, and posteriors from premedial to postlateral along the dental band. Analogs of the intermediates in lamnoids do not exist in carcharhinids. However, some carcharhinid genera, especially those in the advanced and intermediate groupings mentioned below, show strong disjunct monognathic heterodonty and have medials, alternates, symphysials, anteriors, laterals, and posteriors. Other genera (as *Hemitriakis*) have disjunct variation only between the medials or alternates at the symphysis and the adjacent parasymphysial rows, which may be termed anteroposteriors.

Two additional types of heterodonty can be defined here. Ontogenic heterodonty is a gradient phenomenon in which tooth morphology at a functional series position in a single row or many rows changes with replacement of teeth during growth. Gynandric heterodonty, or dental sexual dimorphism, includes differences in morphology of teeth in approximately similar series and row positions between two individuals or groups of individuals of opposite sex and same species at about the same developmental stage.

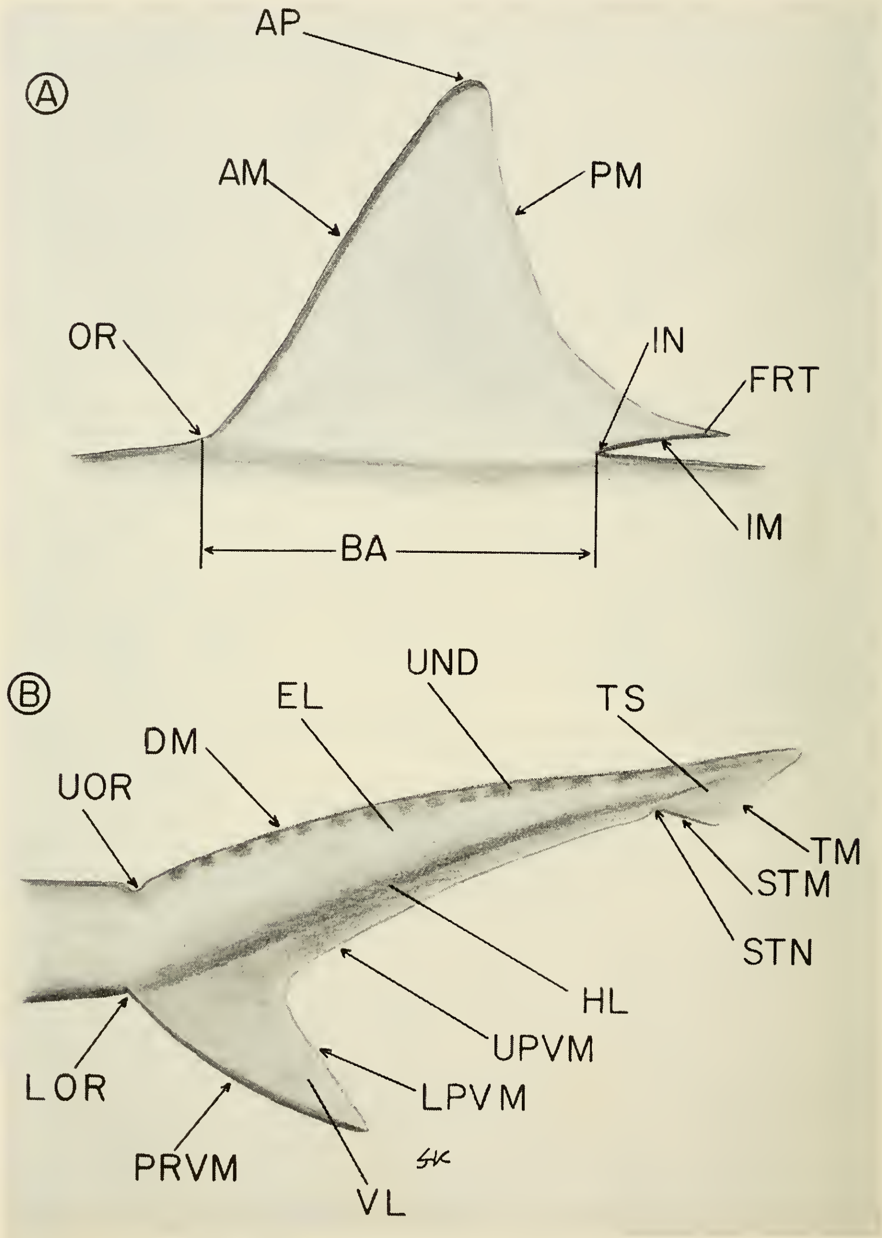

FIGURE 6. Carcharhinid fin terminology. A. Idealized first dorsal fin. B. Caudal fin. Abbreviations: AM, anterior margin; AP, apex; BA, base; DM, dorsal margin; EL, epural lobe; FRT, free rear tip; HL, hypural lobe; IM, inner margin; IN, insertion; LOR, lower origin; LPVM, lower postventral margin; OR, origin; PM, posterior margin;

Vertebrae. Terminology for vertebral calcified parts follows Ridewood (1921).

Springer and Garrick (1964) subdivided the vertebral complements of sharks into precaudal and caudal centra. They noted that an alternative grouping into monospondylic and diplospondylic centra was possible, but this was not utilized in their study.

For present purposes the Springer and Garrick dichotomy of vertebral types is modified into a three-group system of monospondylic precaudal (MP), diplospondylic precaudal (DP), and diplospondylic caudal (DC) centra. This trichotomy is applicable to most carcharhinids, but breaks down in sharks such as *Galeorhinus zyopterus* where alternating long and short centra of a "stutter zone" mark the transition from MP to DP centra. Springer and Garrick's method of delimiting the caudal centra at the upper precaudal pit or upper caudal origin is followed here despite its shortcomings.

In some instances it is useful to compare relative numbers of centra in different vertebral groups of sharks with differing total vertebral counts. A system used here divides the MP, DP, and DC counts by the MP count to give DP/MP and DC/MP ratios that vary sufficiently between carcharhinid genera and species to be of systematic value (MP/MP = 1.00). An alternate system is to divide MP, DP, and DC counts by total count and multiply by 100 to obtain percent total count for each vertebral group.

Fins. The terminology used here for carcharhinid fins is explained by fig. 6. The following terms apply to paired and unpaired fins other than the caudal: Origin; anterior margin; apex; posterior margin; free rear tip; inner margin; insertion; and base. The caudal fin terminology includes: Hypural lobe; epural lobe; terminal sector; subterminal notch; ventral lobe; dorsal margin; terminal margin; subterminal margin; upper postventral margin; lower postventral margin; preventral margin; upper origin; and lower origin.

Genus **Hemitriakis** Herre, 1923

Type species. *Hemitriakis leucoperiptera* Herre, 1923, by original designation.

Species. There are two named species: *H. leucoperiptera*, from the Philippine Islands (detailed distribution in Herre, 1953); and *H. japanica* (Müller and Henle), from Japan, Taiwan, and Amoy (Chen, 1963).

Hemitriakis japanica was placed in the genus *Galeorhinus* Blainville (or its junior synonyms, *Galeus* Cuvier, 1817, not Rafinesque, 1810, and *Eugaleus* Gill)

←

PRVM, preventral margin; STM, subterminal margin; STN, subterminal notch; TM, terminal margin; TS, terminal sector; UND, undulations in dorsal caudal margin; UOR, upper origin; UPVM, upper postventral margin; VL, ventral lobe.

by all previous writers (summarized in Fowler, 1941, and Chen, 1963). The species was named *Galeus japanicus* by Müller and Henle (1841).

Specimens of *Galeorhinus japanicus* were compared with specimens of *Galeorhinus australis*, *G. chilensis*, *G. galeus* (type species of *Galeorhinus*), *G. zyopterus*, and with specimens and Herre's (1923) description of *Hemitriakis leucoperiptera*. This indicated that "*japanicus*" does not belong to *Galeorhinus* but is congeneric with *Hemitriakis leucoperiptera*.

The two *Hemitriakis* species are close but *H. leucoperiptera* differs from *H. japanica* in having the first dorsal origin over inner pectoral margin (*H. japanica* with origin posterior to free rear tip of pectoral). The distance from pectoral free rear tips to pelvic origins about equal to first dorsal length from origin to free rear tip in *H. leucoperiptera* but much greater in *H. japanica*. *Hemitriakis leucoperiptera* also has fewer vertebrae, with about 144–146 total count (2 specimens) and 34–35 MP centra (*H. japanica* with 156–161 total and 41–43 MP centra for 7 specimens).

An undescribed *Hemitriakis* species may be represented by 4 specimens (SU–40097) that differ from the sympatric *H. leucoperiptera* in various proportions, fin shapes, and in their strikingly barred and spotted coloration (*H. leucoperiptera* and *H. japanica* have a nearly plain coloration).

REDEFINITION AND DESCRIPTION OF THE GENUS *Hemitriakis*. Head flattened dorsoventrally, its length from snout tip to 5th gill opening about ⅕ of total length. Eyes high on sides of head, above horizontal head rim and level of nostrils by a space equal or greater than eye height (fig. 7A). Strong subocular ridge present, in dorsal view separating eyes from horizontal head rim by a wide space (fig. 1A). Eyes not visible in ventral view of head (fig. 1D). Eyes elongate, their apertures over twice as long as high, with a notch present posteriorly in adults and subadults. NLE external (fig. 7A), with its edge horizontal. Edge of SLE strongly differentiated. Subocular pouch shallow but well defined, with its interior surface covered with denticles.

Spiracles present, slitlike or porelike, 1/5 to 1/7 of eye length. External gill openings short, the longest (3rd) less than eye length. Gill rakers absent from internal gill openings.

Nostrils narrow, far apart, a nostril width about 2½ times in internarial width. Anterior nasal flap a short rounded lobe, not a pointed barbel. Nostrils about half as far from mouth as from snout tip. Nasoral grooves absent.

Mouth crescentic, broad, at least 2⅓ times as wide as long. Large papillae absent from buccal cavity. Moderately long labial furrows present, upper about 1½ times as long as nostril width, the lower ⅓ to ⅔ of upper. Upper labial furrows extending anteriorly to below first ¼ of eye.

Dignathic heterodonty weak, with upper anteroposterior teeth slightly larger and with higher crowns and more erect cusps than lowers; upper medials smaller

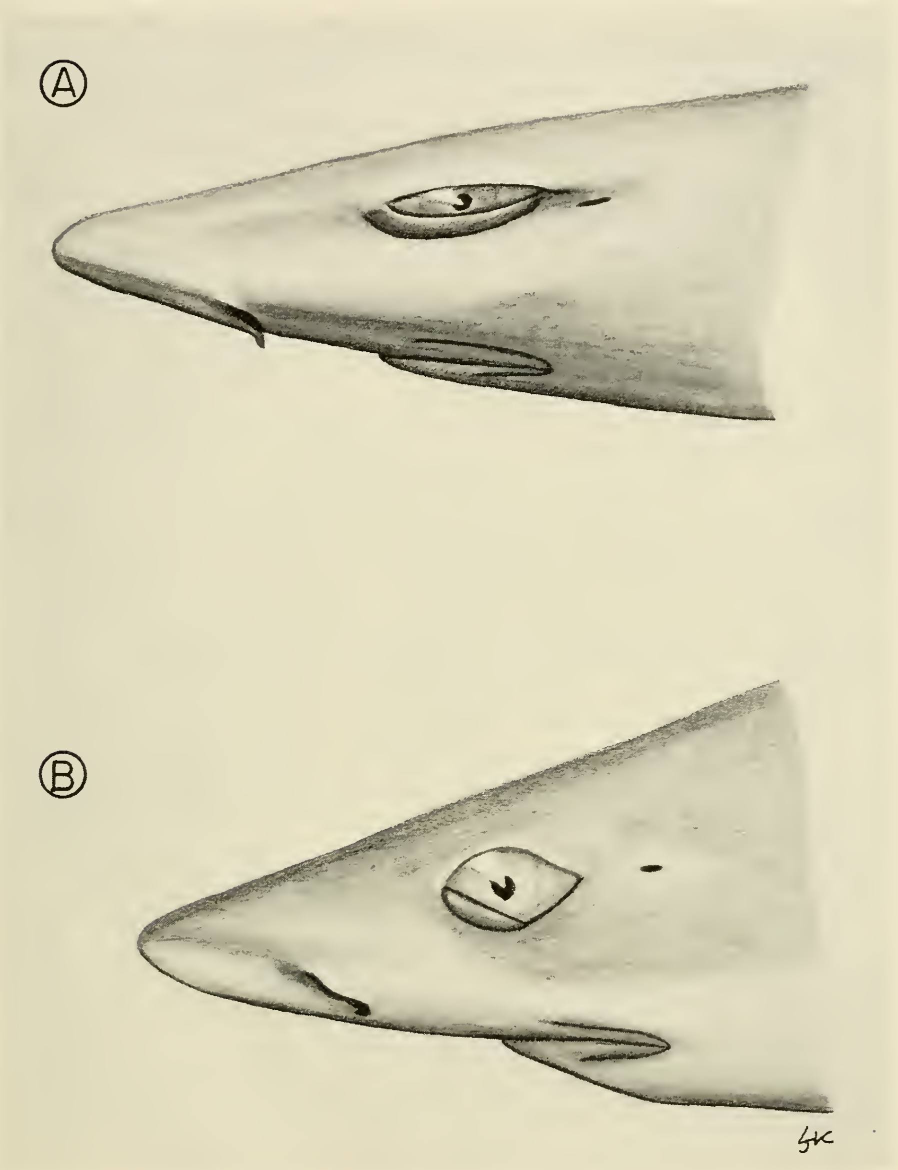

Figure 7. Lateral view of carcharhinid heads. A. *Hemitriakis japanica* (SU-12677). B. *Galeorhinus zyopterus* (LJVC-0238).

than lower ones. Disjunct monognathic heterodonty indicated by differentiation of 3 to 6 rows of medials in upper and lower jaws. Medial teeth differ from anteroposteriors in their lesser size and erect primary cusps, flanked by 1 or 2 premedial and postlateral cusplets. The sharp-edged anteroposteriors are larger, compressed, bladelike cutting teeth with a strong oblique primary cusp and no premedial cusplets (fig. 3). Anteroposteriors show strong gradient monognathic heterodonty. In more premedial teeth in adults and subadults the primary cusp is large and has 2 to 4 postlateral cusplets flanking it. From premedial to postlateral the crowns of teeth become lower, the primary cusps become more oblique, and the postlateral cusplets become fewer and finally disappear. The most postlateral anteroposteriors have primary cusps reduced or absent and are very low and sharp-keeled. Ontogenic heterodonty present in more premedial teeth of anteroposteriors. These teeth gain more postlateral cusplets with growth, so that late embryos have no cusplets and adults have 2 to 4 cusplets. Gynandric heterodonty not apparent.

Teeth moderately large, base width of longest lower anteroposteriors about 0.356–0.405 percent of total length in *H. japanica*. Tooth rows relatively few; Chen (1963) gives 23–29/27–33 (4 specimens) and Tang (1934) gives 35/33 (1 adult male) total tooth row counts for *H. japanica*. The 7 examples of *H. japanica* studied here have 33–38/29–33 rows. Herre (1923) gives 18/34 rows for the holotype (adult female) of *H. leucoperiptera*, but this may be erroneous as 33/30 rows were counted in one of the SU–27118 specimens (late embryo). One to 5 series functional along jaw edges. Teeth of adjacent rows in the alternate overlap pattern of Strasburg (1963). Serrations absent from crown edges. Crown premedial edge not indented and differentiated. Crown foot with a strong basal ledge overlapping a deep basal groove. Transverse ridges present on basal ledge only, not extending onto primary cusp. Roots low, deep, with strong transverse groove dividing attachment surface into 2 lobes and extending through extreme rim of root to form strong transverse notch. Teeth not noticeably protruding when mouth is closed.

Trunk not compressed, subcylindrical. Interdorsal ridge present. Lateral dermal keels absent from caudal peduncle. No precaudal pits. Head-trunk length from snout tip to cloaca equal to, or somewhat shorter than, tail length from cloaca to caudal tip.

Denticles from sides of body below first dorsal fin small, with crowns much longer than wide at all sizes. A single strong medial cusp and bifurcated longitudinal ridge with a weak lateral ridge on each side of crowns of adult denticles. In late embryos to subadults medial ridge not bifurcated and lateral ridges absent. A pair of weak lateral cusps often present on denticles, but these are not constant.

Pectorals moderately large, pectoral area slightly greater than first dorsal area. Pectoral anterior margin about 1½ times as long as combined base and inner margin lengths. Apex of adpressed pectoral slightly posterior to its free rear tip when pectoral inner margin is held parallel to body axis. Origin of pectoral below or slightly anterior to fourth gill opening. Pectoral skeleton projecting about ⅖ to ½ of pectoral anterior margin length into the fin. Distal pectoral radials slightly longer than proximal ones, with broad, truncate tips.

Pelvics relatively small, their anterior margins less than ½ the length of pectoral anterior margins. Pelvic bases closer to 1st dorsal base than to 2nd dorsal base.

Midpoint of 1st dorsal base almost equidistant between pelvic and pectoral bases or definitely closer to pectoral bases. First dorsal free rear tip anterior to pelvic origins.

Second dorsal nearly as large as first one, with its height 70 to 80 percent of 1st dorsal height. Posterior margin of 2nd dorsal strongly concave.

Anal much smaller than 2nd dorsal, its height ½ that of 2nd dorsal and its base only ⅔ to ¾ of 2nd dorsal base. Anal posterior margin strongly concave in adults, shallowly concave in late embryos. Anal origin posterior to 2nd dorsal origin by about ⅓ of the 2nd dorsal base length. Anal insertion varying from under 2nd dorsal insertion to much less than ⅕ of 2nd dorsal base length posterior to it.

Caudal with preventral and postventral margins expanded as a short ventral lobe in adults and subadults, but scarcely developed in late embryos. Preventral caudal margin over ⅓ of dorsal caudal margin in adults and subadults, slightly shorter in young. Postventral margin differentiated into upper and lower parts in subadults and adults, with upper postventral margin ⅓ to ⅖ of dorsal caudal margin. Subterminal caudal margin long, over ½ of terminal caudal margin length. Caudal short, dorsal margin about equal to head length and less than ¼ of total length. No lateral undulations in dorsal caudal margin. Terminal sector of caudal short; distance from subterminal notch to caudal tip only about 2½ to 3 times in dorsal caudal margin. Vertebral axis of caudal slightly raised above body axis.

Vertebrae moderately numerous, total count 144–161. Separation between MP and DP centra not sharp, gradual along two transitional centra. Vertebral calcification pattern of Applegate's (1967) "carcharhinoid" type.

Chondrocranium very similar to that of *Furgaleus ventralis* as illustrated by Whitley (1948) and to that of *Mustelus* species described and illustrated by Gegenbaur (1872) and Holmgren (1941). Supraorbital crest of cranium strongly developed and entire.

Intestinal valve of spiral type, with 6 to 8 turns in the spiral.

Hemitriakis is livebearing and probably viviparous. Yolk-sac placentae are present on the SU–40097 (late embryo) specimens.

FAMILIAL CLASSIFICATION OF *HEMITRIAKIS*

The familial classification of the genus *Hemitriakis* is troublesome because one of its species, *H. japanica*, is conventionally placed in the family Carcharhinidae as delimited by Bigelow and Schroeder (1948). In contrast, *H. leucoperiptera* is usually placed in the family Triakidae. *Hemitriakis* cannot simultaneously reside in both families, but the problem goes beyond deciding in which family this genus belongs. This is because *Hemitriakis* is almost exactly intermediate between the Triakidae and Carcharhinidae as defined by modern writers. Hence the selection of a family for *Hemitriakis* is dependent on the validity of separating the Triakidae from the Carcharhinidae.

According to Bigelow and Schroeder (1948) and to Garrick and Schultz (1963), triakids differ from carcharhinids only by NLE morphology and dentition. The triakids are supposed to have rudimentary, external, and transitional NLE types (except for *Leptocharias* and *Triaenodon* with an internal NLE), whereas carcharhinids have an internal NLE. The teeth of triakids are small, crushing molariform or bladelike multicuspidate types that are present in several functional series on the jaw sides. Carcharhinid teeth are small to large, bladelike, with not more than 1 or 2 series of teeth functional at the sides of the jaws.

As noted by Garrick and Schultz, the separation of the two families is confounded by the seemingly intermediate positions of *Triaenodon*, *Leptocharias*, and *Hemitriakis japanica*. *Triaenodon* especially strains the classification by having "triakid" teeth and an internal NLE. However, Gohar and Mazhar (1964) claimed that *Triaenodon* belonged in the Carcharhinidae because it has a scroll intestinal valve as in *Carcharhinus* and other advanced genera. An unpublished study of the morphology of *Triaenodon obesus* confirms Gohar and Mazhar's results on the valvular intestine and also demonstrates that *Triaenodon* is very different from other "triakids" in its cranial morphology, pectoral fin skeletal structure, head morphology, and many other characters. Of the various triakid and carcharhinid genera, *Negaprion* is evidently closest to *Triaenodon*. The teeth of *Triaenodon* superficially resemble those of other "triakids" only in having premedial and postlateral cusplets flanking a primary cusp, but are otherwise strikingly different in the advanced morphology of their crowns and roots. It is probable that the "triakid" characters of *Triaenodon* are convergent ones.

Even without *Triaenodon* to complicate the issue, the familial separation of Triakidae from Carcharhinidae, using the traditional characters, fails when other genera are considered. Thus, *Hemitriakis* had bladelike, sharp-edged anteroposterior teeth in 1 to 5 functional series that closely resemble those of *Galeorhinus*, but has medials with multiple premedial and postlateral cusplets closely resembling "triakid" teeth. Its NLE is external, as in many, but not all, supposed triakids. *Furgaleus* combines *Galeorhinus*-like upper anteroposterior teeth, *Hemigaleus*-like lower anteroposteriors with one erect primary cusp and no cusplets, and an external NLE. *Furgaleus* is conventionally placed in the Triakidae. Another triakid, *Leptocharias*, has an internal NLE and anterolateral teeth with primary cusps, premedial cusplets, and postlateral cusplets in the "triakid" pattern. In the genus *Galeorhinus* (a presumed carcharhinid), young specimens of *G. australis*, *G. chilensis*, *G. galeus*, and *G. zyopterus* have a transitional NLE, but half-grown to adult individuals have these structures internal. Finally, *Triakis semifasciata* and *T. scyllia* have an external NLE in young specimens but this changes to a transitional or fully internal one in adults and subadults. Adult and subadult *Mustelus* commonly have a transitional NLE, but large *M. canis* may have the internal type (Garman, 1913; Bigelow and Schroeder, 1948). The teeth of *Triakis semifasciata* are arranged in only 3–4 functional series on the jaw edge. Also, in *T. semifasciata* the teeth show considerable ontogenic heterodonty, with loss of premedial and postlateral cusplets as the dentition is replaced until many to almost all of the teeth in adult specimens have only a strong, oblique primary cusp. *Triakis maculata* also shows a similar type of ontogenic heterodonty (Kato, Springer, and Wagner, 1967).

The orthodox distinction of Triakidae from Carcharhinidae is untenable at present because the supposedly diagnostic and traditional characters used to separate these families fail to do so. As the above examples show, there are enough transitional genera and species to make the retention of the two families Triakidae and Carcharhinidae an arbitrary choice based on tradition and convenience. I prefer to submerge the Triakidae in the Carcharhinidae. This has the obvious disadvantage of creating a huge, unwieldy, and heterogeneous complex that combines advanced forms with scyliorhinoid genera. However, it may be possible eventually to divide the family Carcharhinidae as here constituted into a number of lesser families using new characters of comparative morphology that are now being investigated.

Hence, the genus *Hemitriakis* is considered a member of the expanded family Carcharhinidae.

COMPARISON WITH OTHER GENERA

This section demonstrates the distinctness of *Hemitriakis* from other carcharhinid genera. A series of synoptic keys is presented in which allied groups of genera are compared and contrasted with *Hemitriakis*. A general key to carcharhinid genera is not offered here as revisional studies on the family are incomplete at present.

To facilitate comparison of *Hemitriakis* with certain genera, it was necessary to include some species rearrangements within them in the following discussions. This primarily involved removal of some species from the heterogeneous genera *Triakis* and *Galeorhinus* and proposal of tentative new generic arrangements to accommodate them.

Advanced and Intermediate Carcharhinids. A large proportion of carcharhinid genera comprise the two groups here termed the advanced and intermediate carcharhinids. The advanced genera include *Aprionodon*, *Carcharhinus*, *Galeocerdo*, *Hypoprion*, *Isogomphodon*, *Lamiopsis*, *Loxodon*, *Negaprion*, *Prionace*, *Rhizoprionodon*, *Scoliodon*, and *Triaenodon*. The intermediate genera are *Hemigaleus* (including *Chaenogaleus*, *Negogaleus*, and *Paragaleus*) and *Hemipristis* (including *Dirrhizodon* and *Heterogaleus*).

The advanced carcharhinids are so named because they depart furthest of all genera in the family from the morphology of generalized scyliorhinid genera widely thought to occupy the most primitive position among carcharhinoid sharks. The Sphyrnidae (hammerheads) is closely allied to the advanced carcharhinids but is not included for comparison with *Hemitriakis* because of its unique and obvious specializations. The intermediate genera are very similar to the advanced ones in many characters, but retain some generalized features in the morphology of the cranium, fins, dentition, and intestinal valve.

The advanced and intermediate carcharhinids are grouped together for brevity to compare them with *Hemitriakis*. The following synopsis covers only a representative sample of numerous differences between these genera and *Hemitriakis*.

1a. Eyes low on head, their ventral margins meeting or extending across the horizontal head rim. Subocular ridge weak or obsolete. NLE always internal, with slanted edge. Subocular pouch very deep, with inner surface of SLE and bottom of pouch lacking denticles. Crowns of teeth without a strong basal ledge and groove (except in lower teeth of *Hemigaleus*). Transverse ridges virtually absent from crown foot. Denticles of adults as wide or wider than long, with three or more subequal cusps and ridges. Precaudal pits present always at upper caudal origin and usually at lower origin also. Pectoral skeleton projecting at least ⅔ of pectoral anterior margin length into fin, with distal radials much longer than proximals. Distal radials with tapering, acute tips. Anal large relative to 2nd dorsal, its height 70 per cent or more of 2nd dorsal height. Lateral undulations present along dorsal caudal margin (except in young of some species and in *Scoliodon* where undulations are indifferently developed). Intestinal valve a scroll in advanced carcharhinids, but a spiral with only 2–6 turns in *Hemigaleus* and *Hemipristis*. Chondrocranium with isolated preorbital and postorbital processes only, without an intermediate supraorbital crest . . . Advanced and Intermediate Carcharhinids.

1b. Eyes high on head, their ventral margins widely separated from the horizontal head rim in ventral view. Subocular ridge very strong. NLE external, with edge horizontal. Subocular pouch shallow, with denticles covering its internal surface. Crowns of teeth with strong basal groove and ledge. Transverse ridges irregularly present on crown foot. Denticles of adults longer than wide, with a very strong medial ridge and cusp and flanking weak lateral ridges also; weak lateral cusps irregularly present. Precaudal pits absent. Pectoral fin skeleton projecting only ⅖ to ½ of pectoral anterior margin distance into fin, with distal radials slightly longer than proximals. Distal radials with parallel articulating edges and truncate tips. Anal relatively small in relation to second dorsal, its height only ½ that of second dorsal height. Lateral undulations of dorsal caudal margin absent. Intestinal valve a spiral, with 6–8 turns. Chondrocranium with strong supraorbital crest between preorbital and postorbital processes .... *Hemitriakis*.

Galeorhinus and Allied Genera. Recent workers have included the following species in *Galeorhinus*: *G. galeus* (Linnaeus, 1758); *G. japanicus* (Müller and Henle, 1841); *G. australis* (Macleay, 1881); *G. zyopterus* (Jordan and Gilbert, 1883); *G. chilensis* (Perez Canto, 1886), including *G. molinae* (Philippi, 1887); *G. omanensis* (Norman, 1939); *G. hyugaensis* Miyosi, 1939; *G. vitaminicus* de Buen, 1950; and *G. zanzibariensis* Smith, 1957. Of these nine species, four are sufficiently different to require removal from *Galeorhinus*. *"Galeorhinus" japanicus* has been already transferred to *Hemitriakis*. *G. hyugaensis* and the closely similar *G. zanzibariensis* are placed in the genus *Hypogaleus* and discussed below. *"Galeorhinus" omanensis,* as suggested by its describer (Norman, 1939), is not congeneric with *Galeorhinus* and will be discussed in a forthcoming paper by Mr. Stewart Springer and myself. It is included in the synopsis below to distinguish it from *Hemitriakis*.

The remaining 5 nominal species comprise the genus *Galeorhinus* as here delimited. Garman (1913), Fowler (1929, 1941), and Bigelow and Schroeder (1948) considered *G. zyopterus* a junior synonym of *G. galeus*, while Kato, Springer, and Wagner (1967) tentatively synonymized *G. chilensis* with *G. zyopterus*. McCoy (1885) compared *G. australis* with *G. galeus* and listed several proportional differences between a few specimens of *G. australis* and one of *G. galeus*. However, comparison of a pair of equal sized specimens of *G. galeus* and *G. australis* suggests that most, if not all, of McCoy's differences were allometric ones based on comparison of dissimilar sized specimens. *G. vitaminicus*, as described by De Buen (1950), is hardly different from other *Galeorhinus* species. It may be that all 5 species are synonyms, as Smith (1957b) maintained, but the validity of this hypothesis cannot be tested at present because of insufficient material.

Smith (1957b) proposed the subgenus *Hypogaleus* for its type, *Galeorhinus* (*Hypogaleus*) *zanzibariensis* Smith, 1957, and for *Hemitriakis japanica*. According to Smith, *Hypogaleus* species have teeth without the transverse notch on their roots, but in *Galeorhinus* (including only *G. galeus*) the notch is present. In *Galeorhinus* the caudal terminal sector is large, about ½ caudal length, but much smaller and less than ½ caudal length in *Hypogaleus*. *Hypogaleus* has the second dorsal at least twice as great in area as anal, but *Galeorhinus* has these fins subequal in size. In *Galeorhinus* the pelvic fins of adults are inserted behind the middle of the total length; in *Hypogaleus* the pelvics of adults are inserted well in advance of the middle of the total length.

Apparently Smith used only literature descriptions for *Hemitriakis japanica*. Although most of the fin characters for *Hypogaleus* fit *Hemitriakis japanica*, the dentitional character does not, as this species has a strongly developed transverse notch. Also, Smith's tooth photographs of *G.* (*Hypogaleus*) *zanzibariensis* seem to indicate that this species has much higher roots and obsolete basal ledges and

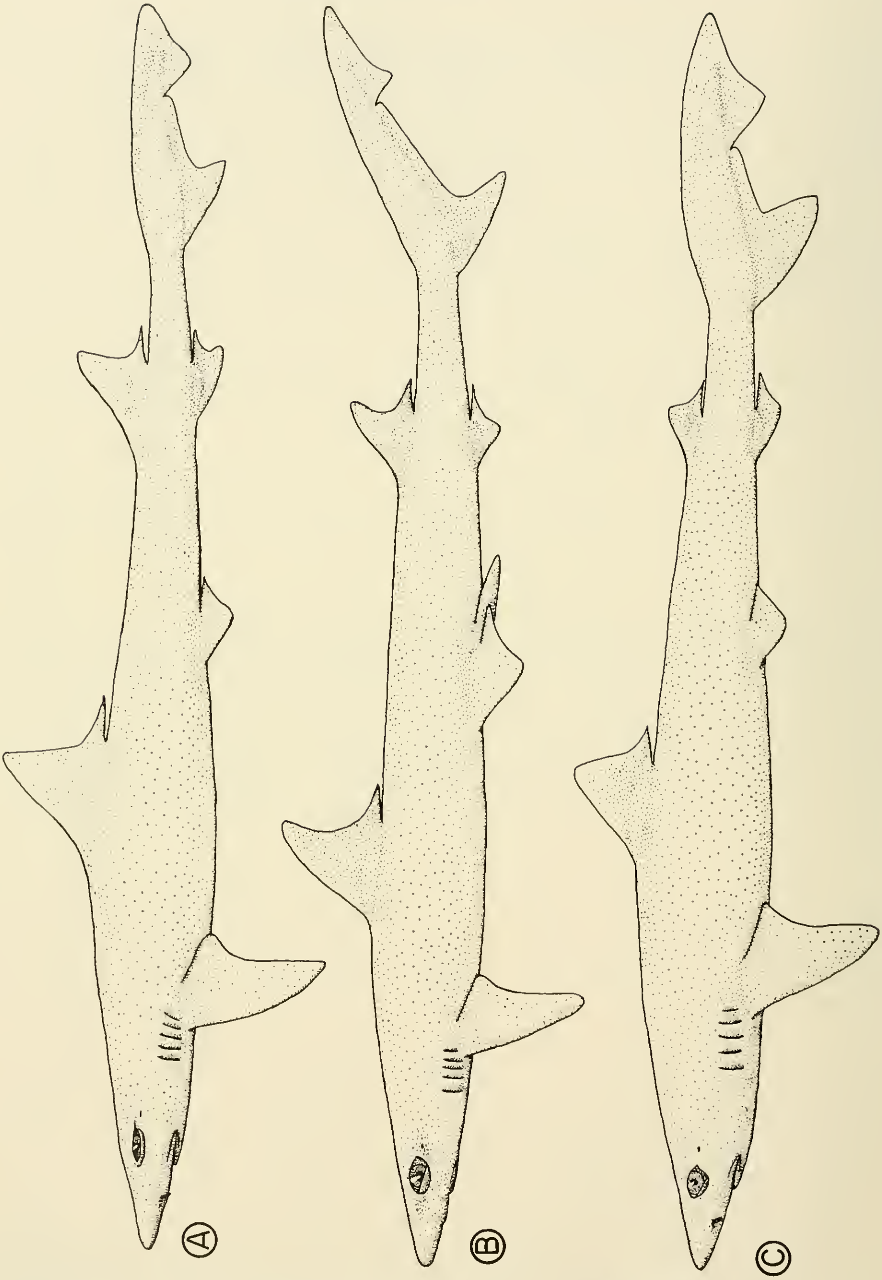

FIGURE 8. Lateral views of carcharhinid sharks. A. *Hemitriakis japanica* (SU-12677). B. *Hypogaleus zanzibariensis* (modified from Smith, 1957b). C. *Galeorhinus zyopterus* (LJVC-0238).

grooves on its teeth (figs. 4B, 4E). *Galeorhinus* and *Hemitriakis* as presently delimited have low roots and strong basal ledges and grooves (figs. 3, 4A, 4D).

Also, Smith did not examine Miyosi's (1939) description of *Galeorhinus hyugaensis*. Comparison of the accounts of *G. hyugaensis* by Miyosi and by Chen (1963) with those of *G. zanzibariensis* by Smith (1957b) and by D'Aubrey (1964) indicates that these species are virtually identical in all important details of morphology (including dentition) and coloration. Indeed, it will be necessary to compare specimens of the two species to determine what differences, if any, exist between them.

Galeorhinus zanzibariensis and *G. hyugaensis* are close to *Galeorhinus* proper and to *Hemitriakis* but are sufficiently different to merit generic status. Hence I propose to raise *Hypogaleus* Smith from subgenus to genus and include in it the two nominal species *H. hyugaensis* (Miyosi, 1939) and *H. zanzibariensis* (Smith, 1957).

The Australian genus *Furgaleus* is included here because its two species, as described and illustrated by Whitley (1943a, 1943b, 1944, 1948), have upper anteroposterior teeth that strongly resemble those of *Hemitriakis*, *Hypogaleus*, and *Galeorhinus*. *Furgaleus* is closest to *Hemitriakis* but is easily distinguished.

The following is a synopsis of *Galeorhinus* and allied genera (including *Hemitriakis*).

1a. Postlateral cusplets absent from anteroposterior teeth in upper jaw. Upper medial teeth without cusplets. First dorsal fin far forward, with origin over anterior half of pectoral base. Caudal fin without ventral lobe in adults .... "*Galeorhinus*" *omanensis*.

1b. Postlateral cusplets present on upper anteroposterior teeth. Upper medials with both premedial and postlateral cusplets. First dorsal origin posterior to pectoral base insertion. Caudal with moderate to strong ventral lobe in adults .... 2.

2a(1b.). Nostrils larger and closer together, their widths about twice in internarial width. Nostrils equidistant between snout tip and mouth. Anterior nasal flap formed into a long, slender barbel. Dignathic heterodonty strong, with upper anteroposteriors having oblique primary cusps and postlateral cusplets while lowers have erect primary cusps and no cusplets .... *Furgaleus*.

2b(1b.). Nostrils smaller and farther apart, their width 2½ times in internarial width or more. Nostrils much closer to mouth than to snout tip. Anterior nasal flap not produced into a barbel. Dignathic heterodonty weak; upper and lower anteroposteriors with oblique primary cusps and postlateral cusplets .... 3.

3a(2b.). Eyes high on sides of head, above level of nostrils by a space equal to or greater than eye height. Eyes over twice as long as high. NLE external in adults and subadults, with horizontal edge. Anterior nasal flap moderately large, expanded as a rounded lobe. Posteriormost anteroposterior teeth elongate, carinate. Interdorsal ridge present. Adult and subadult denticles with crowns much longer than wide and with lateral cusps and ridges weak. Caudal with short ventral lobe in adults and subadults (fig. 8A) .... *Hemitriakis*.

3b(2b.). Eyes lower on sides of head, above level of nostrils by a space less than eye height. Eyes twice as long as high or less. NLE internal in adults and subadults, with diagonal edge. Anterior nasal flap reduced, expanded as a minute, pointed lobe. Posteriormost anteroposterior teeth not elongate, carinate. Interdorsal ridge absent. Denticles of adults and subadults with crowns nearly as long as wide and with strong lateral cusps and ridges. Caudal with long ventral lobe in adults and subadults .... 4.

4a(3b.). Head very short, about ⅙ of total length in adults (fig. 8B). Subocluar ridge strong; in dorsal view eyes separated from horizontal head rim by a moderately wide space. Transverse notch absent from tooth roots (fig. 4B). First dorsal as large or larger than pectoral. Second dorsal about ⅔ as high as first dorsal and about twice as high as anal. Terminal sector of caudal about 2.6 in dorsal caudal margin. Upper postventral margin nearly ½ as long as dorsal caudal margin .... *Hypogaleus.*

4b(3b.). Head longer, over ⅕ of total length in adults (fig. 8C). Subocular ridge obsolete; in dorsal view ventral eye margins contact horizontal head rim. Transverse notch present on tooth roots (fig. 4A). First dorsal much smaller than pectoral. Second dorsal less than half as high as first one and subequal to the anal in height. Terminal sector of caudal about 2.0 in dorsal caudal margin. Upper postventral margin only about ¼ as long as dorsal caudal margin. .... *Galeorhinus.*

LEPTOCHARIAS AND *SCYLLIOGALEUS.* Two aberrant, monotypic African genera, *Leptocharias* and *Scylliogaleus*, differ greatly from *Hemitriakis.* While *Scylliogaleus* is apparently closest to typical *Mustelus* species, the taxonomic position of *Leptocharias* is quite isolated in the Carcharhinidae.

Leptocharias, *Hemitriakis*, and *Scylliogaleus* are compared in the following synopsis. Additional data on *Scylliogaleus* is from Boulenger (1902) and Smith (1957c).

1a. Eyes low on sides of head, above level of nostrils by less than eye height. Subocular ridge obsolete; ventral margin of eyes touching horizontal head rim in dorsal view. Eyes less than twice as long as high, with a slant-edged, internal NLE (fig. 2D). Spiracles minute, porelike, less than ⅒ of eye length. Anterior nasal flap expanded as a pointed barbel. Gynandric heterodontia strong, expressed by presence of about 4 tooth rows of hypertrophied "anteriors" in both jaws on either side of weakly differentiated medials in adult males but not females. Teeth other than anteriors with slender, erect primary cusps and both premedial and postlateral cusplets, not bladelike or molariform. Vertebrae very numerous, 198–213 total centra (9 examples; data for 2 from Springer and Garrick, 1964). Spiral intestinal valve with about 16 turns. Supraorbital crest absent from cranium, with isolated preorbital and postorbital processes only .... *Leptocharias.*

1b. Eyes higher, above level of nostrils by an eye height or more. Subocular ridge strong; eyes separated from horizontal head rim by a wide space. Eyes over twice as long as high, with horizontal-edged and external NLE (fig. 7A). Spiracles larger, ⅓ to ⅐ of eye length. Anterior nasal flap not formed into a barbel. Gynandric heterodonty not apparent. Teeth either molariform or bladelike, without premedial cusplets (except on medials of *Hemitriakis*). Vertebrae fewer, 143–161 total centra (10 examples). Spiral valve with 6 to 8 turns. Supraorbital crest present on cranium .... 2.

2a(1b.). Snout bluntly rounded, semicircular in shape. Anterior nasal flaps greatly enlarged as broad triangular lobes extending posteriorly to overlap mouth. Nostrils very large and separated by a distance much shorter than a nostril width. Deep nasoral grooves present. Teeth with crowns flattened and rounded to form a crushing pavement as in typical *Mustelus* species. Teeth not differentiated into medials and anteroposteriors. Tooth rows 60–72 in each jaw; 9–10 series functional in upper jaw, 16–17 in lower (Smith, 1957c).

Pelvics large, anterior margin lengths ½ or more of pectoral anterior margin lengths. Free rear tip of first dorsal over or posterior to pelvic origins .... *Scylliogaleus.*

2b(1b.). Snout narrower, parabolic in shape. Anterior nasal flaps small truncate lobes, terminating far anterior to mouth. Nostrils smaller, further apart, their widths about 2½ times in internarial width. Nasoral grooves absent. Teeth differentiated into medials and anteroposteriors, not forming a pavement. Anteroposteriors sharp-edged, bladelike teeth, with oblique primary cusps and postlateral cusplets; medials are not bladelike and have premedial cusplets also. Tooth rows fewer, 18(?)–39/27–34; only 1 to 5 series functional along jaw edges. Pelvics smaller, their anterior margins less than ½ length of anterior pectoral margins. Free rear tip of first dorsal anterior to pelvic origins .... *Hemitriakis.*

TRIAKIS AND ASSOCIATED GENERA. Included here are those species placed by Bigelow and Schroeder (1948) and by Kato (1968) in the genera *Triakis*, *Mustelus*, *Eridacnis*, and *Calliscyllium.*

The systematics of *Triakis* and its relatives is unsatisfactory at present. This is in part due to the interpretations of *Triakis* by Garman (1913), Fowler (1929, 1941), Bigelow and Schroeder (1944, 1948), Garrick (1954), Kato (1968), and Springer (1968), which included several scyliorhinid-like species in this genus that are clearly not congeneric with typical *Triakis* species (as *T. scyllia* and *T. semifasciata*). Also, the separation of *Triakis* from *Mustelus* on differences in tooth crown morphology seems untenable, as there are many dentitionally intermediate species between "typical" extremes of these genera. Bigelow and Schroeder (1940) and Kato (1968) have discussed the latter problem in detail, but left the two genera separate.

Smith (1957a) proposed a solution to the *Triakis* heterogeneity problem. He removed *Calliscyllium venustum* Tanaka from *Triakis* and reinstated *Calliscyllium* Tanaka as a monotypic genus for it. Also, he proposed the genus *Neotriakis* for his *N. sinuans* and for *Triakis barbouri* Bigelow and Schroeder. Finally, he transferred *Triakis henlei* (Gill) to *Mustelus.*

Smith's separation of *Calliscyllium* and *Neotriakis* from *Triakis* is undoubtedly correct, as species included in these scyliorhiniform genera exhibit many differences from typical *Triakis.* Unfortunately, Smith retained two anomalous species, *Triakis attenuata* Garrick and *Hemitriakis leucoperiptera* Herre, in the genus *Triakis. Triakis attenuata* is closer to *Calliscyllium* and *Neotriakis* in the sense of Smith than to *Triakis* proper, and its presence in *Triakis* makes separation of that genus from *Neotriakis* especially difficult with the limited and ambiguous generic characters utilized by Smith to define these genera. Finally, placement of *Triakis henlei* in *Mustelus* further undermines the classical tooth crown differences purported to separate *Triakis* from *Mustelus*; however, *T. henlei* is closer to typical forms of *Mustelus* than to those typical of *Triakis* in many respects. Smith was evidently unaware of the *Triakis-Mustelus* continuity problem, as he later (1957c) gave *Mustelus* familial separation from *Triakis* in his family Scylliogaleidae (along with *Scylliogaleus*).

A tentative reclassification of *Triakis* and associated genera is presented here, subdividing these taxa into two groups: 1. Typical forms of *Triakis*, intergrading species, and typical *Mustelus* forms. 2. Scyliorhiniform triakoids, including as subgroups: A. Genus *Proscyllium*; B. Genus *Eridacnis*; C. *Triakis fehlmanni*; D. *T. attenuata*.

Triakis, *Mustelus*, and intermediates (or *Triakis-Mustelus*) are closer to *Hemitriakis* than are other carcharhinids. *Triakis-Mustelus* includes *Triakis scyllia*, *T. semifasciata*, *T. maculata*, *T. acutipinna*, *Mustelus henlei*, and the various other *Mustelus* species.

Typical species of *Triakis*, with strongly cuspidate teeth (*T. scyllia*, *T. semifasciata*), form one extreme of a dentitional continuum with molariform-toothed *Mustelus* species at the other extreme. The continuum is filled by a host of dentitionally intermediate forms, as *T. maculata*, *T. acutipinna*, *Mustelus nigropunctatus*, *M. henlei*, *M. dorsalis*, *M. megalopterus*, *M. natalensis*, and *M. higmani*, that exhibit various stages of cusp and cusplet reduction on tooth crowns. Also, examination of small (150–450 mm. total length range) specimens of typical *Mustelus* species, as *M. canis*, *M. californicus*, *M. manazo*, *M. mustelus*, *M. lunulatus*, and *M. griseus*, indicates that cusps are often well developed on the teeth of small individuals and that cusp obsoleteness in larger examples probably results from ontogenic heterodonty.

Although condition of tooth cusps has been the only character regularly utilized in separating *Triakis* from *Mustelus*, extremes of the former genus differ from typical members of the latter by a number of additional characters. These include: 1. Absence of peg on inner face of crown and root. 2. Lesser number of tooth rows. 3. Lesser number of tooth series. 4. Absence of a tooth pavement. 5. Bluntly rounded, short snout (versus long, pointed or paraboloid snout in *Mustelus*). 6. Very short, arcuate mouth (versus longer, more angular mouth in many *Mustelus* species). 7. Reproduction ovoviviparous (viviparous in at least some *Mustelus*, including *M. henlei*). In addition, there are about a dozen cranial differences between *Triakis semifasciata* and 3 species of *Mustelus* (*M. henlei*, *M. californicus*, and *M. lunulatus*, which are virtually identical cranially). The brain, cranial nerves, and sense organs of *T. semifasciata* also differ in several respects from those of *M. henlei*.

The tooth peg is found in many *Mustelus* species (including *M. henlei*), but not in *Triakis maculata*, *T. scyllia*, or *T. semifasciata*. Its condition is not confirmed for all species of *Triakis-Mustelus* and cannot be used to separate the two genera at present. Tooth row and series counts apparently vary along a continuum as in crown morphology, with an added complication that in at least some *Mustelus* (if not all forms) the tooth row and series counts increase with size increase. Tooth pavementization, snout shape, and mouth morphology evidently show a similar variation spectrum. Data on cranial, neural, and reproductive characters is not available for many to most *Triakis-Mustelus* species, making it impossible to judge their utility in separating the two genera.

External morphology suggests that *Triakis* is not separable from *Mustelus*, but merging the two genera here would be premature with incomplete knowledge of promising anatomical characters. However, *Triakis-Mustelus* is treated as a single unit here for comparison with *Hemitriakis*.

The scyliorhiniform triakoids include species formerly placed in the genera *Proscyllium*, *Calliscyllium*, *Eridacnis*, *Neotriakis*, and *Triakis*. They are divisable into four subgroups, two of which are provisionally ranked as genera.

The first genus, *Proscyllium*, is a structural link between the Carcharhinidae and Scyliorhinidae but is placed in the former family because of its anteriorly positioned first dorsal fin.

The systematic treatment of *Proscyllium* and its synonym, *Calliscyllium*, by various writers has been highly variable and extremely confusing. Hilgendorf (1904) proposed *Proscyllium* as a subgenus of *Scyllium* Cuvier (= *Scylliorhinus* Blainville), with a single new species, *S.* (*Proscyllium*) *habereri*, from Formosa. Later Tanaka (1912) described a new genus and species, *Calliscyllium venustum*, from Japan. Tanaka did not mention Hilgendorf's very similar species in his account. Although Tanaka considered *Calliscyllium* a scyliorhinid, Garman (1913) placed it in his family Galeorhinidae (= Triakidae) and synonymized it with *Triakis*. Garman also placed *Scyllium* (*Proscyllium*) *habereri* in the Catulidae (= Scyliorhinidae) and raised the rank of *Proscyllium* to genus. Schmidt (1930) described and illustrated a Japanese specimen of *Proscyllium habereri*. His account is of special interest as he compared his specimen with measurements and photographs of the holotype of Hilgendorf's species and found no significant differences between the two specimens. Schmidt's account of *Proscyllium habereri* closely matches Tanaka's description of *Calliscyllium venustum*, but for unknown reasons Schmidt did not refer to Tanaka's account or to his own (1928) description of an Okinawan specimen of *Calliscyllium venustum*. White (1937) recognized both *Calliscyllium venustum* and *Proscyllium habereri* as scyliorhinids in a broad sense but placed the former in her family Halaeluridae and the latter in her family Catulidae. Fowler (1929, 1941) followed Garman in placing *Proscyllium* in Scyliorhinidae and placed *Triakis venusta* (Tanaka) in the subfamily Triakiinae of the family Eulamiidae or Galeorhinidae (= Carcharhinidae). Bigelow and Schroeder (1948) placed *Proscyllium habereri* in the family Triakidae, but did not discuss its generic status in that family. These writers followed Garman's synonymy of *Calliscyllium* with *Triakis*. Garrick (1954) discussed *Triakis venusta*, but not *Proscyllium habereri*. Smith (1957a) recognized *Calliscyllium* as distinct from *Triakis*, but also overlooked *Proscyllium habereri*. Lindberg and Legeza (1959) synonymized *Proscyllium* with *Triakis*, but considered

Triakis habereri distinct from *T. venusta.* Chen (1963) placed both *Proscyllium habereri* and *Triakis venusta* in the family Triakidae, but separated *Proscyllium* from *Triakis* by supposed absence of the NLE in the former genus. Finally, Kato (1968) removed *Calliscyllium* from synonymy of *Triakis* on reproductive differences, but did not mention *Proscyllium.*

Comparison of accounts of *Proscyllium habereri* and *Calliscyllium venustum* with each other and with specimens indicates that Lindberg and Legeza were correct in regarding these species as congeneric. However, "*venustum*" and "*habereri*" are not congeneric with typical species of *Triakis* and are placed here in the genus *Proscyllium. Calliscyllium* is therefore a junior synonym of *Proscyllium.* The two species *P. venustum* and *P. habereri* are possibly synonyms also, as the small differences between them listed by Lindberg and Legeza (1959) may be of only variational and allometric significance.

The genus *Eridacnis* includes a few species of deepwater sharklets allied to *Proscyllium* but sufficiently different to merit generic status.

Eridacnis was established by Smith (1913) for *E. radcliffei,* a new shark from the Philippine Islands. *Eridacnis* was supposed to differ from *Triakis* Müller and Henle by lacking labial furrows, but, as Kato (1968) pointed out, the holotype of *E. radcliffei* has vestigial labial furrows presumably overlooked by Smith. Bigelow and Schroeder (1944) described as *Triakis barbouri* a similar but specifically distinct shark from Cuba, but did not compare it with *Eridacnis radcliffei.* Misra (1950) described a third form, *Proscyllium alcocki,* from the Andaman Sea. Data from Misra's account indicates that "*alcocki*" does not belong in *Proscyllium* as here defined but falls in *Eridacnis* instead. The species "*alcocki*" closely resembles *E. radcliffei* and therefore it is quite possible that these two names are synonymous (Norman, 1939, reported *E. radcliffei* from the Gulf of Aden, which is *west* of the type localities of both *E. radcliffei* and "*alcocki*"). Smith (1957a) described a new genus, *Neotriakis,* for his new South African species *N. sinuans.* Smith included *Triakis barbouri* in *Neotriakis* but overlooked *Proscyllium alcocki* and did not compare *Neotriakis* species with the closely similar *Eridacnis radcliffei.* Kato (1968) considered the characters used to separate *Neotriakis* and *Eridacnis* from *Triakis* to be untenable, and synonymized the three genera. However, Kato regarded the species "*radcliffei,*" "*barbouri,*" and "*sinuans*" as closely related to each other within the genus *Triakis.* Kato's synonymy was adopted unchanged by Springer (1968).

The genus *Eridacnis* is revived here for the species *E. racliffei, E. alcocki, E. barbouri,* and *E. sinuans,* with *Neotriakis* considered as a junior synonym.

Triakis fehlmanni, a small shark recently described by Springer (1968) from Somalia, forms a third group closely similar to *Proscyllium* and *Eridacnis* in many details. Its vertebral calcification pattern and relatively short broad caudal are as in *Proscyllium,* but its vertebral count, vertebral group ratios, short body cavity, nostril spacing, pectoral fin position, first dorsal size, and anal base size fit *Eridacnis.* The blotched and spotted color pattern, extremely short precaudal tail (distance from cloaca to lower caudal origin about twice in distance from snout tip to cloaca), broad head, and stout body distinguish "*fehlmanni*" from both *Proscyllium* and *Eridacnis.* Mode of reproduction and clasper morphology are unknown for the species. *Triakis fehlmanni* seems closer to *Eridacnis* than *Proscyllium* but may require subgeneric or generic separation from typical *Eridacnis* species. It does not belong to *Triakis-Mustelus* as here limited and cannot be confused with *Hemitriakis.* Generic placement of "*fehlmanni*" is problematical at present; therefore the species must be left as a tentative and possibly dubious appendage to *Eridacnis.*

The New Zealand *Triakis attenuata*, as described by Garrick (1954), agrees with *Proscyllium*, *Eridacnis*, and *T. fehlmanni* in its NLE type, detailed tooth morphology, eye position, and large second dorsal, but differs from these forms in its elongate snout, narrower and more widely spaced nostrils, longer labial furrows, more numerous tooth rows, more anterior position of first dorsal fin, origin of second dorsal anterior to anal origin, exceptionally small anal fin with base only half length of second dorsal base, weak ventral caudal lobe, and larger size. Unfortunately nothing is known of its cranium, pectoral fin skeleton, vertebral calcification pattern, vertebral counts, vertebral group ratios, clasper morphology, and buccal cavity. *Triakis attenuata* presumably forms a tentative fourth group of scyliorhiniform triakoids allied to, but distinct from, *Proscyllium-Eridacnis-T. fehlmanni.* The species is remote from *Hemitriakis* and is sufficiently different from *Triakis-Mustelus* to be excluded from that group. Separate generic status may be required for *T. attenuata*, but insufficient data on the species prohibits a decision on the matter for now.

The following generic synopsis compares *Hemitriakis* to *Triakis-Mustelus*, *Proscyllium*, and *Eridacnis* (excluding *T. fehlmanni*).

1a. NLE rudimentary in adults (fig. 2A.). Labial furrows vestigial, confined to corners of mouth. All teeth with erect cusps and usually cusplets also (some species have teeth near symphysis lacking cusplets). Posterior teeth polycuspidate, comblike in shape (fig. 4C). Gradient monognathic heterodonty present, in which premedial cusplets increase in number from symphysis to rictus and displace primary cusp from central position on crown foot to a postlateral location. Cusps and cusplets do not become obsolete with age. First dorsal fin with midpoint of its base closer to pelvic origins than to pectoral insertions. Second dorsal origin over or posterior to anal origin. Pectoral fin skeleton as in scyliorhinids, with distal radials much shorter than proximal ones. Vertebral centra of thoracic region in adults with peripheral calcifications of the intermedialia only, not developed into strong lateral and vertical wedges between halves of calcified primary double cone (figs. 5A, 5B.). Diagonal calcified lamellae of double cone, when present, in form of rounded lobe opposite each basidorsal and basiventral. Large papillae present on dorsal and ventral surfaces of buccal cavity and pharynx posterior to teeth, forming dermal gill rakers along internal branchial apertures .... 2.

1b. NLE external, transitional, or internal in adults. Labial furrows well developed, extending far onto jaws. Teeth either cuspless or with cusps that range from erect to strongly oblique and often showing monognathic heterodonty in increasing obliqueness toward ends of dental band. Posterior teeth carinate, molariform, or weakly monocuspidate, not comblike (fig. 4F.). Increase of premedial cusplets and displacement of primary cusp postlaterally not apparent in species with cuspidate teeth, but instead cusps and cusplets tend to become less prominent postlaterally and may be completely absent on posteriormost teeth. Many species (not including *Hemitriakis*) tend to reduce or lose cusplets or even cusps with age. First dorsal fin with base midpoint equidistant between pectoral insertions and pelvic origins or closer to pectoral insertions. Second dorsal origin well anterior to anal origin. Pectoral fin skeleton with distal radials equal in length to, or longer than, proximal ones. Vertebral centra of thoracic region of adults and subadults with intermedialia extending as strong lateral and vertical wedgelike calcifications between halves of calcified primary double cone (figs. 5C, 5D.). Diagonal calcified lamellae well developed, extending as thin plates into the basidorsals and basiventrals. Papillae absent from buccal cavity, pharynx, and internal branchial apertures .... 3.

2a(1a.). Nostrils very close together, internarial width only ½ nostril width. Distance from hind edge of anterior nasal flaps to mouth only about ⅙ of nostril width. Head length from snout tip to 5th gill opening shorter than body length from pectoral insertion to pelvic origin. First dorsal length from origin to free rear tip less than ½ length of interdorsal space. Anal base length only ½ of distance between anal insertion and lower caudal origin. Caudal short, less than ⅕ of total length. Greatest height of caudal about ¼ of upper caudal margin. Vertebrae more numerous, total count 146–168 (6 examples). DP/MP ratios 1.58–1.82; DC/MP 1.08–1.28. Diagonal calcified lamellae of trunk centra present as four rounded lobes extending slightly into areas of basidorsals and basiventrals (fig. 5B.). Claspers of adult males with a row of recurved clasper hooks along external flap of hypopyle. Color pattern of scyliorhinid-like spots and stripes present. Reproduction oviparous .... *Proscyllium.*

2b(1b.). Nostrils farther apart, internarial width about equal to nostril width. Distance from hind edge of anterior nasal flaps to mouth about ½ of nostril width. Head length longer than body length from pectoral to pelvic. First dorsal length ⅗ to ⅘ of interdorsal space. Anal base length subequal to distance between anal insertion and lower caudal origin. Caudal longer, over ¼ of total length. Greatest height of caudal less than ⅕ of upper caudal margin. Vertebrae less numerous, total count 113–135 (26 examples). DP/MP ratios 1.05–1.45; DC/MP 1.29–1.53. Diagonal calcified lamellae not developed in trunk centra (fig. 5A.). Claspers without hooks. Coloration plain or with a few obscure stripes confined to tail. Reproduction ovoviviparous as far as is known .... *Eridacnis.*

3a(1b.). Nostrils narrow and farther apart; nostril width about 2½ times in internarial width. Teeth larger, basal width of largest lower anteroposteriors about 0.356 to 0.405 percent of total length (*H. japanica*, 4 examples). Teeth differentiated into medials and anteroposteriors. The latter are strongly compressed, bladelike cutting teeth with an oblique primary cusp and a few small postlateral cusplets only. Fewer tooth rows present, ?18–38/24–34. Pelvic fins with anterior margins less than half as long as pectoral anterior margins .... *Hemitriakis.*

3b(1b.). Nostrils wider, closer together; nostril width 2 times or less in internarial. Teeth smaller, those of species with largest teeth (*Triakis semifasciata*) only 0.172 to 0.262 percent of total length (largest lower teeth, 11 examples) and considerably smaller in other species. Teeth not differentiated into distinct medials and anteroposteriors, but showing regular gradient monognathic heterodonty between rows in symphysial and parasymphysial regions. Teeth corresponding to anteroposteriors of *Hemitriakis* either cuspless or having an erect or oblique median primary cusp and usually both premedial and postlateral cusplets when cusplets are present. Teeth more weakly compressed, not sharp-edged, modified for grasping or crushing. More tooth rows present, 44–80+/33–80+. Pelvic fins larger, with anterior margins over ½ as long as pectoral anterior margins .... *Triakis-Mustelus.*

SUMMARY

The shark *Galeus japanicus* Müller and Henle, long considered a species of *Galeorhinus* Blainville (or one of its synonyms), is placed in the genus *Hemitriakis* Herre, which is removed from the synonymy of *Triakis* Müller and Henle and redefined. *Hemitriakis* contains two described species, *H. japanica* (Müller and Henle) and *H. leucoperiptera* Herre.

The familial position of *Hemitriakis* is discussed and the separation of the families Triakidae and Carcharhinidae is rejected on present evidence. *Hemitriakis* is placed in the expanded family Carcharhinidae.

Other carcharhinid genera are compared with *Hemitriakis* in synoptic keys, and several tentative systematic rearrangements of species in certain genera are presented to facilitate comparison with *Hemitriakis.* The genus *Galeorhinus* is restricted to the nominal species *G. galeus, G. australis, G. zyopterus, G. chilensis,* and *G. vitaminicus,* while a former subgenus, *Hypogaleus* Smith, is accorded generic rank. *Hypogaleus* contains two nominal species, *H. zanzibariensis* (Smith) and *H. hyugaensis* (Miyosi). Consideration of *Galeorhinus omanensis* (Norman) is postponed for another paper.

In addition to *Hemitriakis,* four tentative groups of scyliorhiniform triakoids are removed from *Triakis.* The first is the genus *Proscyllium* Hilgendorf, of which *Calliscyllium* Tanaka is a junior synonym. *Proscyllium* has two nominal species, *P. habereri* (Hilgendorf) and *P. venustum* (Tanaka). The genus *Eridacnis* Smith forms the second group, with *E. radcliffei* Smith, *E. barbouri* (Bigelow and Schroeder), *E. sinuans* (Smith), and the dubious *E. alcocki* (Misra) as its constituent species. The last two groups contain *Triakis fehlmanni* Springer and *T. attenuata* Garrick; these are not given genus-group names because of insufficient evidence on the generic relationships of their species.

The problem of separating the restricted genus *Triakis* from *Mustelus* Linck is discussed, but no solution is seen at present and the two genera are considered as one unit for comparison with *Hemitriakis.*

A terminology for head morphology, nictitating lower eyelid structure, dentition, vertebral groups, and fin morphology is proposed for use with carcharhinids.

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NOTES ON THE NATURAL HISTORY OF SNIPE EELS

By

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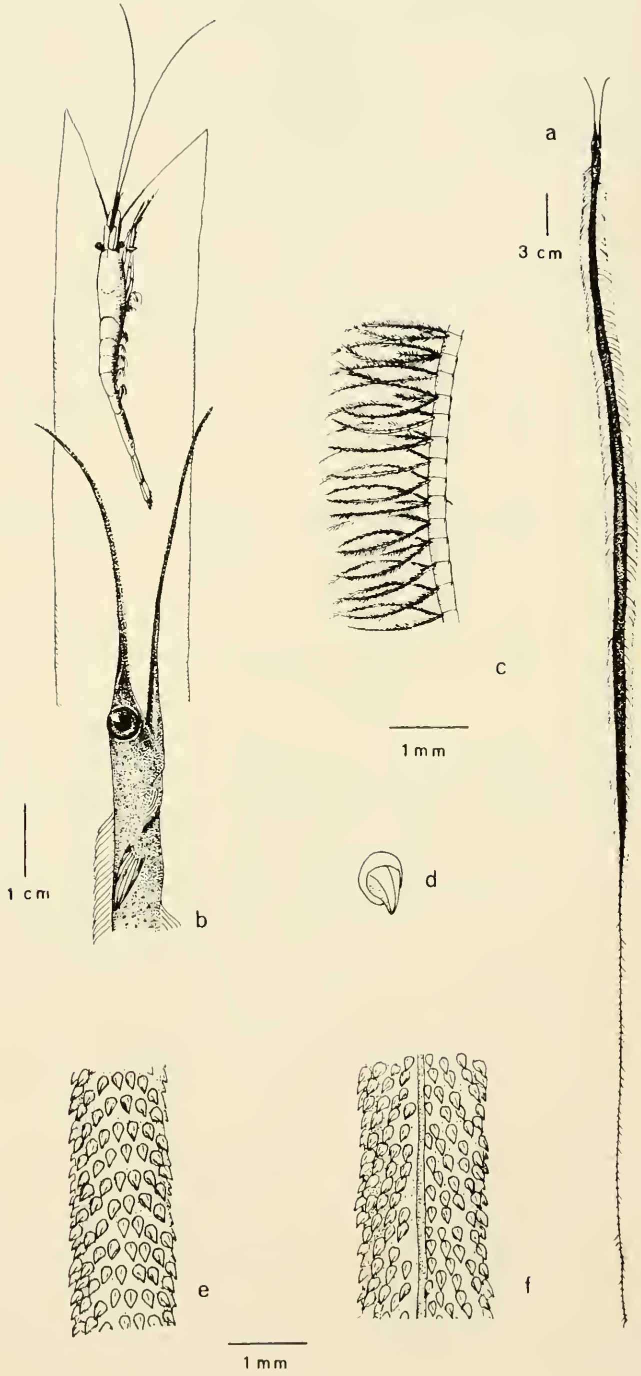
One cannot fail to be impressed by the adaptations for midwater life developed by the mesopelagic eels, an assemblage doubtless derived from a benthic ancestor. In most the body has become far more attenuated than that of the most elongate of their benthic relatives, the terminal part of many being filamentous and apparently composed of little more than minute and poorly ossified vertebrae covered by thin skin and supporting fine and hair-like fin rays. This attenuation is accomplished by an increase in number of vertebrae rather than an increase in the length of each. An apparently intact specimen of *Nemichthys* taken during the International Indian Ocean Expedition of 1964 had 670 vertebrae—certainly a record number among the vertebrates. Equally extreme are specializations in mouth parts. The teeth, for example, vary vastly in form, number and position.

The more extreme genera such as *Nemichthys, Labichthys,* and *Avocettina* are of concern here. All have greatly prolonged jaws (fig. 1b) that bear numerous small teeth laterally as well as dorsally or ventrally (fig. 1d–f), and are usually tipped by flattened bony pads that bear teeth or rugosities on all sides. The jaw teeth are arranged in chevron-shaped consecutive series or, in others, in quincunx. The two halves of the lower jaw are loosely conjoined laterally for most of the length of the mandible. The principal part of the upper jaw, in


a
3 cm
c
1 mm
1 cm
b
d
e
f
1 mm

contrast to other fishes, is composed of the vomer; and the biting elements of other lower fishes, the maxillae, are reduced to lateral struts that support the base of the prolonged vomerine bar (Beebe and Crane, 1937). The positional relationship of these jaws has been particularly enigmatic, for they diverge forward from the gape so that their tips, and often as much as half of the total length of the jaws, cannot be brought into contact with each other when the mouth is as far closed as it can be. These fishes can but partially close their mouths, yet the distal ends of their jaws, that cannot possibly be brought into contact with each other, bear thousands of small chisel-shaped posteriorly inclined teeth (fig. 1d–e) reminiscent of the shagreen of an elasmobranch. What can be the function of such a structure?

That these jaws are used to funnel microplankton toward the mouth as the eel swims through the water seems unlikely. Lateral movement of the prey by but a millimeter or two would take it beyond the grasp of the predator. To feed in this way, structural adaptation similar to that in the herrings would be more in order. It has also been suggested that these prolonged jaws simply provide greater surface area, and might be considered adaptations for flotation. While we would consider the attenuated but fin-bearing shape of the body the result of selection toward greater surface area that serves the interests of flotation, we are reluctant to so consider the development of well ossified structures richly endowed with small but dense teeth. Such a beak would also seem to be the antithesis of a structure developed in aid of streamlining or locomotion. Nichols and Murphy (1944) repeated a report by Mowbray (1922) of a snapper captured in Bermuda with a 265 mm. representative of *Nemichthys scolopaceus* attached by its slender jaws to the posterior margin of the snapper's caudal fin. Mowbray concluded, "The specimen being taken in this way gives good reason to believe that grasping the tails of fishes is the function of the divergent mandibles of these eels."

We can suggest an alternative function for these diverging and nonocclusable jaws, a suggestion emanating from observations made at mid-depths from the late D.S.R.V. *Alvin* and catches made concurrently by a supporting vessel, R.V. *Gosnold*, both of the Woods Hole Oceanographic Institution. These dives were made between October 2 and 6, 1967, in Slope Water of the western North Atlantic in an attempt to observe visually certain sound-scattering targets at

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Figure 1. a. Snipe eel, *Nemichthys scolopaceus*, in typical vertical position as observed from the D.S.R.V. *Alvin*. b. Vertically oriented specimen of *N. scolopaceus* and sergestid shrimp, *Sergestes (Sergestes) arcticus*, drawn from specimens taken by R.V. *Gosnold* concurrent with D.S.R.V. *Alvin* observations. c. Distal portion of antenna of *S. (S.) arcticus*. d. Tooth from upper jaw of *N. scolopaceus*. e. Inner surface of upper jaw of *N. scolopaceus*. f. Inner surface of lower jaw of *N. scolopaceus*.

mid-depth (see Backus *et al.*, 1968). Concurrent with these dives, R.V. *Gosnold* fished similar depths with a 10-ft. Isaacs Kidd Midwater Trawl.

Observers aboard *Alvin* frequently saw snipe eels (*Nemichthys*) at depths below 300 m. and confirmed the observations of others that these eels are usually oriented vertically in the water, motionless or but slightly undulating, and usually with their divergent jaws directed upward. Among the other more spectacular animals seen at comparable depths were relatively large sergestid decapods. These too were often suspended vertically in the water, their bright orange-red stomachs and organs of Pesta prominent, the short pleopods beating furiously, and their long antennae extending upward and outward away from the body and then turning abruptly to follow a course parallel to the axis of the body to a point considerably below the tail. Neither eels nor sergestids appeared to be disturbed by the lights of the submarine.

Both sergestids and snipe eels were caught by the nets of the *Gosnold*. The eels belong to *Nemichthys scolopaceus* Richardson, 1848, and the sergestids, kindly identified for us by Mr. Peter Foxton of the National Institute of Oceanography, Godalming, belong to *Sergestes* (*Sergestes*) *arcticus* Kröyer, 1855. Representatives of *Nemichthys*, as usual, were present in the catch with beaks entangled in everything present, living or not. Several were hanging by their beaks from the upper part of the netting as the trawl was raised above the water, the red stomachs of ingested sergestids visible through the semitransparent stomachs and body walls. This material was returned to Woods Hole and to the Museum of Comparative Zoology, Harvard University, for study and is deposited in the latter institution.

The stomach contents of about 160 specimens of *Nemichthys* were examined. In addition to the *Gosnold* collection these included others variously collected in the western North Atlantic and those from the Indian Ocean and off central Chile that were caught during Cruises VI and XIII, respectively, of R.V. *Anton Bruun*. Most stomachs were empty. Those which were not, contained crustacean remains exclusively. An examination of the specimens of *Sergestes* which were available and published accounts of others (Burkenroad, 1934, 1937; Foxton, 1969; Hardy, 1956) revealed the complexity of the prolonged antennae with their multiple sensory hairs, structures admirably suited to aid in flotation.

We believe that the function of the beak of the snipe eels can be added to the list of features in which these eels are unique among vertebrate animals, for we suggest here that these animals feed by entanglement. Given the vast extent and thread-like nature of some appendages of many mesopelagic crustaceans and the set and structure of snipe eel dentition, the evolution of structures adapted for the feeding of one on the other seems reasonable. The antennae of a sergestid if brushed across the bed of teeth of a snipe eel would almost certainly become entangled, and struggle by the prey would only worsen its plight, shorten the distance between shrimp and fish; and ultimately bring the prey within that more posterior part of the jaws capable of crushing and swallowing movements.

Such a feeding mechanism is consistent with present concepts of midwater ecology. Food in the deep ocean is scarce and energy precious. Hovering and darting, or luring types of predation tend to replace the roving activities more prevalent near the surface. Intake per unit of energy expended must be high if a predator is to survive. What finer an example of adaptation to these conditions can there be than that of these eels: hanging effortlessly with flotation facilitated through attenuation of the body, and with jaws covered by myriads of denticles exquisitely designed to entangle the appendages of passing crustacea, be they moving laterally or, with some, rising or descending as a part of their daily routine.

ACKNOWLEDGMENTS

This note owes its existence to an invitation to one of us to dive aboard *Alvin* and we thus record our grateful appreciation to the Woods Hole Oceanographic Institution and especially to Dr. Richard H. Backus of that institution for that opportunity. In addition to identifying the sergestids, Mr. Peter Foxton, National Institute of Oceanography, Godalming, reviewed the manuscript, as did Drs. Backus, R. L. Haedrich, and J. E. Craddock of the Woods Hole Oceanographic Institution. This paper is contribution number 2351 from the Woods Hole Oceanographic Institution.

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THE ZOOGEOGRAPHY OF THE HERPETOFAUNA OF THE PHILIPPINE ISLANDS, A FRINGING ARCHIPELAGO

By

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and

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INTRODUCTION

Inger, in his essay on the zoogeography of the Philippine amphibia (1954, pp. 448–510), presented the first major distributional paper for any part of the herpetofauna since Taylor's essay (1928). The first part of Inger's paper is concerned with the geological history of the Philippines, and the origins and degree of endemism exhibited by the amphibian fauna. Secondly, he discusses the pathways of entry into the Philippines in terms of the location of the nearest relatives and possible time of entry into the Philippines. He notes, for example, that the present distribution of the genus *Platymantis* (replaces *Cornufer*, Zweifel, 1967) suggests two speciation centers, one in the New Guinea-Solomons region and one in the northern Philippines; but by analogy, in comparison with some other amphibians, suggests a Papuan origin and subsequent dispersal into the Philippines. Inger therefore regards these two present centers as peripheral isolated concentrations of a once more widely distributed genus (1954, pp. 494, 497). He suggests that the bulk of the amphibians entered the Philippines by 2 major routes, the Palawan or Sulu-Mindanao routes. He discusses relative time of entry of different components of the amphibian fauna primarily in terms of extent of endemism and distance from areas occupied by presumed nearest relatives. Within the Philippines, Inger recognizes only 2 somewhat doubtful zoogeographic subdivisions. In his discussion of dispersal (pp. 475–484), he notes that both dispersal by way of earlier land connections and over-water dispersal must be considered, and he also notes, in general descriptive terms, possible routes within the Philippines.

Leviton (1963) provides the most recent discussion of zoogeography of the terrestrial snake fauna of the Philippine archipelago. His discussion is primarily concerned with extraterritorial origins, time of entry and endemism, present distributions, and the taxonomic relationships of species within the Philippines. These are considered in terms of past changes in island configurations, and probable internal pathways. He states (p. 377), contrary to Inger's views relative to the dispersal of the amphibians (Inger, 1954, p. 484), that the present distribution of the snakes can, for the most part, be explained on the basis of former land connections. He recognizes 5 faunal (serpentine) subregions within the archipelago at the present time.

Both authors very ably discuss the present distribution of the faunal element with which they are concerned in terms of traditional concepts of extraterritorial origins, pathways of entry and internal dispersal as governed by probable geological changes, time of entry, and means of dispersal.

Darlington (1957, pp. 476–541) discusses the Philippine ichthyological and herpetological faunas in the more general context of distributions on fringing archipelagoes. Immigrant patterns of distribution, where the species are distributed along the migration route with dropouts occurring linearly as determined by distance and relative dispersal abilities, are, he believes, the primary patterns exhibited in fringing archipelagoes. This basic pattern is modified for older relict groups by concentration of species on distal or proximal islands within the archipelago (p. 533).

MacArthur and Wilson (1963) propose the hypothesis that the number of species on an island represents a balance between number of species reaching the island and number of species becoming extinct per unit of time. They point out that a number of interacting variables will determine the point at which these 2 curves intersect. These include distance from source of immigrants, the species pool of immigrants, area of island concerned, or some other limiting factor such as unfavorable climate. They further propose that in time secondary radiation centers should increase with distance of islands from the major source of the fauna, when corrections are made for area or other limiting variables. They also note that the number of species decreases more rapidly for large than for small islands with increasing distance from source of colonization.

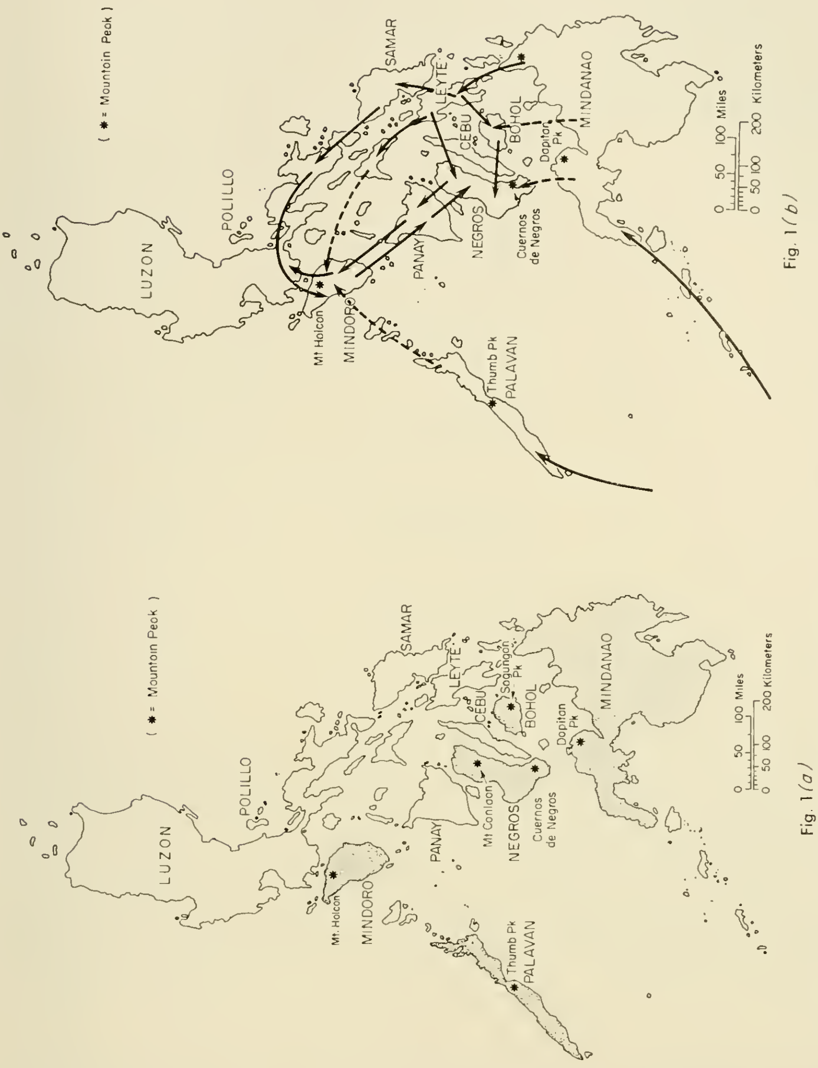

Figure 1. a. Islands surveyed during our recent expeditions, 1958–1963. b. Entryways and proposed dispersal routes within the Philippine Archipelago.

PROBLEMS AND METHODS

Recent intensive exploration of the herpetofaunas of 5 Philippine islands, Palawan, Mindanao, Bohol, Negros, and Mindoro (fig. 1a), makes possible more critical examination of many of the zoogeographic hypotheses suggested by previous authors. Factors which we believe make this possible are: 1) intensive sampling techniques which provide more accurate estimates of species-diversity; 2) choice of islands from proximal, distal, and intermediate regions of the archipelago (fig. 1a); 3) range in size from 5,000 to 95,000 square kilometers

TABLE 1. *Intensively explored areas on the five islands included in the recent survey.*

Mountain Region	*Altitude (meters)*	*Island*	*Island Area (sq. km.)*	*Exploration Date*
Cuernos de Negros	1,903	Negros (southern part)	12,700	March—May 1958 (about 7 weeks)
Mt. Canlaon	2,463	Negros (northern part)	"	March—April 1962 (about 4 weeks)
Dapitan Peak	2,199	Mindanao (Zamboanga Peninsula)	94,600	March—May 1959 (about 6 weeks)
Thumb Peak	1,286	Palawan (central part)	11,800	April—May 1961 (about 7½ weeks)
Mt. Halcon	2,580	Mindoro (northern part)	9,750	April—May 1963 (about 4 weeks)
Sagungan Mountain	870	Bohol (southeastern part)	4,100	April—May 1962 (about 4 weeks)

(table 1); 4) choice of islands which encompass sufficiently large areas of original and/or secondary lowland forest as to make negligible differences in diversity which might be due to major differences in the dominant type of plant community (see Brown and Alcala, 1964).

The techniques stressed intensive sampling of arboreal, surface, and subterranean strata in the lowland forest whenever possible, as well as selected mountains. The expeditions to each of the 6 mountain areas on the 5 islands were carried out by crews of 8 to 10 men over 4 to 7½ week periods (table 1).

TABLE 2. *Number of species recorded for the islands included in this study. The number in parentheses is the number of species belonging to the group of 23 widely distributed species associated with man's economy or beach communities. The number in brackets is the number of relict species.*

	Palawan	*Mindanao*	*Bohol*	*Negros*	*Mindoro*	*Leyte*	*Luzon*
Caecilians	1	1					
Frogs	22 (4)[1]	34 (4)[3]	21 (3)[4]	16 (4)[4]	12 (4)[2]	16 (3)[3]	21 (4)[6]
Lizards	23 (11)[1]	52 (10)[6]	31 (11)[4]	33 (11)[4]	27 (11)[2]		34 (8)[7]
Snakes	33 (9)[0]	39 (9)[2]	20 (8)[1]	29 (9)[2]	19 (8)[1]	18 (7)[1]	39 (9)[3]
Total	78 (24)[2]	125 (23)[11]	72 (22)[9]	78 (24)[10]	58 (23)[5]		94 (21)[15]

Table 3. *Amphibians known from Palawan, Mindanao, Bohol, Negros, Mindoro, Leyte, and Luzon islands.*

	Palawan	*Mindanao*	*Bohol*	*Negros*	*Mindoro*	*Leyte*	*Luzon*
1. *Ichthyophis monochrous*	×	×					
2. *Barbourula busuangensis*	×						
3. *Ansonia mcgregori*		×					
4. *Ansonia mulleri*		×					
5. *Bufo biporcatus*	×						
6. *Leptobrachium hasselti*	×	×	×		×		
7. *Megrophrys monticola*	×	×	×			×	
8. *Platymantis cornutus*							×
9. *Platymantis corrugatus*		×	×	×	×	×	×
10. *Platymantis dorsalis*		×	×	×	×	×	×
11. *Platymantis guentheri*		×	×	×		×	×
12. *Platymantis hazelae*				×			×
13. *Platymantis ingeri*			×				
14. *Platymantis subterrestris*							×
15. *Micrixalus mariae*	×						
16. *Ooeidozyga diminutiva*		×					
17. *Ooeidozyga laevis*	×	×	×	×	×	×	×
18. *Rana cancrivora*	×	×	×	×	×	×	×
19. *Rana erythraea*				×			
20. *Rana everetti*		×		×		×	×
21. *Rana leytensis*		×	×	×		×	
22. *Rana limnocharis*	×	×		×	×		×
23. *Rana magna*	×	×	×	×	×	×	×
24. *Rana microdisca*	×	×					
25. *Rana nicobariensis*	×						
26. *Rana sanguinea*	×						
27. *Rana signata*	×	×	×		×	×	×
28. *Rana woodworthi*							×
29. *Staurois natator*	×	×	×			×	
30. *Philautus acutirostris*		×					
31. *Philautus bimaculatus*		×	×				
32. *Philautus leitensis*			×			×	
33. *Philautus longicrus*	×						
34. *Philautus pictus*	×						
35. *Philautus schmackeri*					×		
36. *Philautus spinosus*		×	×				
37. *Philautus williamsi*							×
38. *Rhacophorus appendiculatus*		×	×	×			
39. *Rhacophorus everetti*	×						
40. *Rhacophorus emembranatus*		×					
41. *Rhacophorus leucomystax*	×	×	×	×	×	×	×
42. *Rhacophorus lissobrachius*		×	×				
43. *Rhacophorus pardalis*		×	×	×			×
44. *Rhacophorus surdus*		×					×
45. *Pelophryne albotaeniata*	×						

TABLE 3. *Continued.*

	Palawan	*Mindanao*	*Bohol*	*Negros*	*Mindoro*	*Leyte*	*Luzon*
46. *Pelophryne brevipes*		×					
47. *Pelophryne lighti*		×	×				
48. *Chaperina fusca*	×	×					
49. *Kalophrynus pleurostigma*		×	×			×	
50. *Kaloula baleata*	×						×
51. *Kaloula conjuncta*		×		×	×	×	×
52. *Kaloula picta*		×		×	×	×	×
53. *Kaloula rigida*							×
54. *Oreophryne annulata*		×					

The belief that our sampling techniques for these selected mountain areas has provided a realistic estimate of the number of species present in the area is based upon experience in the Cuernos de Negros area in southern Negros Island. The initial survey expedition there in 1958, using the sampling methods noted above, resulted in the recording of 67 herpetofaunal species (Brown and Alcala, 1961, p. 631). Although extensive resampling of this area has occurred during the interim of several years, in connection with our population and other ecological studies, only 7 additional species (*Hemiphyllodactylus typus, Lepidodactylus christiani, L. lugubris, Luperosaurus cumingi, Brachymeles tridactylus, Typhlops cumingi*, and *Boiga angulata*) have been found in the southern Negros area. The 4 remaining species in the present list for Negros (tables 3, 4 and 5) are known only from the northern part of the island. Thus, even though Bohol, Palawan, and Mindoro are not yet widely explored, the presently available data on their herpetofaunal communities, based on past records and on our intensive sampling of selected mountain areas, are believed to be sufficient to realistically approximate their relative positions in terms of diversity.

Utilizing primarily the data from the 6 recently intensively explored mountain areas on 5 islands (table 1), supplemented by available lists of species, largely based on data assembled by earlier explorers, for Leyte and Luzon islands as well as total distributional data for a few genera, we propose to examine: 1) the nature of the relict patterns for some of the older herpetofaunal elements; 2) the probability of secondary radiation zones; 3) the relative importance of probable internal migration routes, using Sorenson's index of similiarity; 4) the probable importance of marine barriers in effecting the present distribution patterns; 5) the relation of island size and distance to diversity of species.

RESULTS

DIVERSITY OF SPECIES

A total of 9,000+ herpetofaunal specimens, ranging from about 1,000 for Mindoro Island to 2,500 for Negros Island, were collected during our recent expeditions. Classification of the collected material when added to earlier records, reveals 197 species: 1 caecilian, 49 frogs, 82 lizards, and 66 snakes for these five islands (tables 2–5). Although the new records ranged from 61 for Bohol to 5 for Mindoro, only 14 were new species or species not recorded from the Philippines prior to our intensive sampling. Most of these 14 were from Palawan and Mindanao, the islands adjacent to Borneo.

The number of species of snakes and frogs recognized from Luzon and Leyte islands are based primarily upon Inger's review of the Philippine amphibia (1954) and Leviton's review of the snakes (1963). The distribution of the species of the genus *Calamaria*, however, is from Inger and Marx (1965). The list of lizards for Luzon is based primarily on the earlier records of Taylor (1922a, 1922b, 1922c, 1923 and 1925) with a few recent additions by the present authors. The inclusion of Luzon adds 23 more species (5 amphibians, 10 lizards, and 8 snakes) to the 197, making a total of 220 species (tables 3–5).

Native Fauna

Twenty-three of the 220 species (4 frogs, 11 lizards, and 8 snakes) are regarded as probably nonnative; that is, as possibly introduced or at least reintroduced by man. We do not presume that this list includes all species which have at any time been introduced by man, intentionally or otherwise. It probably, however, does include most of these species which are readily, perhaps often accidentally, transported from island to island. To be included in this category, the species must meet these criteria: 1) occur on at least 4 of the 5 islands included in our study; 2) exhibit no subspeciation except for the Palawan populations in some instances; 3) be associated with man's habitations, and cultivated lands, or with other lowland beach communities (Brown and Alcala, 1964); 4) be widespread in Borneo and other adjacent areas. It is interesting to note (table 2) that the number of species of this nonnative group, whether we are concerned with frogs, lizards, or snakes, is essentially the same for each of the 7 islands irrespective of distance from entry-point or area of island. This we interpret as further evidence supporting their classification in this category. The 23 species include:

Amphibians:
Ooeidozyga laevis
Rana cancrivora
Rana limnocharis
Rhacophorus leucomystax

Lizards:
Cosymbotus platyurus
Gehyra mutilata
Gekko gecko
Hemidactylus frenatus
Hemiphyllodactylus typus
Draco volans
Dasia smaragdina
Emoia atrocostata
Lygosoma (Leiolopisma) quadrivittatum
Mabuya multifasciata
Mabuya multicarinata

Snakes:
Typhlops braminae
Python reticulatus
Ahaetulla prasina
Dendrelaphis pictus
Chrysopelea paradisi
Elaphe erythrura
Lycodon aulicus
Psammodynastes pulverulentus

TABLE 4. *Lizards known from Palawan, Mindanao, Bohol, Negros, Mindoro, and Luzon islands.*

	Palawan	*Mindanao*	*Bohol*	*Negros*	*Mindoro*	*Luzon*
1. *Cosymbotus platyurus*	×	×	×	×	×	×
2. *Cyrtodactylus agusanensis*		×				
3. *Cyrtodactylus annulatus*		×	×			
4. *Cyrtodactylus philippinicus*				×	×	×
5. *Cyrtodactylus redimiculus*	×					
6. *Gehyra mutilata*	×	×	×	×	×	×
7. *Gekko athymus*	×					
8. *Gekko gecko*	×	×	×	×	×	×
9. *Gekko mindorensis*					×	
10. *Gekko monarchus*	×	×		×		
11. *Gekko palawanensis*	×					
12. *Hemidactylus frenatus*	×	×	×	×	×	×
13. *Hemidactylus garnoti*					×	×
14. *Hemidactylus luzonensis*						×
15. *Hemiphyllodactylus typus*	×		×	×	×	
16. *Lepidodactylus aureolineatus*		×	×			
17. *Lepidodactylus christiani*				×		
18. *Lepidodactylus herrei*				×		
19. *Lepidodactylus lugubris*				×		
20. *Lepidodactylus naujanensis*					×	
21. *Lepidodactylus planicaudus*		×	×			
22. *Luperosaurus cumingi*				×		
23. *Luperosaurus joloensis*	×					
24. *Perochirus ateles*		×				
25. *Pseudogekko compressicorpus*		×	×			×
26. *Pseudogekko brevipes*			×	×		
27. *Ptychozoon intermedia*		×				
28. *Calotes cristatellus*	×	×	×			
29. *Calotes marmoratus*				×	×	×
30. *Draco bimaculatus*		×				
31. *Draco everetti*			×			
32. *Draco mindanensis*		×				
33. *Draco ornatus*		×				×
34. *Draco quadrisi*					×	
35. *Draco rizali*		×	×			
36. *Draco volans*	×	×	×	×	×	×
37. *Gonyocephalus interruptus*					×	
38. *Gonyocephalus semperi*		×	×			
39. *Gonyocephalus sophiae*		×		×		
40. *Hydrosaurus pustulosus*		×	×	×	×	×
41. *Varanus salvator*	×	×		×	×	×
42. *Dibamus argenteus*	×	×		×		
43. *Brachymeles bonitae*					×	×
44. *Brachymeles elerae*						×
45. *Brachymeles gracilis*		×	×	×	×	×
46. *Brachymeles pathfinderi*		×				

Table 4. *Continued.*

	Palawan	*Mindanao*	*Bohol*	*Negros*	*Mindoro*	*Luzon*
47. *Brachymeles samarensis*						×
48. *Brachymeles schadenbergi*		×	×			×
49. *Brachymeles talinis*				×		×
50. *Brachymeles tridactylus*				×		
51. *Brachymeles wrighti*						×
52. *Brachymeles hilong*		×				
53. *Dasia griffini*	×					
54. *Dasia olivaceum*		×			×	
55. *Dasia smaragdina*	×	×	×	×	×	×
56. *Emoia atrocostata*	×	×	×	×	×	
57. *Emoia caeruleocauda*		×				
58. *Emoia ruficauda*		×				
59. *Lygosoma (Leiolopisma) auriculatum*				×	×	
60. *Lygosoma (Leiolopisma) pulchellum*		×	×	×		×
61. *Lygosoma (Leiolopisma) quadrivittatum*	×	×	×	×		
62. *Lygosoma (Leiolopisma) rabori*				×		
63. *Lygosoma (Leiolopisma) semperi*		×				
64. *Lygosoma (Leiolopisma) subvittatum*		×				
65. *Lygosoma (Leiolopisma) vulcanium*		×				
66. *Lygosoma (Leiolopisma) zamboangensis*		×				
67. *Lygosoma (Lygosoma) chalcides*	×					
68. *Lygosoma (Sphenomorphus) acutum*		×	×			
69. *Lygosoma (Sphenomorphus) arborens*				×		
70. *Lygosoma (Sphenomorphus) atrigularis*		×				
71. *Lygosoma (Sphenomorphus) coxi*		×		×		
72. *Lygosoma (Sphenomorphus) decipiens*						×
73. *Lygosoma (Sphenomorphus) diwati*		×				
74. *Lygosoma (Sphenomorphus) fasciatum*		×	×			
75. *Lygosoma (Sphenomorphus) jagori*		×	×	×	×	×
76. *Lygosoma (Sphenomorphus) luzonensis*						×
77. *Lygosoma (Sphenomorphus) mindanensis*		×	×			
78. *Lygosoma (Sphenomorphus) palawanensis*	×					
79. *Lygosoma (Sphenomorphus) steerei*		×	×	×	×	×
80. *Lygosoma (Sphenomorphus) stejnegeri*						×
81. *Lygosoma (Sphenomorphus) varigatum*		×	×			
82. *Lygosoma (Sphenomorphus) wrighti*	×					
83. *Lygosoma (Sphenomorphus) sp.*						×
84. *Mabuya bontocensis*						×
85. *Mabuya multicarinata*	×	×	×	×	×	×
86. *Mabuya multifasciata*	×	×	×	×	×	×
87. *Otosaurus cumingi*		×	×		×	×
88. *Tropidophorus grayi*				×		×
89. *Tropidophorus leucospilos*						×
90. *Tropidophorus misaminus*		×				
91. *Tropidophorus partelloi*		×				
92. *Tropidophorus sp.*		×				

Table 5. *Snakes known from Palawan, Mindanao, Bohol, Negros, Mindoro, Leyte, and Luzon islands.*

	Palawan	*Mindanao*	*Bohol*	*Negros*	*Mindoro*	*Leyte*	*Luzon*
1. *Typhlops braminae*	×	×	×	×		×	×
2. *Typhlops cumingi*				×			
3. *Typhlops canlaonensis*				×			
4. *Typhlops dendrophis*		×					
5. *Typhlops jagori*							×
6. *Typhlops longicauda*		×	×				
7. *Typhlops luzonensis*				×			×
8. *Typhlops mindanensis*		×					
9. *Typhlops ruber*					×		
10. *Typhlops ruficauda*							×
11. *Typhlops rugosa*		×					
12. *Xenopeltis unicolor*	×						
13. *Python reticulatus*	×	×	×	×	×	×	×
14. *Ahaetulla prasina*	×	×	×	×		×	×
15. *Aplopeltura boa*	×	×					
16. *Calamaria bitorques*							×
17. *Calamaria gervaisi*		×		×	×		×
18. *Calamaria lumbricoidea*		×	×			×	
19. *Calamaria palawanensis*	×						
20. *Calamaria virgulata*	×	×					
21. *Chrysopelea paradisi*	×	×		×	×	×	×
22. *Cyclocorus lineatus*		×		×	×		×
23. *Dendrelaphis caudolineatus*	×	×	×	×	×	×	×
24. *Dendrelaphis pictus*	×	×	×	×	×		×
25. *Dryophiops philippina*				×	×		×
26. *Dryocalamus tristrigatus*	×						
27. *Dryocalamus subannulatus*	×						
28. *Elaphe erythrura*	×	×	×	×	×	×	×
29. *Gonyosoma oxycephala*	×		×	×	×		×
30. *Hologerrhum philippinum*							×
31. *Hurria rynchops*	×	×		×		×	×
32. *Liopeltis philippinus*	×						
33. *Liopeltis tricolor*	×						
34. *Lycodon aulicus*	×	×	×	×	×		×
35. *Lycodon dumerili*		×					
36. *Lycodon mulleri*					×		×
37. *Lycodon subcinctus*	×						
38. *Lycodon tesselatus*							×
39. *Myersophis alpetris*							×
40. *Natrix auriculata*		×	×			×	
41. *Natrix chrysarga*	×						
42. *Natrix dendrophiops*		×	×	×	×		×
43. *Natrix lineata*		×					
44. *Natrix spilogaster*							×
45. *Oligodon ancorus*					×		×

Table 5. *Continued.*

	Palawan	Mindanao	Bohol	Negros	Mindoro	Leyte	Luzon
46. *Oligodon maculatus*		×					
47. *Oligodon modestum*		×		×			×
48. *Oligodon vertebralis*	×	×					
49. *Opisthotropis alcalai*		×					
50. *Opisthotropis typica*	×						
51. *Oxyrhabdium leporinum*				×	×		×
52. *Oxyrhabdium modestum*		×	×			×	
53. *Psammodynastes pulverulentus*	×	×	×	×		×	×
54. *Pseudorabdion ater*		×					
55. *Pseudorabdion mcnamarae*				×			×
56. *Pseudorabdion montanum*				×			
57. *Pseudorabdion oxycephalum*				×			
58. *Pseudorabdion taylori*		×					
59. *Sibynophis bivittatus*	×						
60. *Stegonotus mülleri*		×				×	
61. *Zaocys carinatus*	×						
62. *Zaocys luzonensis*				×		×	×
63. *Bioga angulata*		×	×	×		×	×
64. *Bioga cynodon*	×	×				×	×
65. *Boiga dendrophila*	×	×	×				×
66. *Boiga drapiezi*	×						
67. *Boiga philippina*							×
68. *Calliophis calligaster*				×	×		×
69. *Maticora intestinalis*	×	×	×				×
70. *Naja naja*	×	×	×		×	×	×
71. *Ophiophagus hanna*	×	×		×	×		×
72. *Trimeresurus flavomaculatus*		×	×	×	×	×	×
73. *Trimeresurus schultzei*	×						
74. *Trimeresurus wagleri*	×	×	×	×		×	×

In other sections of this paper, certain of the indices are determined, both for the total fauna and for the presumed native fauna following the exclusion of these 23 species.

Relict Patterns and Secondary Radiation Zones

As noted by Darlington (1957, p. 505) endemism at the specific and subspecific levels is high, but at the generic level very low for the Philippine herpetofauna. It is of interest to examine the distributional patterns of these endemic genera, as well as of a few other genera (the presumed earlier arrivals) which, though not limited to the Philippines, exhibit disrupted distributional patterns outside the Philippines, to determine their fit to typical relict or modified immigrant patterns as postulated by Darlington (1957, p. 484 ff.). This selection of endemic genera and those with strongly disrupted distributional patterns does

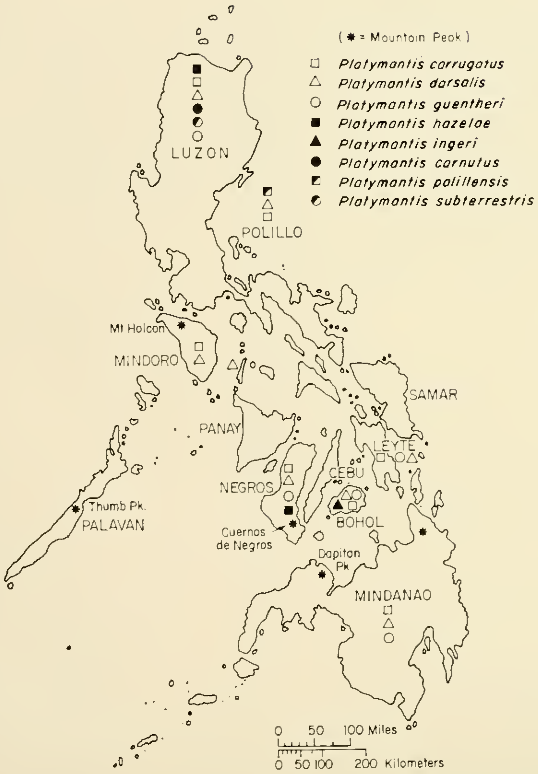

Fig 2

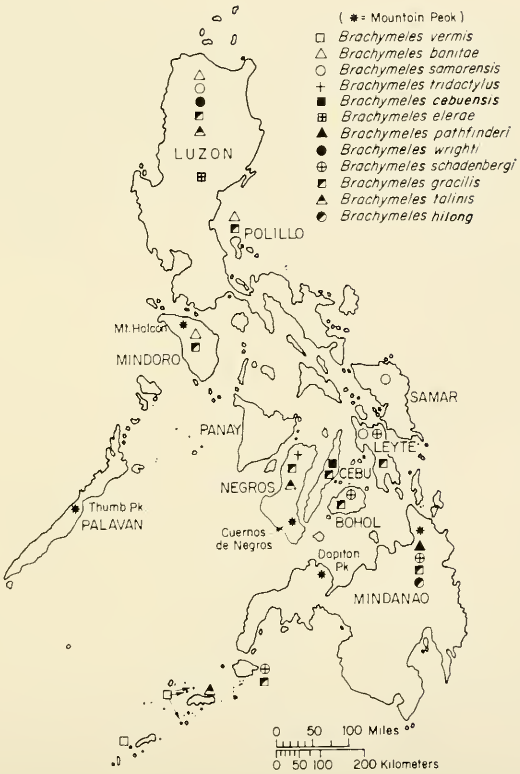

Fig. 3

Figure 2. Distribution patterns of species of the frog genus *Platymantis* in the Philippines.
Figure 3. Distribution patterns of species of the lizard genus *Brachymeles* in the Philippines.

not preclude the possibility that species in other, widely distributed genera may also be relicts of early immigrations, but provides objective criteria for selection.

The endemic genera include *Barbourula*, an amphibian; *Luperosaurus*, *Pseudogekko* and *Brachymeles*, lizards; and *Cyclocorus*, *Hologerrhum*, and *Oxyrhabdium*, snakes. *Platymantis* in the amphibia and *Perochirus* in the squamata, though not endemic, exhibit overall disrupted patterns.

Barbourula and *Perochirus* are limited to single species in the Philippines. *Barbourula* is known only from the Palawan group and *Perochirus* only from Mindanao and Leyte. This pattern of limitation to proximal islands permits 3 alternative explanations: 1) these genera have very low dispersal ability and did not go beyond these proximal islands; 2) they have reached but failed to establish themselves on more distal islands; 3) they still remain to be found on the other islands.

Platymantis, Brachymeles, and *Luperosaurus* exhibit relict patterns (figs. 2, 3, and 4) of the type which may be interpreted as resulting from the partial extinction of an old widespread fauna (Darlington, 1957, p. 485). Each of these genera includes several species. The genus *Platymantis* (as noted by Inger, 1954, p. 496 exhibits a concentration of species on Luzon at the distal end of the archipelago, others with distribution limited to one or two scattered islands, and several species which are widespread throughout the Philippines, though none of these species are known from outside of the archipelago. As proposed by MacArthur and Wilson (1963, p. 386) and Inger (1957, p. 496), such a pattern may also be interpreted as due in part to secondary radiation from the distal island of Luzon as indicated by the present distribution of *P. hazelae* and *P. polillensis*, very closely related species, not necessarily as wholly due to chance extinctions of once widespread species.

The genus *Brachymeles*, as reviewed by Brown and Rabor (1967), includes such widespread species as *B. gracilis* and *B. schadenbergi*, groups of species limited to the proximal or distal islands, and a third very interesting group (the tridactylus-vermis group) which strongly suggests an origin in and radiation from the center of the archipelago. Based on the presumed evolutionary relationships, indicated by the degree of reduction of the limbs and digits, the least specialized members of the group occur in the central islands and those with the greater reduction of limbs and digits in the northern and southern islands. These species include:

Species	Distribution	Digits on fore limbs	Digits on hind limbs
Brachymeles tridactylus	Negros	3	3
Brachymeles cebuensis	Cebu	3	2
Brachymeles samarensis	Leyte, Samar, and Luzon	2	2
Brachymeles bonitae	Luzon and Mindoro	0–1	0–1
Brachymeles vermis	Sulus	0	0

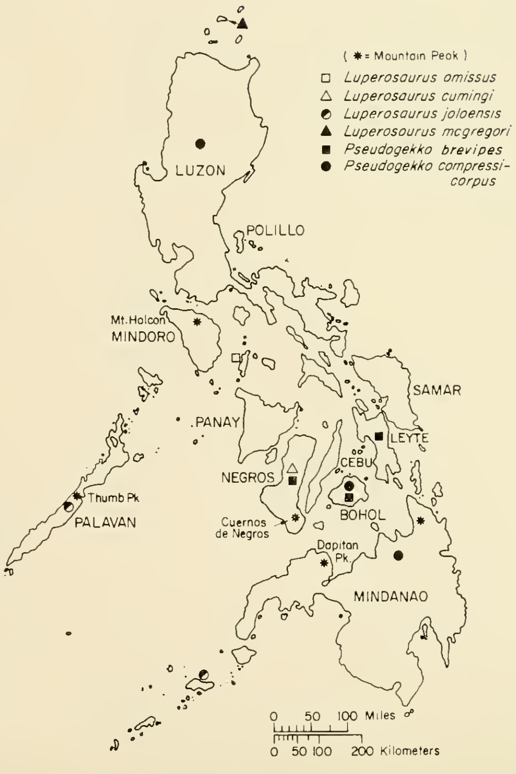

Fig. 4

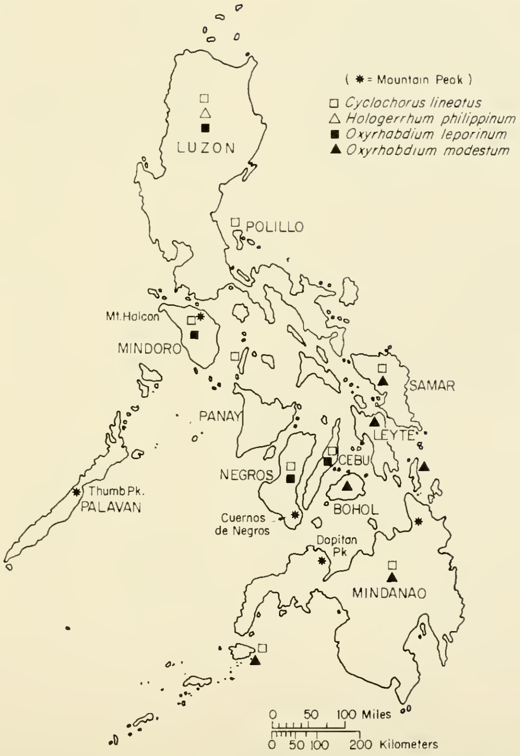

Fig. 5

FIGURE 4. Distribution patterns of the lizard genera *Luperosaurus* and *Pseudogekko* in the Philippines.

FIGURE 5. Distribution patterns of the species of the snake genera *Cyclocorus*, *Hologerrhum*, and *Oxyrhabdium* in the Philippines.

Table 6. *Indices of similarity for amphibians. The index in parentheses is based on the native species after exclusion of common widespread forms associated with man's economy or beach communities. The index in brackets is based on those species remaining after the relicit species are also excluded.*

	Mindanao	*Leyte*	*Bohol*	*Negros*	*Mindoro*	*Luzon*
Palawan	0.429	0.368	0.372	0.263	0.412	0.326
	(0.333)	(0.258)	(0.278)	(0.067)	(0.231)	(0.171)
	[0.364]	[0.296]	[0.323]	[0.080]	[0.261]	[0.214]
Mindanao		0.600	0.691	0.520	0.476	0.509
		(0.588)	(0.667)	(0.429)	(0.368)	(0.426)
		[0.486]	[0.634]	[0.343]	[0.303]	[0.368]
Leyte			0.703	0.687	0.643	0.595
			(0.645)	(0.640)	(0.571)	(0.533)
			[0.583]	[0.556]	[0.500]	[0.476]
Bohol				0.541	0.485	0.429
				(0.467)	(0.385)	(0.343)
				[0.364]	[0.300]	[0.240]
Negros					0.643	0.703
					(0.500)	(0.621)
					[0.429]	[0.526]
Mindoro						0.606
						(0.480)
						[0.471]

Hologerrhum has a relict pattern exhibiting limitation to the distal island of Luzon (fig. 5). *Pseudogekko*, with two species, has a spotty distribution; *Cyclocorus* (1 species) and *Oxyrhabdium* (2 species) have less obvious relict patterns, being more widely distributed throughout the archipelago (figs. 4 and 5).

Internal Migration Routes

When differences in composition as well as diversity are considered, it is possible to compare the relative effectiveness of probable dispersal routes indicated in fig. 1b. In comparing composition of the faunas, we have used the

$$\text{similarity index}\ \frac{\text{twice the number of species common to the two communities}}{\text{the sum of the species comprising each of the communities}}$$

developed by Sorenson (1948) for comparing plant communities in northeast Greenland and in Denmark. A low index of similarity will be the result of either: (1) a large difference in diversity; or (2) when diversities are more or less equal, a small number of species in common.

In addition to the 5 islands upon which this study is primarily based, Leyte Island, as well as Luzon, has been included in this section since the former lies

TABLE 7. *Indices of similarity for lizards. (The index in parentheses is based on the species exclusive of the 23 widespread forms associated with man's economy or beach communities, that in brackets is based on the species remaining after relicit species are also excluded).*

	Mindanao	*Bohol*	*Negros*	*Mindoro*	*Luzon*
Palawan	0.400 (0.185) [0.213]	0.481 (0.125) [0.148]	0.500 (0.176) [0.207]	0.440 (0.000) [0.000]	0.316 (0.053) [0.067]
Mindanao		0.651 (0.548) [0.539]	0.471 (0.313) [0.333]	0.380 (0.207) [0.200]	0.395 (0.265) [0.218]
Bohol			0.562 (0.333) [0.294]	0.552 (0.278) [0.267]	0.491 (0.348) [0.286]
Negros				0.600 (0.368) [0.375]	0.478 (0.333) [0.323]
Mindoro					0.590 (0.429) [0.424]

closest to Mindanao on the most eastern dispersal route. The Leyte indices have been computed only for frogs and snakes, based on lists published by Inger (1954) and Leviton (1963). The lizards are not sufficiently well known to be included at this time, and the snakes are believed to be rather poorly known since several widely distributed species have not yet been reported from this island. This, however, would tend to introduce an error in the direction of a low rather than a high index.

As is evidenced in table 2, Mindanao, at the proximal end of the eastern routes, exhibits a higher diversity for each of the major taxa considered, as well as for the herpetofauna as a whole, than do any of the other 4 islands included in our expeditions. This will depress the similarity index when comparisons are made with the other islands, whereas no such depressing effect will exist in the instance of Palawan at the proximal end of the western entryway, since the diversity of the Palawan herpetofauna is about the same as that of the more distal islands which range from 60 to 80 species in total herpetofauna. Thus, if indices between Mindanao and more distal islands are equal to or greater than the indices between Palawan and these same islands, less isolation of island faunas along eastern routes from Mindanao would be indicated.

All indices, those for each of the taxa, (frogs, lizards, and snakes), as well as those for the total herpetofaunas (tables 6–9), are moderately high when

Table 8. *Indices of similarity for snakes. (The index in parentheses is based on species exclusive of the 23 widespread forms associated with man's economy or beach communities, that in brackets is based on the species remaining after relicit species are also excluded).*

	Mindanao	*Leyte*	*Bohol*	*Negros*	*Mindoro*	*Luzon*
Palawan	0.528 (0.373) [0.385]	0.431 (0.229) [0.235]	0.491 (0.278) [0.286]	0.323 (0.182) [0.190]	0.308 (0.171) [0.176]	0.308 (0.296) [0.314]
Mindanao		0.596 (0.488) [0.474]	0.644 (0.524) [0.513]	0.500 (0.360) [0.348]	0.414 (0.293) [0.268]	0.538 (0.433) [0.436]
Leyte			0.684 (0.609) [0.571]	0.468 (0.305) [0.345]	0.324 (0.182) [0.200]	0.491 (0.341) [0.378]
Bohol				0.531 (0.315) [0.345]	0.462 (0.348) [0.381]	0.542 (0.333) [0.378]
Negros					0.542 (0.516) [0.429]	0.706 (0.640) [0.622]
Mindoro						0.621 (0.585) [0.541]

Palawan and Mindanao are compared, even though the differences in diversity are relatively large. This is the result of the large number of species which these 2 entry-way islands have in common. These common species have either entered the 2 islands relatively recently from Borneo or have continued to reinvade from time to time. The fact that many of these species have not dispersed to more distal islands in the Philippines and yet are conspecific with Bornean populations tends, however, to support the first explanation of more recent entry.

When indices between Mindanao and Mindoro, Leyte, Luzon, or Negros, based on the complete fauna (both native and nonnative species), are compared with the indices between Palawan and these same islands (tables 6–9), those with Mindanao are much higher, with one exception, even though the greater diversity of the Mindanao fauna, almost twice that of Palawan, tends to depress the similarity indices. The exception is the Palawan-Mindoro index for lizards. These differences are more pronounced and the exception ceases to exist when the 23 widespread, nonnative species (p. 111) are excluded. The differences are not quite as great, in most instances, when those classified as older relicts (p. 117) are also excluded; but these latter, small differences can be accounted for by the absence of the relict genera *Platymantis* and *Brachymeles* from Palawan.

TABLE 9. *Indices of similarity for the total herpetofauna. (The index in parentheses is based on species exclusive of the 23 widespread forms associated with man's economy or beach communities, that in brackets is based on the species remaining after relicit species are also excluded).*

	Mindanao	*Bohol*	*Negros*	*Mindoro*	*Luzon*
Palawan	0.453	0.453	0.372	0.382	0.372
	(0.304)	(0.245)	(0.109)	(0.165)	(0.186)
	[0.331]	[0.274]	[0.122]	[0.188]	[0.214]
Mindanao		0.660	0.493	0.415	0.475
		(0.584)	(0.354)	(0.286)	(0.362)
		[0.567]	[0.337]	[0.258]	[0.331]
Bohol			0.547	0.508	0.494
			(0.377)	(0.364)	(0.368)
			[0.345]	[0.342]	[0.337]
Negros				0.588	0.616
				(0.457)	(0.511)
				[0.415]	[0.481]
Mindoro					0.605
					(0.523)
					[0.505]

This indicates that the primary dispersal routes for the native fauna were by way of Mindanao, and that the present herpetofauna of Palawan has not dispersed widely into other areas in the Philippines.

The high indices between Mindanao, Leyte, and Bohol are due to the very large number of species which they hold in common, even though diversity is greatly reduced. This suggests a very high rate of exchange between Mindanao and these 2 nearby islands on the eastern routes. The slightly higher indices between Mindanao and Bohol as compared to those between Mindanao and Leyte may be partly the result of lesser knowledge of the fauna of Leyte. However, it may also be the result of some exchange across a direct Mindanao-Bohol route.

The relatively high Mindoro-Negros index for each taxon, as well as for the total herpetofauna, may be in part due to their positions at the distal end of dispersal routes, and, consequently, the same species have tended to reach both. However, it also suggests an active Mindoro-Panay-Negros dispersal route. The richer fauna of Negros, on the other hand, also indicates that a part of the Negros fauna must have arrived by way of the shorter Mindanao-Leyte-Bohol, or Mindanao-Leyte-Cebu dispersal routes, or in some instances perhaps, a Mindanao-Bohol-Negros route.

The progressively lower indices with Mindanao, as one progresses along the eastern dispersal route to Mindoro, appears to be consistent with the decrease in diversity. The Mindoro-Mindanao index is higher for frogs than for either lizards or snakes. This would be expected in terms of a later arrival, which might be accounted for by their slower dispersal ability where marine barriers have presumably operated.

Evidence for Over-Water Dispersal

In addition to the evidence of barriers to dispersal indicated by the reduction of numbers of species on distal islands as compared to proximal islands, when the size variable is minimized, as suggested in the section on diversity (fig. 2), the data may be further analyzed in terms of the probable differential effect of marine barriers. As noted at the close of the previous section, on biological grounds marine barriers would be expected to affect adversely dispersal of amphibians to a greater extent than that of reptiles. Therefore, on the assumption that the primary entryway into the Philippine archipelago was from Borneo by way of Mindanao, the amphibia might be expected to exhibit a more rapid reduction in number of species than do the reptiles when comparisons are made between Mindanao and the more distal islands such as Bohol, Negros, Mindoro, and Luzon if dispersal did take place wholly or in part across such barriers along these eastern routes. This should become even more evident if, as well as the nonnative, the presumably older endemic relict elements, those which exhibit the typical relict pattern of chance pockets of isolated species and/or secondary radiation centers on distal islands, were also excluded.

To evaluate this, we propose a simple proportional-diversity index. This makes possible an objective comparison of changes in diversity for amphibia relative to changes in diversity for the reptiles. The index is calculated as the ratio of the number of species in the particular taxon (frogs, lizards, etc.) to the number of species in the total herpetofauna.

This index for frogs is indeed lower for Luzon, Negros, and Mindoro, at the distal end, than for Mindanao or Bohol at the proximal end of the dispersal routes. The amphibian index for Bohol is noteworthy in that it is slightly higher than that for Mindanao. This may be, at least in part, a distortion due to a disproportionately poorly known snake fauna (see p. 119).

Since indices for reptiles (both lizards and snakes) tend to increase as the index for amphibians decreases, it is interesting to note that the index for lizards exhibits a greater increase than that for snakes in all instances, except for Luzon Island, when the distal islands are compared with Mindanao at the entryway. For some reason, snakes appear to have been relatively more successful in their dispersal to Luzon, or have suffered fewer extinctions there.

We interpret these changes in the proportional diversity indices as supporting the conclusion that much of the herpetofauna of the Philippines, with the exception of that of Palawan, has been the result of waif dispersal across marine

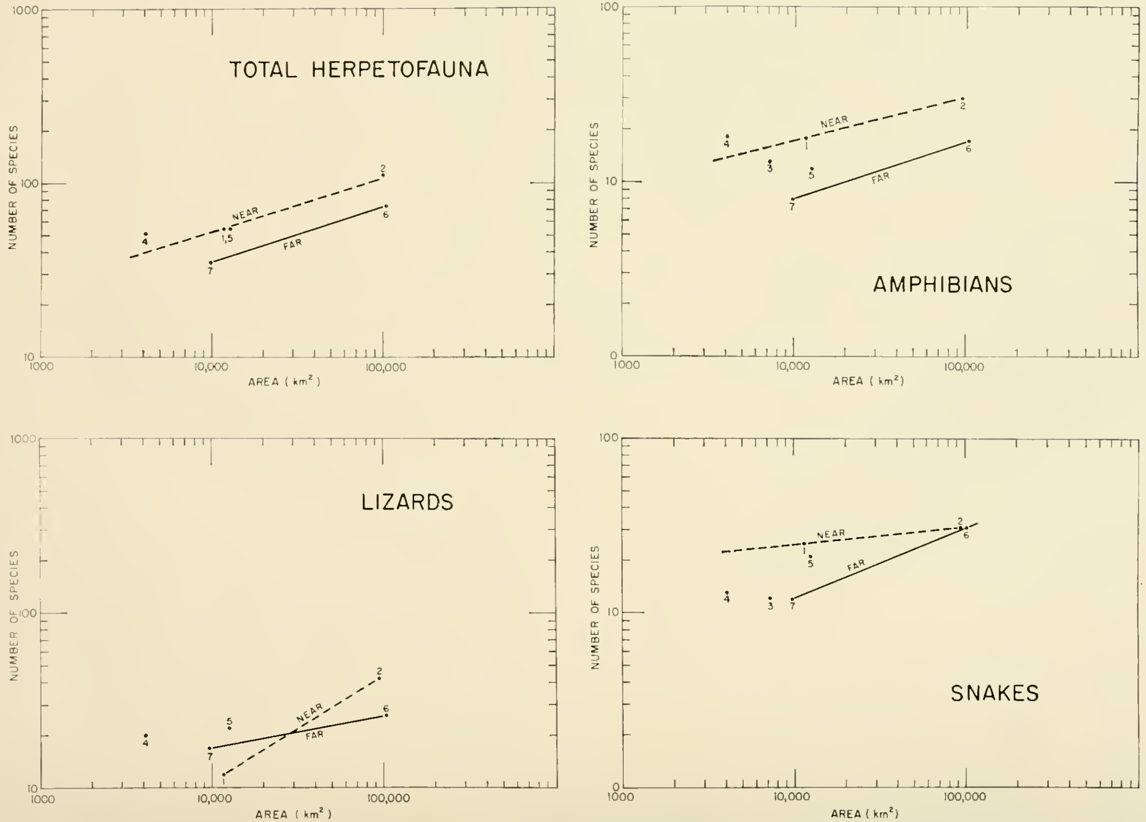

FIGURE 6. Area-species curves for near and far islands: (1) Palawan; (2) Mindanao; (3) Leyte; (4) Bohol; (5) Negros; (6) Luzon; (7) Mindoro.

Table 10. *Proportional diversity indices for caecilians, frogs, lizards, and snakes for selected proximal, intermediate, and distal islands for the total herpetofauna, the fauna with the presumed nonnative species excluded (in parentheses), and with both the nonnative and that element classified as relict included [in brackets].*

	Palawan	*Mindanao*	*Bohol*	*Negros*	*Mindoro*	*Luzon*
Number of Caecilian species	0.013	0.008				
(Total herpetofaunal species)	(0.018)	(0.009)				
	[0.019]	[0.011]				
Number of frog species	0.269	0.272	0.292	0.205	0.207	0.223
(Total herpetofaunal species)	(0.309)	(0.291)	(0.352)	(0.218)	(0.216)	(0.230)
	[0.302]	[0.292]	[0.333]	[0.178]	[0.188]	[0.186]
Number of lizard species	0.295	0.416	0.431	0.423	0.466	0.362
(Total herpetofaunal species)	(0.218)	(0.408)	(0.392)	(0.400)	(0.459)	(0.351)
	[0.208]	[0.391]	[0.381]	[0.400]	[0.469]	[0.322]
Number of snake species	0.423	0.312	0.278	0.372	0.328	0.415
(Total herpetofaunal species)	(0.455)	(0.301)	(0.255)	(0.382)	(0.324)	(0.419)
	[0.422]	[0.315]	[0.286]	[0.422]	[0.344]	[0.492]

barriers from Mindanao Island. This conclusion is most strongly evidenced when nonnative and isolated relict species are excluded leaving the so-called immigrant species (table 10).

Diversity as Related to Area and Distance

Area. When number of native species is plotted against area (fig. 6) for the compact group of islands included in the present study, the curves for amphibians and the total herpetofauna exhibit the expected pattern for overwater dispersal as postulated by MacArthur and Wilson (1963, 1967). Large islands do exhibit a greater diversity (number of species) than small islands and near islands a consistently greater diversity than more distant islands, in terms of the probable migration routes.

The diversity of lizards on Palawan, a near small island, and the diversity of snakes of Mindanao are somewhat less than expected, however, based on the slope of the curves. The diversity of snakes on Luzon, the most distant large island, also appears slightly greater than might be expected. One explanation might be that the relatively short over-water distances obtaining in this compact archipelago have made possible a higher frequency of invasion of snakes along the eastern chain to Luzon or that there are more relict snakes on Luzon. Since lizards of the endemic genus *Brachymeles* are absent from Palawan, this probably accounts in part for the lower diversity of this faunal group on that island. The diversity for amphibians and lizards on Bohol Island is greater than expected and that of the snakes lower. It has been suggested that the latter may be due

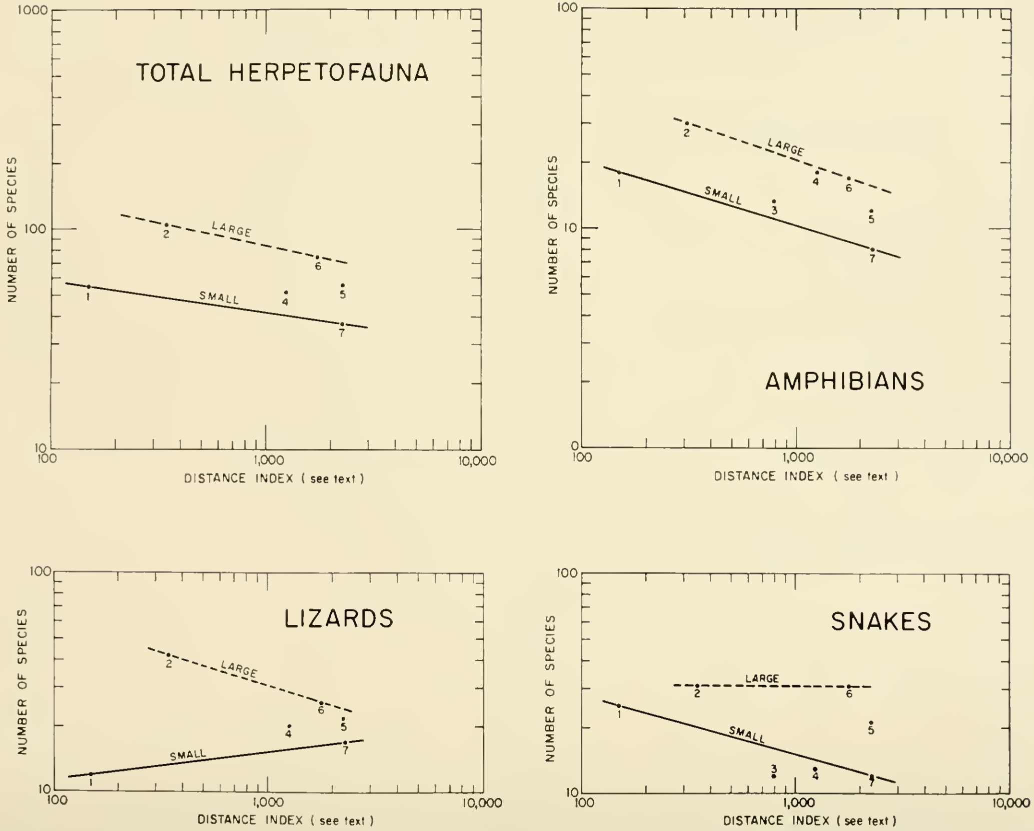

Figure 7. Distance index-species curves for large and small islands: (1) Palawan; (2) Mindanao; (3) Leyte; (4) Bohol; (5) Negros; (6) Luzon; (7) Mindoro.

Table 11. *Calculated distance index for Philippine islands included in this study in relation to Borneo.*

Route	*Weighted number of effective marine barriers*	*Approximate over-water distance by present probable routes (in km.)*	*Weighted distance index*
Borneo—Palawan	(1)	150	150
Borneo—Sulus—Mindanao	(1)	345	345
Borneo—Mindanao—Leyte	(2)	395	790
Borneo—Mindanao—Leyte—Bohol	(3)	420	1260
Borneo—Mindanao—Leyte—Cebu —Negros	(4–5=4½)	505	2272.5
Borneo—Mindanao—Leyte—Samar —Luzon	(4)	440	1760
Borneo—Mindanao—Leyte—Samar —Luzon—Mindoro	(5)	455	2275

to a sampling bias. The high diversity of lizards and amphibians may possibly be the result of the very narrow water gap between Leyte and Bohol.

Distance. Any attempt to measure over-water dispersal distances in this compact, nonlinear archipelago is difficult. If the effective distance is measured as the airline distance from Borneo to the various islands, Leyte is almost as distant as Luzon, and Bohol almost as distant as Mindoro (fig. 1b). If the effective distance is measured as the sum of the breadth of over-water distances between islands, by ways of eastern migration routes for all islands except Palawan, assuming that the islands themselves provide stepping stones of ecologically relatively uniform space, the effective over-water distance between Mindanao and Luzon, the northernmost island, is 75 kilometers as compared to 55 to 90 kilometers as the effective over-water distance between Mindanao and Bohol for example. In an attempt to minimize these sources of error we have derived a weighted index by multiplying the sum of the approximate over-water distances times a value for number of marine barriers (table 11).

When this distance index is plotted against number of species (fig. 7), the shape of the curves are again, with slope opposite to that of the area curves, in keeping with that expected for amphibians and the herpetofauna as a whole, and the curves for large and small islands are nearly parallel. The diversities for snakes on Mindanao and Luzon and for lizards on Palawan also impose effects on the slopes of the curves which are comparable to the effects on the area curves. Bohol and Leyte also exhibit a very low diversity for snakes relative to the curve for other islands in the same general size-category. The general agreement between these curves and those based on area suggests that such a weighted distance index may be useful in the island faunas in similar compact archipelagos.

SUMMARY AND CONCLUSIONS

The existence of relict patterns and secondary radiation centers, the relative importance of possible internal migration routes from alternative entryways, the evidence for over-water dispersal of the "migrant" element, and the effects of island area and distance are considered for the herpetofauna of the Philippines, a compact, fringing archipelago. Evaluations are based primarily on diversities and relationships of the herpetofaunas of 7 of the islands, which have a total of 220 species (54 amphibians, 92 lizards, and 74 snakes). Only in the evaluation of relict distributions is the known herpetofauna of the total archipelago taken into consideration.

The distributional patterns within the Philippines of the endemic, multispecies genera of lizards, *Luperosaurus* and *Brachymeles*, as well as the amphibian genus *Platymantis*, exhibit relict patterns of the type resulting from partial extinction of an old fauna, which has existed as a number of isolated units. *Brachymeles* and *Platymantis* also give evidence of secondary radiation centers in distal islands. Patterns for the endemic genus of lizards *Pseudogekko* and snake genera *Cyclocorus*, *Hologerrhum*, and *Oxyrhabdium* are simpler relict patterns with only 1 or 2 species in each genus. These are rather widely distributed, or, in some instances, limited to either the distal or proximal islands. These patterns are those postulated by Darlington (1957) as patterns which would develop within a chain of islands.

Sorenson's index of similarity is used to evaluate the relative effectiveness of dispersal routes. These indices, particularly when the nonnative fauna is excluded, indicate that the primary dispersal route or routes within the archipelago have been the eastern routes, by way of the Mindanao-Leyte—or possibly, in some instances the Mindanao-Bohol—pathways. The Palawan entryway has contributed very little to the herpetofauna of the rest of the Philippines. High indices of similarity between Negros and Mindoro suggest a relatively active migration route between these two islands.

A proportional-diversity index, based on the presumed lower ability of amphibians to disperse across marine barriers, is used to evaluate the probable effect of marine barriers. The evidence indicates that, with the exception of Palawan Island, much of the herpetofauna has apparently reached the intermediate and distal islands of the archipelago from Mindanao as a result of waif dispersal across marine barriers.

When number of species for the total herpetofauna, and for the amphibians, lizards, and snakes independently, are plotted against area or against a weighted distance value the curves for amphibia and the total herpetofauna exhibit patterns consistent with those projected from MacArthur's and Wilson's thesis (1967) regarding faunal diversity along a chain of islands of varying size. The data indicate, however, that the diversity of the lizard fauna on Palawan island is lower than expected, and that the diversity of the snake fauna is probably somewhat lower for Mindanao and higher for Luzon island relative to the diversity exhibited by the fauna of other islands in the study. The effects of the narrow marine barriers on the present distribution of the amphibian fauna have produced a pattern of island diversities in general agreement with the MacArthur-Wilson hypothesis. The diversities of lizards and snakes for the sample group of islands included in this study exhibit several discrepancies. The relatively narrow over-water barriers between the islands of this compact archipelago, less effectual against reptiles than amphibians, and the several possible migration routes and secondary centers of radiation may be factors in the distribution patterns of these faunal elements. The reasons, however, for the low diversity of lizards of Palawan and for the effectiveness of the barrier between Palawan and Mindoro, a marine channel only about 150 km. in breadth at the present time and broken by small islands, are not readily explained from data.

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TROPICAL SHELF ZOOGEOGRAPHY

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INTRODUCTION

The richest marine fauna is found in the shallow waters of the tropical oceans at depths generally less than 200 meters. Zoogeographically, four great regions may be identified, the Indo-West Pacific, the Eastern Pacific, the Western Altantic, and the Eastern Atlantic. Each region may, in turn, be subdivided into provinces, but these will not be discussed at this time. To the north and south, the tropics are bounded by the 20°C. isotherm for the coldest month in the year. Longitudinally, the tropical regions are separated from one another by barriers that are very effective since each region possesses, at the species level, a fauna that is highly endemic. By studying the operation of these longitudinal barriers, one can learn something about the interrelationship of the regions and can also obtain information leading to a better understanding of zoogeography and evolution.

THE EAST PACIFIC BARRIER

The Indo-West Pacific and Eastern Pacific regions are separated by the East Pacific Barrier, the vast stretch of deep-water that lies between Polynesia and America. In regard to the shore fishes, it was concluded that an eastward colonization movement was taking place across the Barrier and that successful reciprocal migrations were, at least, very rare and might be completely lacking

(Briggs, 1961, 1964, 1966). When the general relationship of the tropical shelf regions was first discussed (Briggs, 1967a), comparable information on the major groups of the shallow-water invertebrates was not available.

Emerson (1967) published a revealing analysis of the distribution of those Indo-West Pacific species of mollusks that have succeeded in penetrating across the Barrier into the Eastern Pacific. He found that such trans-Pacific species were largely restricted, in the Eastern Pacific, to the oceanic islands, the greatest numbers being found at Clipperton (33 species) and at the Galápagos (25 species). It was noted that the gastropods, which greatly outnumbered the bivalves, belonged to groups that were known to have relatively long larval stages. Most important of all, Emerson pointed out that no molluscan species of apparent Eastern Pacific origin were known to occur in Polynesia.

Data on the other invertebrate groups are not as complete, but it is significant that some of the littoral echinoderms (Ekman, 1946), holothurians (Deichmann, 1963), decapod crustaceans (Chace, 1962; Garth, 1965), and hermatypic corals (Emerson, 1967) found in the Eastern Pacific (especially around the offshore islands) are trans-Pacific species of apparent Indo-West Pacific origin. Therefore, it may now be said that for the tropical marine shore fauna in general, including both fishes and invertebrates, it seems likely that successful migration across the East Pacific Barrier takes place in one direction only—from west to east.

THE NEW WORLD LAND BARRIER

The New World Land Barrier, with the Isthmus of Panama forming its narrowest part, is virtually a complete block to the movement of tropical marine species between the Eastern Pacific and Western Atlantic. This state of affairs has existed since about the latest Pliocene or earliest Pleistocene (Simpson, 1965; Patterson and Pascual, 1968) so that, at the species level, the two faunas are well separated. The present Panama Canal has not notably altered this relationship since, for most of its length, it is a freshwater passage forming an effective barrier for all but a few euryhaline species.

The New World Land Barrier is the most effective of the four zoogeographic barriers that separate the tropical faunal regions. It has stood for approximately three million years, but it now appears that man is about to breach this barrier by excavating a sea-level canal somewhere in the vicinity of the Isthmus of Panama. If such a canal is constructed, it would present ample opportunities for marine animals to migrate in either direction. This could result in the Eastern Pacific being invaded by over 6000 species of fishes and invertebrates and the Western Atlantic being invaded by over 4000 species. Since the Western Atlantic species would apparently be competitively dominant, it has been predicted that a large scale extinction would take place in the

Eastern Pacific resulting in the irrevocable loss of a huge number (possibly thousands) of species (Briggs, 1968, 1969).

THE MID-ATLANTIC BARRIER

The broad deep-water barrier that separates the Western Atlantic tropics from those of the West African coast functions in a very interesting manner. An impressive number of shore fishes have managed to traverse the Mid-Atlantic Barrier from west to east. It has been estimated (Briggs, 1967a) that about 118 shore fish species have trans-Atlantic distributions but that only about 24 of them came from the Indo-West Pacific via the Cape of Good Hope. The rest probably evolved in the Western Atlantic and successfully performed an eastward colonization journey across the ocean. Trans-Atlantic species comprise about 30 percent of the shore fish fauna of tropical West Africa.

Works on some of the major groups of West African invertebrates also show that an appreciable number of the species are trans-Atlantic: Dekeyser (1961) found that about 25 percent of the ascidians showed this distribution; Burton (1956), 18 percent of the sponges; Monod (1956), 16 percent of the anomuran and brachyuran crabs; Knudsen (1956), 6 percent of the prosobranch mollusks; Ekman (1953), 16 percent of the starfishes, brittle stars, and sea urchins; and Marcus and Marcus (1966), 29 percent of the opisthobranch mollusks. Furthermore, Chesher (1966), who found 8 trans-Atlantic species of sea urchins in the Gulf of Guinea, stated that gene flow appeared to take place from west to east.

It seems apparent that, in both the fishes and the invertebrates, the great majority of the trans-Atlantic species originated in the Western Atlantic and then migrated eastward. The westward colonization traffic appears to be restricted to certain dominant species that originated in the Indo-West Pacific and then gained access to the Atlantic by rounding the Cape of Good Hope. So far, there are no indications that species originating in the Eastern Atlantic, and belonging to genera typical of that area, have been successful in becoming established on the western side.

THE OLD WORLD LAND BARRIER

The Eastern Atlantic and the Indo-West Pacific regions are separated by the Old World Land Barrier. It has been estimated that the continental masses of Eurasia and Africa have been linked at least since the beginning of the Pleistocene (Gohar, 1954). The Suez Canal is a sea-level passage that has been open since 1869 but migration of marine animals has been inhibited for two reasons: first, the canal connects two areas that are separated by a temperature barrier, the Red Sea being tropical while the Mediterranean is warm-temperate; second, the Bitter Lakes, which form part of the Suez passageway, have a high salinity (about 45 percent). Despite these difficulties, the limited migratory movements that have taken place through the Suez Canal do provide some significant information.

The Mediterranean has been invaded by at least 24 species of Red Sea fishes (Ben-Tuvia, 1966), 16 species of decapod crustaceans (Holthuis and Gottlieb, 1958), and several species in other groups such as the tunicates (Pérès, 1958), mollusks (Engel and van Eeken, 1962), and stomatopod crustaceans (Ingle, 1963). So, while there is ample evidence of intrusions into the eastern Mediterranean, there are no reliable data that indicate any successful reciprocal migration. Also, there are some indications that the invaders from the Red Sea (a part of the Indo-West Pacific Region) are replacing rather than coexisting with certain native species (George, 1966).

The various circumtropical shore species have probably been able to preserve their genetic homogeneity by means of migration around the Cape of Good Hope (in addition to crossing the open ocean barriers in the Pacific and Atlantic). Talbot and Penrith (1962) remarked that surface temperatures of 21°C. are often present round the Cape outside a cold upwelling area. There are about 16 known species of circumtropical shore fishes (Briggs, 1960). Besides these, there are about 15 other species that apparently transgress the Old World Land Barrier at the Cape (Briggs, 1967a). Of the total of 31 fish species, eight are monotypic but all the rest represent genera that are best developed in the Indo-West Pacific.

Apparently, only a few tropical invertebrate species have been able to migrate around the Cape of Good Hope. Monod (1956) in his monographic study of the West African decapods showed that 10 out of 176 shore species occurred in the Indo-West Pacific. Ekman (1953) noted that only 2 percent of the tropical Atlantic echinoderms (Asteroidea, Ophiuroidea, and Echinoidea) extended around the Cape. It appears, especially from the ichthyological evidence, that the colonization movement of tropical shore species around the Cape takes place entirely in a westerly direction, from the Indo-West Pacific into the Atlantic.

RELATIONSHIPS OF THE SHELF REGIONS

Evidence now available about the dispersal of the shallow-water marine invertebrates tends to substantiate the general nature of a remarkable distributional phenomenon that was discovered earlier for the shore fishes (Briggs 1961, 1964, 1967a). Successful (colonizing) migrations across the zoogeographic boundaries that delimit the Indo-West Pacific can apparently take place in one direction only, outward into areas where the fauna is poorer and the competition is less. The realization that the East Pacific and Old World Land Barriers operate as one-way filters enables us to understand better how the Indo-West Pacific Region serves as *the* evolutionary and distributional center for the tropical shore animals of the world. We can see that competitively dominant species continue to migrate, as they probably have for millions of years, from the Indo-West Pacific eastward across the open ocean to America and westward around the Cape of Good Hope into the Atlantic; since 1869, some of them have also been able to pass northward through the Suez Canal into the Mediterranean.

The Western Atlantic Region may be considered a secondary center of evolutionary radiation. Many species evolved in this area have proved capable of migrating eastward to colonize the tropical Eastern Atlantic. However, species originating in the Eastern Atlantic are apparently incapable of successfully invading the western side. Again, the advantage seems to lie with the area that possesses the richer fauna and the higher level of competition.

It can be seen that the completely eastward direction of successful migratory movements across the East Pacific Barrier and the predominantly eastward movements across the Mid-Atlantic Barrier take place in a direction opposite to that of the main flow of the surface waters via the North and South Equatorial Currents. In contrast, the surface and subsurface countercurrents in the tropical Pacific and Atlantic are weakly developed but these smaller currents are obviously the principal means by which successful transport is achieved.

Fell (1967) noted that certain groups of shore species apparently demonstrated speciation gradients in which the number of species gradually diminished around the world in a westward direction. He interpreted this to mean that the direction of successful migrations had also been to the west and that such dispersals had been carried out by the North and South Equatorial currents. Subsequently, it was pointed out that the existence of a gradient in numbers of species (or genera) across a major barrier did not necessarily indicate the direction of the original successful migration (Briggs, 1967b). The fact that colonizations do take place in a direction opposite to that of the major currents is a good indication that biological competition rather than passive transport is probably the most important factor controlling the successful dispersal of tropical marine shore animals.

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A NEW SPECIES OF GLANDULOCAUDINE CHARACID FISH, *HYSTERONOTUS MYERSI*, FROM PERU

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INTRODUCTION

On August 23, 1964, one of the authors (Thomerson), Jerry Anderson, Albert J. Klee, Emanuel Ledecky-Janachek, Winfield Rayburn, and Dr. Richard L. Stone made a collection of fishes taken from a small stream tributary to the Pachitea River (Amazon drainage) at the northeastern outskirts of Tournavista, Province of Huanuco, Peru. Some of these were kept alive for experimental purposes and some were preserved. Among the fishes taken were representatives of the new species described here.

Hysteronotus is a small genus of glandulocaudine characids most recently reviewed by Böhlke (1958) who described a new species, *Hysteronotus hesperus,* amplified our knowledge of the only other known species, *Hysteronotus megalostomus* Eigenmann (1911), and redefined the genus. The characters of the new species described here and an analysis of additional specimens of *H. megalostomus* require a reevaluation of Böhlke's contribution.

Hysteronotus myersi Weitzman and Thomerson, new species.
(Figures 1, 2, 3, 4, and 5.)

Material. Holotype, a male USNM 203697, standard length 49.00 mm. (no. 13 in table 1) from a small stream directly tributary to Pachitea River (itself tributary to Ucayali River) at northeastern outskirts of Tournavista, Huanuco Province, Peru. Elevation approximately 200 meters. Paratypes, originally in two lots, one lot of 8 specimens (nos. 1–4, 7–9, and no. 14 in table 1) with same data as holotype. Second lot of 5 specimens (nos. 5, 6, and 10–12 in table 1) raised in aquaria by Thomerson and bred from specimens in lot 1 and the holotype. Disposition of these lots is as follows: specimens nos. 5, 6, 7, 11, and 14 to Academy of Natural Sciences, Philadelphia (ANSP no. 112326 for nos. 5, 6, and 11, and ANSP no. 112325 for nos. 7 and 14); nos. 1, 2, 3, 4, 8, and 9 to United States National Museum, (USNM no. 203698); nos. 10 and 12 to Tulane University Collections (TU no. 56456).

Description. Proportions as thousandths of standard length appear in table 1. Body elongate, laterally compressed, especially in males; body depth just anterior to dorsal and anal fin 2.7–3.4 times in standard length. Predorsal body profile slightly convex with slight concavity at nape; concavity deepest at posterior termination of supraoccipital spine. Along base of dorsal fin, body surface slightly arched dorsally to accommodate inclinator and other muscles of fin. Posterior to dorsal fin, body profile nearly straight with gentle downward slope to adipose fin. Posterior to adipose fin, body profile a straight level line to procurrent caudal rays in males and a slightly downward slope to these rays in females (compare figs. 1–4). Ventral profile to anus usually gently rounded with steepest inclination ventral to jaws. Ventral profile protrudes ventrally its greatest distance at point ventral to midlength of adpressed pectorals. At anal fin origin (anterior termination of fin base) body profile gently convex, more so in males, and slopes upward to beginning of caudal peduncle just posterior to posterior anal fin termination. At that point profile straight and level or sloping slightly downward to procurrent caudal fin rays. Caudal peduncle deeper in males, least depth in standard length 6.5–6.8 times in males and 7.5–8.5 times in females (compare figs. 1–4).

Length of head 3.7–4.0 times in standard length, this proportion not changing greatly in different sized specimens. Specimen 49.6 mm. (longest) and one 28.3 mm. in standard length both with head 3.9 times in standard length. Eye rather large, somewhat larger in small specimens, 2.8–3.3 times in head length. Snout short, equal to, or shorter than, eye in specimens at hand, 3.3–3.9 times in head length. Snout appears proportionally longer in small specimens (table 1). Least width bony interorbital 2.6–3.0 times in head length, always longer than snout length.

Maxillary long, relatively slender, sloping ventrally and posteriorly to form an angle of 60–80 degrees to longitudinal axis of specimens. Maxillary length

TABLE 1. *Measurements of* Hysteronotus myersi *in thousandths of standard length. Locality: small stream at northeastern outskirts of Tournavista, Huanuco Province, Peru.*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Range	Mean
													Holotype			
Sex	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♂	♂	♂		
Standard length (mm.)	25.3	28.1	28.3	29.0	29.8	30.9	31.5	32.4	32.6	33.8	35.5	36.5	49.0	49.6		
Greatest depth	332	292	311	331	309	334	332	336	338	322	316	372	316	349	292–372	327.14
Snout to dorsal	594	576	586	602	594	576	590	584	586	577	566	594	582	561	561–602	583.43
Snout to pectoral	268	272	289	279	272	275	298	262	267	266	271	271	268	280	262–298	274.14
Snout to pelvic	458	459	459	473	457	478	479	481	454	447	457	477	452	463	454–481	463.86
Snout to anal	601	566	597	597	571	579	590	577	586	592	597	614	582	572	566–614	587.21
Eye to dorsal	442	434	463	469	457	459	467	435	460	456	444	474	445	440	434–474	453.22
Anterior dorsal base to caudal fin base	467	463	428	467	476	472	483	466	460	458	450	482	454	475	428–483	465.07
Depth of peduncle	123	117	120	131	128	126	129	133	120	133	127	148	153	151	117–153	131.35
Length of peduncle	138	146	138	138	138	149	143	145	132	148	141	150	151	131	131–151	142.00
Length of pectoral	233	214	216	224	228	220	228	226	221	224	212	232	247	222	212–247	224.79
Length of pelvic	134	128	127	138	138	124	130	136	129	130	126	159	174	171	124–174	138.86
Height of dorsal	203	196	191	200	184	184	200	198	199	172	166	200	244	231	166–244	197.71
Length of head	268	267	258	258	258	256	266	259	248	261	251	260	253	256	248–268	258.50
Diameter of eye	095	089	088	090	087	091	082	083	089	083	079	079	076	077	076–095	085.57
Length of snout	075	068	067	066	074	074	079	071	068	071	068	074	078	076	066–079	073.50
Bony interorbit	095	089	099	097	094	094	092	093	086	089	085	088	092	093	085–099	091.86
Length of upper jaw	123	121	124	124	124	126	127	126	120	124	124	123	130	133	120–133	124.93

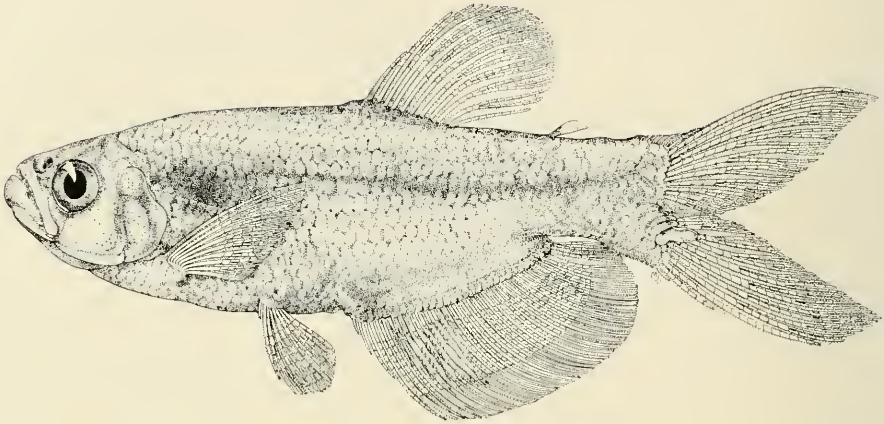

Figure 1. *Hysteronotus myersi*, new species, holotype, USNM 203697, adult male, 49.0 mm. in standard length. Small stream (tributary to Pachitea River, tributary to Ucayali River) at northeastern outskirts of Tournavista, Huanuco Province, Peru.

(measured from tip of snout to posteroventral end of maxillary) 1.9–2.2 times in head length. Teeth 7–10, tricuspid, in single row on maxillary. Four specimens with 7, three with 8, three with 9, and two with 10 teeth on one side. Teeth cover about 60–90 percent of free edge of maxillary. Premaxillary teeth in two series; outer row with 3 teeth except two specimens with 4 teeth on one side and 3 teeth on other side. Inner row with 4 tricuspid or quincuspid teeth in six specimens and 5 teeth in eight specimens. Usually 4 large, most often tricuspid, anterior teeth on each dentary (3 teeth on one side of one specimen). In large male specimens third tooth from anteromedian tooth largest and with secondary cusps reduced or absent. Sometimes other large dentary teeth with reduced cusps. Large teeth followed by 9–13 abruptly smaller and usually tricuspid teeth. No teeth on vomer, palatines, or pterygoids.

Fontanels almost absent, that part anterior to epiphyseal bar (often called frontal fontanel) not detectable, that part posterior to bar (often called parietal fontanel but almost always surrounded by frontal as well as parietal bones and supraoccipital) narrow, almost completely closed joint in all specimens. Gill rakers moderately short, pointed, longest less than ½ length of pupil, 6–8 in upper limb, 10–12 on lower limb. Two specimens with total of 16, four with 17, four with 18, three with 19, and one with 20 rakers on entire first arch of one side. Circumorbital bones well ossified, covering entire cheek area, so-called "great suborbital" (actually infraorbital 3) completely covers cheek, leaving no space between it and preopercle. Suprapreopercular process extends dorsally to level of dorsal fin of fourth infraorbital bone (postorbital of some authors). In large specimens posterior border of fourth infraorbital con-

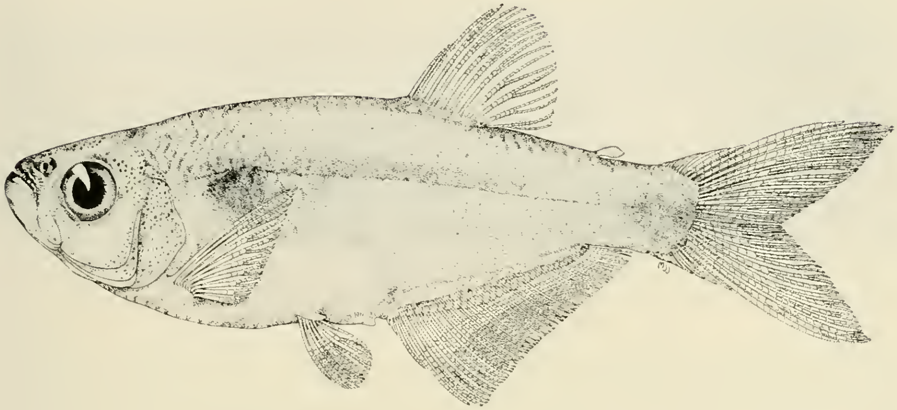

Figure 2. *Hysteronotus myersi,* new species, paratype, USNM 203698, adult female 32.6 mm. in standard length. Same data as holotype.

tacts suprapreopercular process. Small individuals with space between these bones. Fifth infraorbital not in contact with preopercle.

Scales of moderate size, cycloid with concentric circuli and about 8–15 grooves or radii on the exposed posterior field. Lateral line complete, perforating 39 scales in three specimens, 40 in four, 41 in three, 42 in four. Lateral line with slight ventral curve on side of body anterior to position of dorsal fin. Lateral line continues to caudal base along midline. Transverse scale rows between anterior bases of dorsal and anal fins 14–15, often 7 above and 7 below lateral line. Predorsal scale count 21–23; axillary scales present above pectoral and pelvic fins. Basal scale sheath at base of anal fin of about 27–29 scales, usually 2 obvious horizontal rows anteriorly with some accessory scales. One longitudinal scale row along posterior third of anal fin base, and 1½ rows at midregion of fin. Between bases of pelvic fin and anus, scales of both sides of body meet at midline in elongate median acute angle. Scales overlap acute midline angle only anteriorly near base of pelvic fins. No sharp keel between pelvic bases and anus. Area from anterior and posterior medial bases of pelvic fins along midventral line to isthmus, covered by scales. Ventrolateral bases of pectoral fin without greatly enlarged scales. Figure 3 diagrams scales around caudal gland at base of lower caudal fin lobe. Two lateral line scales illustrated just dorsal to posterior base of gland. Glandular tissue and fossa-like structure of gland entirely supported by modified scales, fibrous connective tissue, and skin.

Dorsal fin with ii, 9 rays in ten specimens, ii, 10 in four specimens; origin usually vertically over anterior base of anal fin, sometimes somewhat posterior to anterior anal fin base, nearer margin of opercle than base of caudal fin. Distance from tip of snout to anterior base of dorsal fin 1.7–1.8 times in

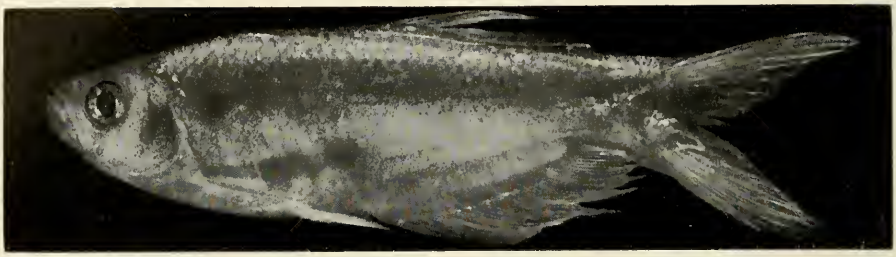

FIGURE 3. *Hysteronotus myersi*, new species, holotype USNM 203697.

standard length. Dorsal fin profile rounded, not "straight topped" as reported for *Hysteronotus hesperus* by Böhlke (1958). Length of longest fin ray (= height of dorsal in table 1) 4.1–6.0 times in standard length; large males with greatest dorsal fin height (4.1 and 4.2 vs. 4.9–6.0 for all other specimens) (see also table 1). Height of dorsal fin appears sexually dimorphic, but relatively short in females and small males.

Anal fin with v, 34 rays in two specimens, v, 35 in eight specimens, and v, 36 rays in four specimens. First unbranched ray not visible externally. Origin at or slightly behind midpoint of standard length. Distance from tip of snout to anal fin origin 1.6–1.8 (1.7 in eleven of fourteen specimens) times in standard length. Ventral margin of anal fin nearly straight in females, convex in males (compare figs. 1 and 2). Males with small dorsally recurved hooks on fourth through eleventh or twelfth branched anal fin rays (see fig. 1).

Pelvic fin rays i, 6 in all specimens, distal end always reaching anterior basal termination of anal fin. Length of pelvics sexually dimorphic, 5.8 times in standard length in largest males, 6.3 in smaller male and 7.4–8.1 in females. Two types of contact organs present, bony hooks and bony spinelets. Hooks of one large, thick, hooklike excresence per ray segment. Spinelets of small, slender spicules of bone, one or more per ray segment. Spinelets easily broken, hooks not easily broken. Hooks confined to anal fin. Retrorse bony spinelets on males very small, and primarily on the first and second branched ray, even in largest male; not nearly as well developed or common as on *Hysteronotus hesperus*. Two to 3 or 4 spinelets per bony segment of each fin ray.

Caudal fin with 10/9 principal caudal rays (17 branched rays) in all specimens; fin deeply forked. Males with small antrorse spinelets on dorsal edge of caudal rays, especially of lower lobe. No caudal spur.

Vertebral counts 38–39 including ural segment. Two specimens with 16 precaudals and 22 caudals, remainder (except for one abnormal specimen for which there is no count) with 16 precaudals and 23 caudals.

COLOR IN ALCOHOL. Humeral spot present, large, diffuse, and centered above fourth through sixth scales of lateral line. Single narrow, black, straight line extends from dorsal border of humeral spot to center of caudal peduncle

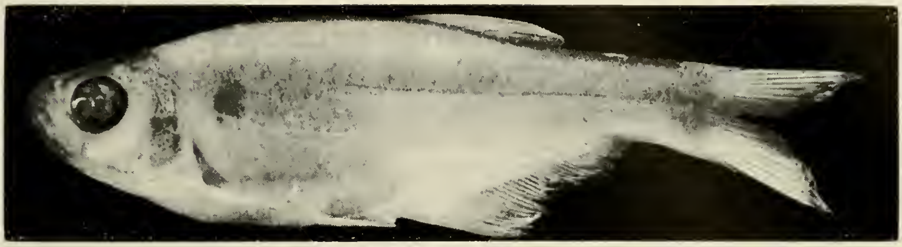

Figure 4. *Hysteronotus myersi,* new species, paratype ANSP 112326, adult female 30.9 mm. in standard length. Bred from specimens collected at the type locality.

where in males line arches dorsally to end at junction of center of upper caudal peduncle muscle mass with upper lobe of caudal fin (fig. 1). Line may be more diffuse than shown in fig. 1, or may be pale in some females as in fig. 2. Caudal blotch present, weak, sometimes absent as in fig. 1; weakly present in fig. 2. In male 36.5 mm. in standard length caudal blotch moderately well developed at center of union of caudal fin with caudal peduncle. Anterior border of blotch diffuse but with some dark pigment extending onto central caudal rays. Never as much pigment as in *Hysteronotus hesperus.* Compare figs. 1 through 4 with fig. 2, plate 3 in Böhlke (1958) for *H. hesperus* and fig. 4, plate 58 in Eigenmann (1927) for *H. megalostomus.* Most of body of *Hysteronotus myersi* pale brown, slightly darker dorsally and lighter ventrally. Top of head dark brown with a narrow band of dark pigment extending from head to dorsal fin base.

Color in life. One of us (Thomerson) has kept two pair of *H. myersi* in aquaria for several months. Their color may be summarized as follows. Females silvery with no prominent markings. Males with humeral spot and dusky stripe or band extending length of body. Both sexes with a distinct greenish iridescence. When males excited, lateral band darkens and 2 distinct pinkish spots appear at upper and lower base of caudal fin.

Further aquarium notes. Fertilization is internal. Eggs slightly oval, approximately 1 mm. in diameter, and translucent. Eggs distributed on aquarium glass, plants, and rocks. More eggs appear attached to underside of plant leaves than on top. Very few eggs deposited near bottom of tank, usually in upper ⅔ of tank (5, 15, and 20 gallon aquaria). Spawning probably occurred in early morning and eggs appear deposited individually.

Species name. This species is named in honor of George S. Myers in recognition of his long and continued interest in characid fishes, and his frequent and helpful council to students of this complicated but fascinating group.

Type locality. *Hysteronotus myersi* is known only from the type locality, a small stream directly tributary to the Pachitea River (Amazon drainage) at the northeastern outskirts of Tournavista, Huanuco Province, Peru. Most

TABLE 2. *Measurements of* Hysteronotus hesperus *in thousandths of standard length. All specimens from eastern Ecuador. See Böhlke (1958, p. 35) for localities; compare original numbers.*

	1	2	3	4	5	6	7	8	Range	Mean
							Holotype			
Sex	♀	♀	♂	♀	♂	♂	♂	♂		
Standard length (mm.)	61.0	62.3	63.4	68.2	75.0	76.0	76.5	81.8		
Greatest depth	328	320	331	320	316	349	318	332	316–349	326.75
Snout to dorsal	640	644	640	650	657	663	612	621	612–663	640.88
Snout to pectoral	271	265	268	258	259	286	274	271	258–286	269.00
Snout to pelvic	492	475	470	469	466	470	464	454	454–492	470.00
Snout to anal	623	623	613	640	597	627	636	606	597–640	620.63
Eye to dorsal	528	518	503	532	539	542	510	514	503–542	523.88
Anterior dorsal base to caudal peduncle	386	401	427	384	376	423	402	412	384–423	401.37
Depth of peduncle	107	106	121	113	127	126	118	127	106–127	118.13
Length of peduncle	134	127	114	114	131	126	131	129	114–134	125.75
Length of pectoral	279	279	265	264	268	271	258	—	258–279	269.14
Length of pelvic	139	135	142	137	136	150	140	142	135–150	140.13
Height of dorsal	134	156	164	180	189	191	191	183	134–191	173.50
Length of head	246	229	248	232	240	268	240	252	229–268	244.37
Diameter of eye	069	069	060	066	065	072	059	061	059–072	065.13
Length of snout	067	075	077	070	076	083	081	073	067–083	075.25
Bony interorbit	090	088	087	088	084	099	089	089	084–099	089.25
Length of upper jaw	107	096	096	101	105	116	094	110	094–116	103.13
Original number	P304	Pi1001	Pi607	P308	P309	Pi1002	P306	P307		

of the specimens were taken from pools in an area of alternating shallow pools and riffles where the width of the stream varied from 1 to 5 meters and from a few centimeters to 0.5 meters deep. The bottom was gravel and sand, with a few snags and broken limbs but no macrophytic aquatic plants. The stream was in a shallow ravine and was shaded by a dense canopy of small trees, brush, and vines. Downstream were several small waterfalls leading to an area of deeper boulder filled pools. Elevation at the type locality is approximately 200 meters. A popular account of this locality is given by Klee (1965a).

Fishes were not abundant, either above or below the waterfalls. Most of the specimens of *Hysteronotus myersi* were taken from midwater in the shallow pools. Representatives of *Rivulus peruanus* Regan and loricariid catfishes were taken from the same pools, but the most abundant macroorganism was a river shrimp, *Macrobrachium brazilense* (Heller). Klee (1965b) characterized the water at the type locality as ". . . . clear, clean, cool, moving water containing little or no vegetation. It is very soft, well oxygenated, and contains little in the way of dissolved materials." These observations and the collection of the specimens of *Hysteronotus myersi* were made during the last week of August and first week of September 1964, during the dry season.

Relationships. Böhlke (1958) reviewed in detail our knowledge of *Hysteronotus.* At that time Böhlke distinguished the two known species, *H. hesperus* and *H. megalostomus,* by contrasting 14 characters. In most of these characters, *H. myersi* appears closest to *H. megalostomus* but differs from that species in many other respects. A new comparison is made of these 14 characters plus additional characters based on new data for *H. megalostomus,* new counts and measurements of *H. hesperus* (so that all counts and measurements are consistent), and data from *H. myersi.* Tables 1, 2, and 3 present a comparison of measurements as thousandths of standard length for the three species.

Character 1, size of males: Standard length 63.4–81.8 mm. in *Hysteronotus hesperus*; 36.5–49.6 mm. in *H. myersi*; 29.0–41.8 mm. in *H. megalostomus.* All males at these various sizes appear fully adult. Both *H. megalostomus* and *H. myersi* appear to be relatively small species and the large adult males of *H. myersi* lived at least nine months in aquaria with little growth and are presumably large specimens of the species. *Hysteronotus megalostomus* may reach a larger size and perhaps these size differences between adult males of *H. myersi* and *H. megalostomus* do not reflect a real species difference. Character 2, bony hooks on anal fin of male: *H. hesperus* with true hooks on last unbranched and first 8–9 branched rays. Böhlke (1958) reported hooks extending back to third ray from posterior termination of fin; however, these are spinelets. *Hysteronotus myersi* with hooks confined to fourth through about twelfth branched rays, mostly on fifth through eleventh. *Hysteronotus megalostomus* with hooks on first through eleventh to twelfth branched rays. Character 3, pelvic fin rays: Rays i, 7 in *H. hesperus*; i, 6 in *H. myersi* and *H. megalostomus.* Character 4, humeral spot: Small, round, clearly defined in *H. hesperus*; diffuse and large in *H. myersi*; large, sharply defined, and vertically elongate in *H. megalostomus.* Character 5, outer and inner rows of premaxilliary teeth: Outer premaxillary teeth 4–6, usually 5 in *H. hesperus*; 3–4, usually 3 in *H. myersi*; and 3–5 in *H. megalostomus.* Inner premaxillary teeth 4–5, usually 4 in *H. hesperus*; 4–5, slightly more often 5, in *H. myersi*; and 5–6, usually 6 in *H. megalostomus.* Character 6, maxillary teeth: Teeth 6–9 and very strong, dorsal teeth sometimes quincuspid, ventral teeth tricuspid in *H. hesperus*; 7–10 strong, tricuspid teeth in *H. myersi*; 5–6 strong (especially dorsally in large specimens) tricuspid teeth in *H. megalostomus.* Character 7, caudal fin of males split to its base: Not split to base in male of *H. hesperus* and *H. myersi* but split to base in *H. megalostomus.* Character 8, pectoral rays: Normally i, 11 in *H. hesperus*; i, 9 in *H. myersi*; and i, 9 (12 specimens) or i, 10 (6 specimens) in *H. megalostomus.* Character 9, lower limb gill rakers: 12 or, usually, 13 in *H. hesperus*; 10–12, usually 11, in *H. myersi*; and 10–12, usually either 11 or 12, in *H. megalostomus.* Character 10, eye in head length: 3.4–4.3 times in *H. hesperus*; 2.8–3.3 in *H. myersi*; and

Table 3. *Measurements of* Hysteronotus megalostomus *in thousandths of standard length. Specimens 1–15 are from 3 to 4 km. northwest of Loĝoa Santa, Minas Gerais, Brazil. Specimens 16–18 are from a tributary of Rio das Velhas near Laĝoa Santa, Minas Gerais, Brazil.*

	1	2	3	4	5	6	7	8	9	10
Sex	♀	♂	♂	♀	♂	♀	♀	♂	♀	♂
Standard length (mm.)	28.4	29.0	29.3	29.7	29.8	29.9	29.9	30.5	31.3	31.4
Greatest depth	274	314	324	320	329	278	291	348	294	344
Snout to dorsal	612	600	604	616	584	586	612	604	600	596
Snout to pectoral	264	268	272	262	278	251	264	256	268	268
Snout to pelvic	431	428	447	438	449	438	438	443	447	440
Snout to anal	545	507	550	515	547	522	553	535	565	522
Eye to dorsal	510	473	485	482	474	458	478	482	489	468
Anterior dorsal base to caudal fin base	382	427	406	407	413	398	415	400	400	420
Depth of peduncle	104	128	123	118	121	100	106	125	105	124
Length of peduncle	139	155	154	135	138	137	134	148	137	146
Length of pectoral	243	241	259	239	252	224	240	229	236	246
Length of pelvic	104	126	137	128	121	100	113	131	102	131
Height of dorsal	182	186	188	192	185	177	174	194	179	185
Length of head	246	231	246	246	248	244	256	239	239	242
Diameter of eye	083	076	085	084	084	080	080	082	083	086
Length of snout	076	079	082	081	084	077	080	082	083	083
Bony interorbit	090	097	097	094	098	087	097	098	096	096
Length of upper jaw	115	107	123	118	128	107	110	121	118	111
Color of pelvics			black		part black			part black		

Table 3. *Continued.*

	11	12	13	14	15	16	17	18	Range	Mean
Sex	♂	♂	♀	♂	♂	♂	♂	♂		
Standard length (mm.)	31.6	32.1	32.2	32.8	41.8	32.3	34.0	35.0		
Greatest depth	352	339	298	342	316	356	338	312	274–356	320.50
Snout to dorsal	614	592	582	598	630	597	606	600	582–630	601.83
Snout to pectoral	272	268	254	262	271	276	270	263	251–278	265.94
Snout to pelvic	446	442	432	452	440	434	456	414	414–456	439.72
Snout to anal	544	534	534	534	524	545	535	503	503–565	535.61
Eye to dorsal	478	472	475	479	505	483	462	446	446–510	477.72
Anterior dorsal base to caudal fin base	422	436	422	424	411	440	400	374	374–440	410.94
Depth of peduncle	133	122	102	125	117	124	124	111	100–133	117.33
Length of peduncle	149	157	137	137	146	149	144	140	134–157	143.44
Length of pectoral	250	—	229	232	254	251	248	223	223–259	241.41
Length of pelvic	111	131	096	137	127	127	118	108	096–137	119.50
Height of dorsal	190	181	176	183	196	179	197	177	174–197	184.50
Length of head	246	242	220	250	239	242	236	228	220–256	241.11
Diameter of eye	089	081	078	086	084	078	082	074	074–089	081.94
Length of snout	079	075	075	079	074	074	074	069	069–084	078.11
Bony interorbit	101	097	090	095	083	093	088	080	080–101	093.16
Length of upper jaw	123	115	112	116	100	118	118	114	100–128	115.22
Color of pelvics	black	black				yellow	red	black		

2.8–3.1 in *H. megalostomus.* Character 11, length of upper jaw in head length: 2.3–2.6 in *H. hesperus*; 1.9–2.2 in *H. myersi*; and 1.8–2.3 in *H. megalostomus.* Character 12, length of pelvics: 6.2–7.4 in males, 7.2–7.6 in females of *H. hesperus*; 5.8–6.3 in males, 7.3–8.1 in females of *H. myersi*; and 7.3–9.2 in males, 7.8–10.4 in females of *H. megalostomus.* Character 13, anterior dentary teeth: Quincuspid in *H. hesperus,* tricuspid in *H. myersi* and *H. megalostomus.* Character 14, fine bony spinelets of male pelvic fins: Numerous and on both sides of ray segments, usually several per segment in *H. hesperus*; not numerous, 1 or 2 per segment (sometimes up to 4 in *H. myersi*) and on one side of ray only in both *H. myersi* and *H. megalostomus.*

Other characters useful in comparing these species are as follows: Character 15, numbers of vertebrae: 40–42 vertebrae in *H. hesperus* with 17 precaudals in all specimens, 23 caudals in one specimen, 24 caudals in two specimens, and 25 caudals in five specimens; 38–39 vertebrae in *H. myersi,* with 16 precaudals in all specimens, 22 caudals in two specimens and 23 caudals in eleven specimens; 40–42 vertebrae in *H. megalostomus* with 15 precaudal vertebrae in almost all specimens and 25 caudal vertebrae in eight specimens, 26 in seven specimens, and 27 in two specimens. One specimen of *H. megalostomus* with 14 precaudal and 27 caudal vertebrae. Character 16, scales around caudal fin: *H. hesperus* with 14 (15 in one specimen) longitudinal rows of scales around caudal peduncle, *H. myersi* and *H. megalostomus* with 18. Character 17, predorsal scales: This count difficult and inaccurate but *H. hesperus* with 23–25 scales, *H. myersi* with 20–23, and *H. megalostomus* with 21–25.

Character 18, tip of snout to dorsal fin origin in thousandths of standard length (see tables 1–3): Range of *H. hesperus* (612–663), mostly beyond ranges of other two species, (561–602) for *H. myersi* and (584–614) for *H. megalostomus.* Character 19, snout to anal distance in thousandths of standard length: Ranges of *H. myersi* (566–614) and *H. megalostomus* (507–565) partly contiguous, that of *H. hesperus* (597–640) begins at upper limit of range of *H. myersi,* not approaching that of *H. megalostomus.* Character 20, eye to dorsal distance in thousandths of standard length: Range of *H. hesperus* (503–542) nearly falls outside that of other two species (434–474 for *H. myersi* and 446–510 for *H. megalostomus*). Character 21, distance between dorsal origin and base of caudal fin in thousandths of standard length: Ranges of *H. hesperus* (384–423) and *H. megalostomus* (374–440) broadly overlap; that of *H. myersi* (428-483) stands apart from that of *H. hesperus* and overlaps upper range of *H. megalostomus.* Character 22, length of caudal peduncle in thousandths of standard length: Ranges of *H. myersi* (131–151), and *H. megalostomus* (134–157) broadly overlap, while that of *H. hesperus* (114–134) barely overlaps their lower limit. Character 23, caudal gland: This gland is different in *H. myersi* and *H. megalostomus* (compare figs. 5 and 6). The gland of *H. hesperus* is very similar to that of *H. myersi* (compare fig. 5 with fig. 6 in Böhlke 1958. Also see discussion below under Status of the Genus *Hysteronotus*). Character 24, caudal fin split to its base: The caudal fin is normally split to its base in *Pseudocorynopoma doriae* and *Hysteronotus megalostomus* but it is not split in *H. hesperus* or *H. myersi.*

The determination of the closest relative of *H. myersi* is difficult. As can be seen in the above characters, for example spinelets on the pelvic and caudal fins, number of ventral fin rays, number of outer row premaxillary teeth, number of cusps on maxillary teeth and large dentary teeth, number of pectoral rays, size of eye in relation to head length, length of the upper jaw, number of longitudinal rows of scales around caudal peduncle, proportional distance between snout tip and dorsal fin origin, proportional length of the caudal peduncle, and small scales at pectoral base, *H. myersi* more closely approaches *H. megalostomus* than it does *H. hesperus.* In a very few presumably important characters, for example caudal fin not split to its base and caudal gland structure, *H. myersi* more closely approaches *H. hesperus* than it does *H. megalostomus.*

In a few characters, for example length of pelvics in males, and relative distances between the dorsal origin and caudal fin base, *H. hesperus* and *H. megalostomus* are more similar to each other than either is to *H. myersi.* In some characters, for example in number of precaudal vertebrae, structure of glandular tissue within caudal gland, size and shape of the humeral spot, no bony hooks on first through third branched anal fin rays, relatively long pelvics in males, ventrally convex anal fin margin, and extremely rounded, convex male dorsal fin profile, *H. myersi* is unique and unlike either *H. hesperus* or *H. megalostomus.*

With our present unclear knowledge of the phyletic and genetic stability of the caudal fin organ, or gland, it is difficult to weigh the significance of this structure in showing a close relationship between *H. hesperus* and *H. myersi* in contrast to the many characters that indicate *H. myersi* is closer to *H. megalostomus.* The caudal glands of glandulocaudine characids are in need of detailed comparative study, both in their histology and gross structure. The best review of this subject to date is by Nelson (1964). See Géry (1964, fig. 4) for figures of *Glandulocauda,* and Nelson (1964, figs. 3–5) for figures of *Pseudocorynopoma, Argyropleura, Gephyrocharax, Landonia, Corynopoma,* and *Glandulocauda.* Eigenmann and Myers (1927, plates 84, 86, and 88) illustrated *Corynopoma, Landonia, Pseudocorynopoma,* and *Gephyrocharax.* Unfortunately, at present we do not know enough about either caudal glands or other characteristics of glandulocaudine characids to utilize these glands as valid, generic differences. The formation of the glandular tissue and scales in *Hysteronotus megalostomus* on the one hand, and *H. hesperus* and *H. myersi* on the other, is very different (compare figs. 5 and 6). The

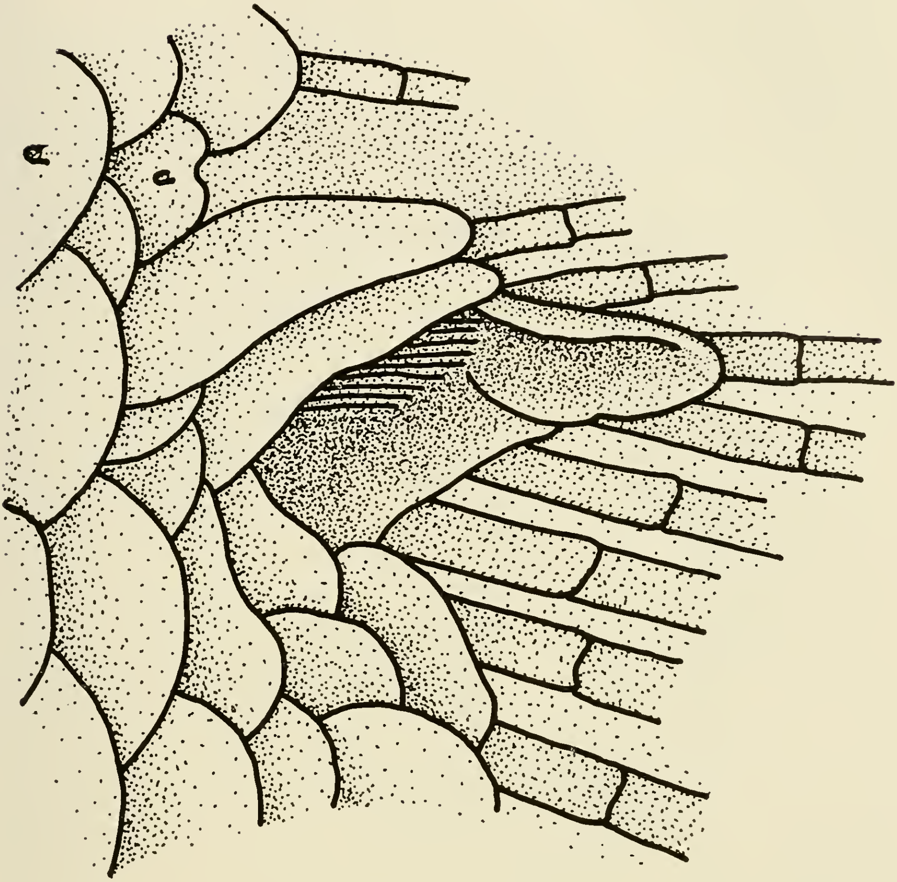

Figure 5. Lateral view of caudal gland of holotype of *Hysteronotus myersi.*

gland of the latter two species is surrounded in part by several modified scales and the glandular tissue lies over the lateral surface of two modified scales which curve dorsally over the glandular tissue forming a deep longitudinally oriented fossa. This fossa is open on its lateral and ventral surface. The gland of *H. megalostomus* is very different and has a very modified scale oriented ventrally around glandular material. The gland in *H. megalostomus* most closely resembles that of *Pseudocorynopoma,* see Eigenmann and Myers (1927, pl. 84, figs. 4–5). In gross dissection of *H. megalostomus* no obvious modified glandular tissue is present, but thickened skin lies over the dorsal surface of the ventral, furrowed scale, this skin being also attached medially to the fin rays. The same structure is found in *Pseudocorynopoma doriae* Perugia. The pouch of the gland in *H. megalostomus* extends anteriorly four to five scale

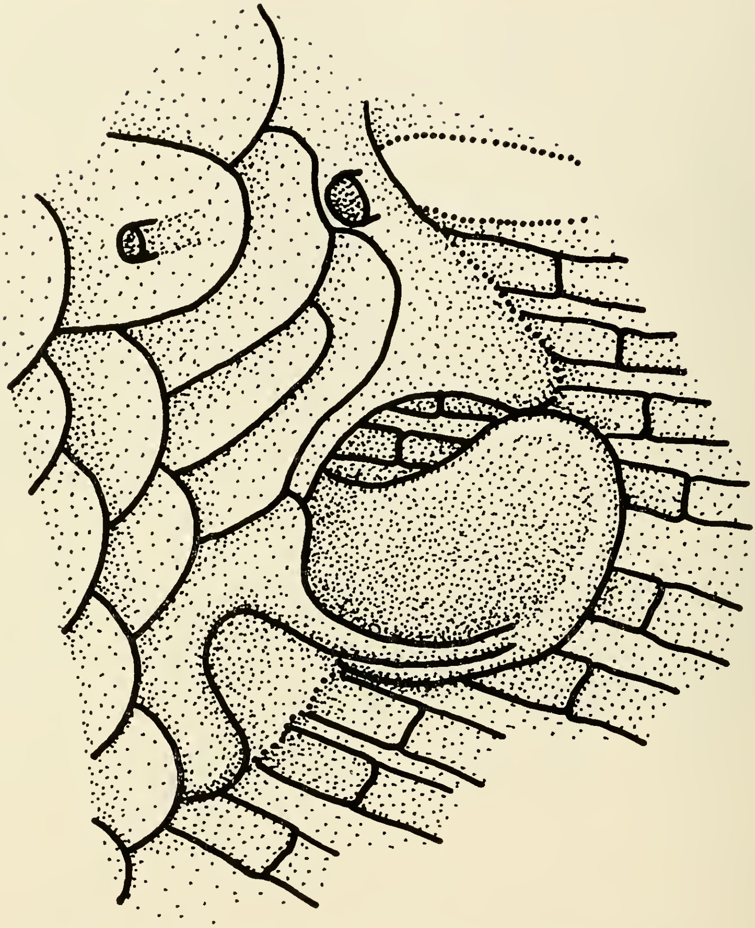

FIGURE 6. Lateral view of caudal gland of a specimen of *Hysteronotus megalostomus* 34.0 mm. in standard length from a tributary to Rio das Velhas near Lagôa Santa (19°39'S. longitude, 43°44'W. latitude), Minas Gerais, Brazil. This is the male with red pelvics in table 3.

rows between the scales just ventral to the lateral line and the musculature of the caudal peduncle. The external opening of the pouch is held lateral and open by the modified ventral scale and two elongate scales just anterodorsal to it. In *H. myersi* the pouch extends medially and anteriorly beneath five or six scale rows. The striated glandular tissue within the pouch turns sharply dorsally just within the pouch. This tissue ends under the area of the termination of the lateral line. In *H. hesperus* the pouch and scale structure is about the same as in *H. myersi*; however, the apparent glandular tissue in the specimens at hand is not striated and only slightly thickened. It lies in the same area as the striated tissue in *H. myersi.*

Polychromatism in *Hysteronotus megalostomus.* Myers (1953) collected, preserved and labeled separately 3 males belonging to *H. megalostomus* because one had black pelvic fins, one had red, and the other yellow pelvic fins. Böhlke (1958, pp. 39–42) suggested that these 3 fishes represented 3 closely related species. He devised a key to separate them using the characters discussed below, but did not describe any of the three as a new species distinct from *H. megalostomus.* The senior author has reexamined these 3 specimens and compared them with 15 other specimens of *H. megalostomus* (table 3).

Böhlke found the body depth different in the 3 males, 3.1 for the black-finned fish, 2.9 for the red and 2.8 for the yellow. Remeasurement of these 3 specimens gives 3.1, 3.0, and 2.9 respectively, but relative differences are valid. In the additional collection of *H. megalostomus* investigated, the black-finned males have a depth of 2.8, 2.9, 3.0, 3.0, and 3.1. Two of these specimens (nos. 5 and 8 in table 3) have much less black on their pelvics than Böhlke's specimen (no. 18 in table 3). Three of the additional male specimens in table 3 have colorless (color in life unknown) pelvics and a body depth of 3.0, 3.1, and 3.2 (2.9 and 3.0 in the yellow and red specimens). These males include specimens larger and smaller than Böhlke's. Thus body depth is not a function of body length in the sizes examined. Böhlke correlated the number of pectoral rays (i, 9 in red pelvics and i, 10 in yellow pelvics) with color and believed it may be a species difference. There is no information on the red and yellow color of the pelvics in the new collection; however, of all specimens available with black pelvics, three have 9 branched rays and three have 10 branched rays; of the three colorless males, one has i, 10, two have i, 9. Böhlke found that the dorsal fin of the red-pelvic-finned male extended to the base of the adipose fin, but fell considerably short of the adipose fin in the yellow-finned male. In the additional males, the dorsal never reaches the adipose fin; however, the height of the dorsal fin varies considerably (table 3). Specimen no. 10 has a dorsal fin proportionally almost as high as specimen no. 17, the red-finned male; the dorsal of no. 10 nearly reaches the adipose fin and dorsal fin length does not separate these fishes into two groups. Böhlke reported 3 maxillary teeth in the red-finned fish and 4 and 5 maxillary teeth in the yellow-finned fish. We confirm his counts but the number of maxillary teeth is variable in several of the specimens at hand. Two specimens had 1, five had 2, four had 3, and three had 4 maxillary teeth. One specimen is damaged. Böhlke counted 31 branched anal rays in the red-finned fish and 33 rays in the yellow-finned fish. We again confirm Böhlke's counts, but in the additional specimens the branched ray counts vary from 29–33 and black-finned specimens exhibit this whole range of counts. Finally, Böhlke reported the yellow-finned fish with 43, and the red-finned specimen with 41 perforated lateral line scales. In the specimens at hand this scale count ranges from 40–45.

All known male specimens of *H. megalostomus* have black pigment in the form of large melanophores on the body just dorsal to the pelvic fin rays; some have more of this than others. The amount of black pigment on the pelvic fins is variable and one specimen (not recorded as part black in table 3) has a few large melanophores on one pelvic fin. Perhaps the thickened fleshy interradial membranes unique to the pelvics of the yellow-finned fish studied by Böhlke are correlated with sexual activity and vary with sexual activity. In view of the above facts, we suggest that all the specimens examined, including those previously examined by Böhlke, belong to *H. megalostomus,* a single, somewhat variable, species with polychromatic pelvic fins in the males.

STATUS OF THE GENUS *HYSTERONOTUS*

Böhlke's definition of *Hysteronotus* (1958, pp. 33–34) includes the new species here described with little difficulty. In his key to the glandulocaudine genera (p. 44) Böhlke used one character of the genus, dorsal fin origin nearer the caudal base than to the eye, to separate *Hysteronotus* from four other rather unrelated genera. This statement is supported by data for *H. megalostomus* and *H. hesperus* but 12 out of 14 specimens of *H. myersi* (table 1) have the dorsal fin origin nearer the eye than the caudal base. We thus expand the definition of *Hysteronotus* to include fishes showing this character, however a revision of Böhlke's key to the glandulocaudine characid genera should be deferred until a complete and detailed review of the species involved is available.

A more questionable decision is that to include species with such diverse caudal gland structure (figs. 5 and 6) in a single genus. If caudal gland structure is strongly conservative in glandulocaudines then perhaps *H. myersi* and *H. hesperus* should be generically separated from *H. megalostomus,* a species closer to *Pseudocorynopoma* in this character. On the other hand, the three species here referred to *Hysteronotus* share a number of unique characters and the differences in caudal gland structure may have little phyletic significance. We think it best to retain *Hysteronotus* as here defined with three known species, *H. myersi, H. hesperus,* and *H. megalostomus,* until a more penetrating analysis of the phyletic significance of characters found in glandulocaudine characids can be made.

ACKNOWLEDGMENTS

We are indebted to Dr. James E. Böhlke of the Academy of Natural Sciences, Philadelphia, for his generous loans of specimens of *Hysteronotus* and for comments on the manuscript. Jerry Anderson, Albert J. Klee, Emanuel Ledecky-Janachek, Winfield Rayburn, and Dr. Richard L. Stone assisted

Thomerson in collecting the specimens here described. Dr. Alfred E. Smalley, Tulane University, kindly identified the river shrimp. The collection was made during Thomerson's tenure as a National Aeronautics and Space Administration Predoctoral Fellow at Tulane University and collecting expenses were partially supported by a grant from the Society of Sigma Xi. The drawing for figure 2 was paid for by a grant from the Graduate School, Southern Illinois University. Figures 1 and 2 are by Marion Johnson; figures 5 and 6 are by the senior author. Radiographs were prepared by Edgar N. Gramblin and Masaw L. Williams.

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REDISCOVERY OF THE LORICARIID CATFISH, *ACESTRIDIUM DISCUS* HASEMAN, NEAR MANAUS, BRAZIL

By

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More than fifty years ago John D. Haseman (1911, p. 319, pls. 50 and 51) described and figured a very small elongate loricariid catfish which he collected near Manaus, Brazil, as a new genus and species, *Acestridium discus.* He distinguished the genus from *Farlowella* principally on the basis of the expanded, disclike end of the snout and the presence of many series of delicate, spiny ridges (with intervening depressions) on all of the scutes. Haseman had 3 examples, the largest (holotype) was 72 mm. in total length. The types are now in the Field Museum of Natural History, Chicago. With the exception of a restatement by Miranda Ribeiro (1912) of Haseman's original description and the inclusion by Gosline (1945) of the species in his catalog of Central and South American catfishes, the species, so far as is known, has not been reported again.

During a recent visit, Dr. Jacques Gery presented the Stanford Collection with 2 examples of *A. discus* (fig. 1 a,b) collected on 23 October 1965, by E. Fittkau and himself in a small tributary of the Igarapé Castanha, which meets the right (southwestern) bank of the Rio Negro at a point two hours by boat upstream from Manaus. The specimens (SU 64202) measure 49 and 51 mm. in total length. A search of the Stanford Collection revealed 9 other specimens of the same species collected by Dr. Carl Ternetz in 1924

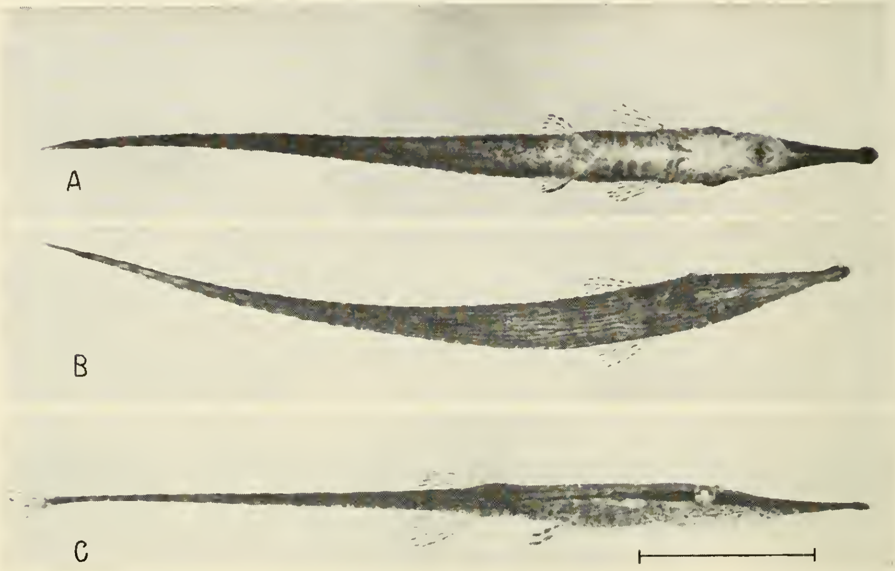

Figure 1. *Acestridium discus,* SU 64202, 49 and 51 mm total length; a, ventral; b, dorsal; c, lateral. Scale 1 cm.

from the Igarapé do Mai Joana, also near Manaus. These 9 specimens (SU 64095) range in total length from 48 to 65 mm. The total known range of the species then includes 3 tributaries of the Rio Negro near Manaus.

The specimens fit Haseman's description and illustrations with but one exception. The length of the snout, as usually measured from the anterior of the orbit to its tip, is about 2.25 rather than 4 times in the distance from its tip to the anus. Apparently Haseman measured the snout length differently, as this same measurement made on his drawings is about 2.25. Perhaps he, like Regan (1904, p. 303), used the distance between the tip of the snout and the anterior border of the naked area containing the mouth. This snout measurement, as determined from Haseman's drawings, does yield about 4 times in the distance from snout tip to anus.

Several characteristics in Haseman's description require discussion. The large retrose hooks on the dorsal and ventral surfaces of the expanded tip of the snout (fig. 2) are set in 4 rows of 3–4 hooks. One row lies on either side near the margin of the disc, the other parallel to it and situated a short distance from the margin. The first pelvic spine of many of the Loricariidae, including *Farlowella,* is covered with many small hooks. In *Acestridium,* the structure is comblike (fig. 3) with enlarged toothlike hooks in about 3 series confined to the median surface of the spine, the rest of the spine being naked. With the fins erected, the hooks point toward each other, and, with the at-

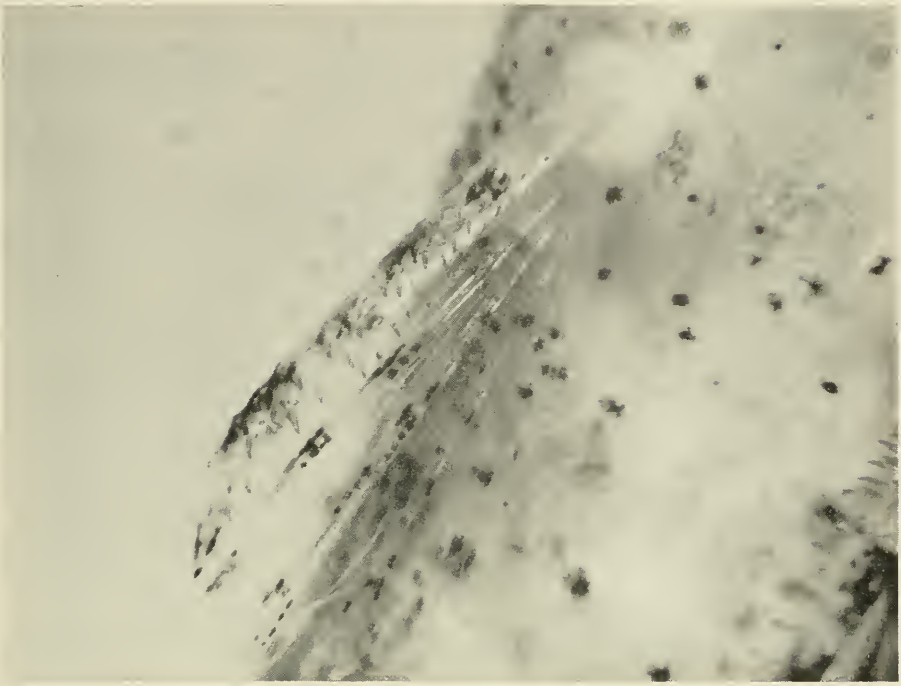

Figure 2. Pelvic fin. 38×.

tached fin membranes and supporting rays curving inward toward the midline, the whole structure appears like a small basket. This structure was common to all specimens of both sexes examined. Although sex was not easily determined because of the small size of the fish and, in some specimens, a lack of any recognizable feature of the gonads, the structure does not appear to be a secondary sexual character. Regan (1904, p. 198) describes the sexual characteristics in males of this family as being generally confined to enlarged bristles on the sides and top of the head or on the pectoral fins. But he makes no mention of the pelvic fins.

The body (fig. 1b) is finely striped with brown above, pale below (fig. 1a) with the black spots on the lower lateral sides (fig. 1c) forming a dark border in the abdominal region and continuing completely across on the snout and the caudal peduncle. A broad, brown, lateral stripe (fig. 1c) extends posteriorly on either side of the head from the snout through the eye and tapers to a point above the posterior edge of the pelvic base. Each of the rather bulging eyes bears a smooth-margined operculum on the dorsal part of the iris.

Acestridium discus differs from all known species of *Farlowella* not only in the sharply expanded snout-tip with its series of hooks and the definite spiny

Figure 3. Expanded disclike snout with rows of retrose hooks. 60×.

ridges of the scutes, which are fewer in number (25–27) than in any known species of *Farlowella* (33–34), but also in its generally smaller size; the rounded caudal fin; the absence of filamentous extensions on the main, terminal upper and lower caudal rays; the rounded (rather than acutely pointed) dorsal, anal, and pelvic fins; the straight vertical margins of the lateral scutes of the long caudal peduncle; five rather than six plates between the dorsal plate and the supraoccipital; and in having the ventral surface of the abdomen covered with two rather than three series of plates.

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THE AMPHIBIANS AND REPTILES OF AFGHANISTAN, A CHECKLIST AND KEY TO THE HERPETOFAUNA

By

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In 1950 the Academy received a collection of reptiles from Afghanistan. Though small, the collection was of considerable interest, having come from a little-visited region of the Dasht-i-Margo desert. It was reported on by Leviton in 1959. Subsequently, significant collections of Afghanistan reptiles have been made, notably by John Gasperetti in 1961 (Leviton and Anderson, 1961a and 1963), Richard and Erica Clark in 1964 and 1968 (Clark, Clark, Anderson and Leviton, 1969, and Clark and Clark, in preparation [for 1968 collections]), and the William Street Expedition of the Field Museum of Natural History in 1965 (Anderson and Leviton, 1969). These, together with new materials acquired by other museums, some of which we have seen, have formed the basis of the following preliminary attempt at a checklist and key to the herpetofauna of the entire country.

The growth of knowledge about the Afghan herpetofauna may be measured by the fact that in 1959 Leviton included 67 nominal species in his checklist. One additional species, *Calotes versicolor*, an error of omission at that time, should have been included to bring the total to 68. In the accompanying key and checklist, 101 nominal species and subspecies are listed, an increase of 50 percent in the number of species currently known from that country. Of the 33 new additions, five have been described as new since 1960. We believe it safe to say that our knowledge of the Afghan herpetofauna is still very incomplete and we expect that many interesting animals remain to be discovered, especially in the mountains of the Hindu Kush.

We must emphasize that problems exist. For example, we are not satisfied with our treatment of the species of *Eryx*, *Cyrtodactylus*, or those of the genus *Coluber*. However, rather than postpone publication of this work indefinitely until all problems are solved, an unlikely event in any case, we beg the indulgence of our colleagues and hope they will find this account useful as a point of departure for extending their own researches.

We have included in both the key and the checklist several nominal species whose presence in Afghanistan, though reasonable to expect, has yet to be authenticated. In the key these species are indicated by having an asterisk (*) immediately following the name; in the checklist the asterisk precedes the name.

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KEY TO THE AMPHIBIANS AND REPTILES OF AFGHANISTAN

1. Body, and limbs (if present), covered with scales or a shell (reptiles) 2
   Body and limbs without scales or shell (amphibians) 4
2. Shell present (turtles) ..... *Testudo horsfieldii*
   Shell absent 3
3. Limbs absent, eyes without movable lids (snakes) 79
   Limbs present, or if absent, eyes with movable lids (lizards) 9
4. Tail present in fully metamorphosed individuals; hind limbs approximately same length as forelimbs; larvae resembling adults, possessing teeth in both jaws (salamanders) ..... *Batrachuperus mustersi*
   Tail absent in fully metamorphosed individuals; hind limbs considerably longer than forelimbs; larvae unlike adults, never possessing true teeth until metamorphosis (frogs and toads) 5
5. Large, raised gland (paratoid) between shoulder and eye; no maxillary teeth 6
   Paratoid gland absent; maxillary teeth present 7
6. Tarsal ridge well developed, smooth; tympanum, when distinct, about half or less than half diameter of eye ..... *Bufo viridis*
   Tarsal ridge marked by small tubercles; tympanum ⅔ diameter of eye ..... *Bufo andersonii*
7. Skin of back with thickened dorsolateral ridge on each side; frequently with light vertebral stripe; toes not fully webbed (terminal phalanx of 4th toe free of web) ..... *Rana ridibunda*
   Back without dorsolateral ridges; usually no light vertebral stripe; toes fully webbed 8
8. Tympanum as large as eye or larger; heel reaching anterior to eye; prominent light stripe on hinder surface of thigh; males with external vocal sacs; males without pectoral glandular areas (mammata) ..... *Rana cyanophlyctis*
   Tympanum smaller than eye; heel not reaching anterior to eye; no prominent light stripe on hinder surface of thigh; males without external vocal sacs; males with prominent pectoral glandular areas (mammata) ..... *Rana sternosignata*
9. Limbs absent; eyelids movable; deep longitudinal fold on each side of body ..... *Ophisaurus apodus*
   Limbs present 10
10. Pupil of eye vertically elliptical; skin soft, with granules, rarely imbricate scales, no paired shields on top of head, which is covered by granules; neither suborbital nor frontosquamosal arch present on skull; clavicles broadened, forming loop at inner end; tongue smooth or covered by threadlike papillae (geckos) 11
    Pupil of eye round or slightly oval; skin covered by scales, plates, or granules, not soft; if head not covered by paired plates, then by juxtaposed scales or granules; either suborbital and/or frontosquamosal arch present on skull; clavicles not broadened at inner end, or if clavicles broadened, tongue covered by imbricate, scalelike papillae, or by oblique folds 28
11. Eyelids movable; digits not dilated; procoelous vertebrae ..... *Eublepharis macularius*
    Eyelids immovable (spectacle); digits dilated or not; amphicoelous vertebrae 12

12\. Digits with expanded subdigital lamellae forming pads, lamellae paired .... *Hemidactylus flaviviridis*
Digits without expanded subdigital lamellae; lamellae not divided 13

13\. Digits with well defined lateral, comblike, flexible fringe of pointed scales 14
Digits without lateral fringe of pointed scales, though scales may be denticulate, forming serrate border 19

14\. Dorsal scales small, granular or imbricate, intermixed with larger rounded tubercles 15
Dorsal scales large, uniform, cycloid, imbricate 17

15\. Back with small, irregular, dark spots and dots; dorsolateral dark stripe extending from behind eye to just beyond forelimb or about ⅓ distance between fore- and hind limbs; tail with dark blotches above .... *Crossobamon eversmanni*
Back with dark crossbars or longitudinal stripes 16

16\. Back with dark crossbars; hind limb reaching beyond axilla; ventral scales smooth .... *Crossobamon lumsdeni*
Back with longitudinal stripes (or dots arranged in regular longitudinal rows); hind limb reaching axilla; ventral scales keeled; dorsolateral stripe extending from behind eye to, or almost to, insertion of hind limb; light dorsal stripe extending length of posterior ⅔ of tail, bordered by serrated brown dorsolateral stripes .... *Crossobamon maynardi*

17\. Cycloid scales on back extending on to hinder part of head .... *Teratoscincus scincus*
Cycloid scales on back not extending beyond shoulders 18

18\. Cycloid scales on back feebly imbricate; about 100 scales round middle of body .... *Teratoscincus microlepis*
Cycloid scales on back strongly imbricate; about 50 scales round middle of body .... *Teratoscincus bedriagai*

19\. Dorsal scales uniform, small, juxtaposed; granular, without enlarged tubercles present (Afghanistan specimens only) .... *Alsophylax pipiens*
Enlarged dorsal tubercles present among granular scales 20

20\. Chin shields (postmentals) absent 21
Chin shields present 22

21\. Tail tapering gradually, covered below by small scales only; subdigital lamellae with several small tubercles, or denticulate on distal margin .... *Bunopus tuberculatus*
Tail cylindrical, very slender, of almost uniform diameter from base to tip, with median series of enlarged subcaudal plates; subdigital lamellae smooth .... *Agamura persica*

22\. Rostral excluded from border of nostril .... *Agamura femoralis*
Rostral forming anterior border of nostril 23

23\. Tubercles usually present among granules of lower surface of thigh, in short row of 1–6, some often in contact with posterior row of large imbricate scales; males with continuous series of preanal and femoral pores 24
No subfemoral tubercles; males with preanal pores only 26

24\. 37–40 abdominal scales across middle of belly (19–25 in distance across belly equal to length of snout); series of pores separated on midline by 1–2 scales not containing pores; 35–46 pores in males (total of both sides) .... *Cyrtodactylus* species
23–34 abdominal scales across middle of belly (10–16 in distance across belly equal to length of snout); no separation between right and left series of pores; 24–41 pores in males (total of both sides) 25

25\. 24–29 strongly keeled, nonmucronate trihedral or subtrihedral tubercles in paravertebral row from occiput to level of vent; males with 28–41 (32–40 in Afghan specimens examined) preanal and femoral pores (total of both sides) .... *Cyrtodactylus fedtschenkoi*

20–23 strongly keeled, distinctly mucronate trihedral tubercles in paravertebral row from occiput to level of vent; males with 23–31 (24–29 in Afghan specimens examined) preanal and femoral pores (total of both sides) .... *Cyrtodactylus caspius*

26\. Subcaudal scales 1 head-width behind vent small, not enlarged and platelike (in distal part of tail, more than 2 head-widths posterior to vent, median series becomes enlarged, but much narrower than width of tail); tubercles on dorsal surface of tail arranged around middle of each caudal segment, not in terminal scale row .... *Cyrtodactylus russowii**

Subcaudal scales 1 head-width behind vent enlarged, platelike, in single median series covering nearly full width of tail; tubercles on dorsal surface of tail forming terminal ring of each caudal segment 27

27\. 25–47 abdominal scales across middle of belly (more than 12 scales across belly in distance equal to length of snout) .... *Cyrtodactylus watsoni*

15–23 abdominal scales across middle of belly (7–10 scales across belly in distance equal to length of snout) .... *Cyrtodactylus scaber*

28\. No large paired shields on top of head, which is covered by granules or small scales or tubercles 29

Enlarged paired plates on top of head (some granules may be present, but enlarged shields predominate) 54

29\. Venter covered by imbricate scales, not granules; tongue broad and short, smooth or covered with villose papillae, not deeply forked; dorsum covered by imbricate scales or combination of imbricate scales and granules (agamids) 30

Venter covered by small granules or juxtaposed quadrangular scales; tongue deeply divided, long and slender, smooth, retractile into sheath at base; dorsum covered with numerous small granules or juxtaposed scales (varanids) 53

30\. Well marked dorsal crest, at least on neck .... *Calotes versicolor*

No dorsal crest 31

31\. Femoral pores present; tail strongly depressed through most of length, dorsal surface of tail with transverse rows of very large spinous tubercles rounded at base 32

Femoral pores absent; tail depressed only at base, without transverse rows of very large spinous tubercles rounded at base, although rings of large spiny scales may be present, forming more or less distinct caudal segments 33

32\. Back without greatly enlarged pointed tubercles; caudal spines small, 20–24 in cross-series at base of tail .... *Uromastyx hardwickii*

Back with transverse series of large pointed tubercles; caudal spines large, 8–10 in cross-series at base of tail .... *Uromastyx asmussi*

33\. Tympanum exposed, i.e. ear opening visible 34

Tympanum concealed or absent, no visible external ear opening 45

34\. Caudal scales in oblique rows, not forming rings; tympanum deeply sunk 35

Caudal scales forming more or less distinct rings; tympanum large, superficial 36

35\. Dorsal scales subequal in size and disposed in regular rows .... *Agama agilis*

Dorsal scales unequal, large dorsal scales twice as large as smallest, irregularly arranged .... *Agama ruderata megalonyx*

36\. Enlarged dorsal scales smooth or faintly keeled 37

Enlarged dorsal scales strongly keeled 39

37. Caudal segments with 2 whorls of scales 2 head-widths posterior to vent .... *Agama caucasica*

Caudal segments with 3 whorls of scales 2 head-widths posterior to vent, or segmentation of tail indistinct 38

38. 19–24 scales around tail at level of 5th complete whorl; scales on flanks distinctly larger than ventral and dorsolateral scales .... *Agama badakhshana*

25–35 scales around tail at level of 5th complete whorl; scales on flanks small, not larger than ventrals, grading into granular dorsolateral scales .... *Agama himalayana*

39. Caudal scales small, 30 or more in whorl 5 rows posterior to vent 40

Caudal scales large, usually less than 30 in whorl 5 rows posterior to vent 41

40. Forelimb and tibial portion of hind limb covered above with scattered, greatly enlarged spinous scales surrounded by much smaller or granular scales, large scales neither grouped in patches nor imbricate; largest scales on dorsum twice as large as largest ventral scales, vertebral and paravertebral groups of scales heterogeneous .... *Agama nuristanica*

Forelimb and tibial portion of hind limb covered with regularly arranged, enlarged imbricate and strongly keeled scales; largest scales on dorsum not larger than ventrals, vertebral and paravertebral groups of scales homogeneous .... *Agama tuberculata*

41. Flanks lacking enlarged scales .... *Agama nupta*

Flanks with numerous enlarged scales intermixed with smaller scales 42

42. Scales of chest and throat strongly keeled and mucronate .... *Agama erythrogastra*

Scales of chest and throat smooth or weakly keeled, not mucronate 43

43. Each caudal segment 1 head-length posterior to vent, with 2 whorls of scales .... *Agama caucasica*

Each caudal segment 1 head-length posterior to vent with 3 whorls of scales 44

44. Scales on snout and forehead smooth or faintly keeled; large mid-dorsal scales in 4 longitudinal rows, intermixed with smaller scales; greatly enlarged dorsolateral and flank scales in small, separate clusters forming longitudinal rows .... *Agama lehmanni*

Scales on snout and forehead strongly keeled; large mid-dorsal scales in regular longitudinal rows not intermixed with smaller scales, though vertebral row of small scales may separate enlarged scale rows into 2 paravertebral groups; no greatly enlarged dorsolateral scales; enlarged flank scales forming large patch on mid-flank .... *Agama agrorensis*

45. Large cutaneous fold at corner of mouth .... *Phrynocephalus mystaceus*

No large cutaneous fold at corner of mouth 46

46. Dorsal scales heterogeneous, small scales intermixed with strongly enlarged scales 47

Dorsal scales subequal, homogeneous (but in *P. reticulatus* clusters or single scales may appear to be of different size than surrounding scales because they are swollen and tubercular and with upraised posterior margins; if striking difference is observed, see 47.) 48

47. Enlarged dorsal scales flat, not tubercular, posterior border not sharply upturned; sides of back of head and neck with long, flexible, spinous or fringelike scales; both sides of 4th toe with long, well developed fringes; tail without dark crossbars, tip black on ventral surface in adults, in very small juveniles not black but with single black spot on ventral surface of tail .... *Phrynocephalus luteoguttatus*

Some enlarged dorsal scales nail-like, large portion of scale raised free of back; sides of back of head and neck without long spinous or fringelike scales; 1 side of 4th toe with short fringe; tail with dark crossbars always present at least on ventral surface, tip not black .... *Phrynocephalus scutellatus*

48. Flexible, fringelike scales prominent in temporal region 49
No fringelike scales in temporal region 50

49. No crossbars on tail, tip of tail black; large, prominent black spots on back and top of head, group of 4 especially conspicuous in scapular region .... *Phrynocephalus euptilopus*
Tail with distinct black crossbars on ventral surface, tip black; no conspicuous large, black spots on dorsum .... *Phrynocephalus interscapularis*

50. Nasal shields separated by 1-3 series of scales 51
Nasal shields in contact or partly separated 52

51. Scattered scales or clusters of scales on dorsum with upraised posterior margins, often swollen, tubercular; scales of upper surfaces of limbs and midline of back prominently keeled .... *Phrynocephalus reticulatus boettgeri*
No upraised, swollen scales on dorsum; scales of upper surfaces of limbs and back smooth to indistinctly keeled in young, scales of limbs distinctly keeled in adults .... *Phrynocephalus maculatus*

52. Distinct, dark-margined, light dorsolateral stripe from posterior angle of eye along body onto tail; single, very elongate suborbital scale 2–3 times as long as adjacent scales .... *Phrynocephalus clarkorum*
No light stripe along side of body; 3 suborbital scales of about equal size .... *Phrynocephalus ornatus*

53. Tail round in cross-section, or slightly compressed posteriorly, without double-toothed crest above; abdominal scales in 110–125 transverse series from collar fold to groin .... *Varanus griseus*
Tail compressed, with low, double-toothed crest above; abdominal scales in 90–110 transverse series from collar fold to groin .... *Varanus bengalensis*

54. Abdominal scales similar to dorsals; no femoral or preanal pores (skinks) 55
Abdominal scales subquadrangular or quadrangular, in 8–18 longitudinal rows across venter, very distinct from dorsal granules; femoral pores present (except in *Eremias aporosceles*) (lacertids) 65

55. Body elongate; limbs present but greatly reduced, 3–4 fingers, 3 toes 56
Body not serpentine; 4–5 fingers, 5 toes 57

56. Fingers 3 .... *Ophiomorus tridactylus*
Fingers 4 .... *Ophiomorus brevipes*

57. Lower eyelid scaly; palatine bones separated on midline of palate 58
Lower eyelid with transparent disc or lids not movable; palatine bones meeting on midline of palate 60

58. 21–23 scales around body; postnasal present; single broad vertebral scale row, much broader than adjacent rows .... *Eumeces taeniolatus*
26–30 scales around body; no postnasal; 2 median rows of dorsal scales broader than those on flanks 59

59. 1 azygous postmental .... *Eumeces blythianus**
2 azygous postmentals .... *Eumeces schneideri*

60. Eyelids immovable (spectacle) 61
Eyelids movable 63

61. Ear hidden beneath scales .... *Ablepharus grayanus**
Ear opening small but distinct 62

62. Frontoparietal single .... *Ablepharus pannonicus*
Frontoparietal divided .... *Ablepharus bivittatus lindbergi*

63. Supranasals absent; pterygoid bones in contact anteriorly, palatal notch not reaching to level of centers of eyes .... *Scincella himalayana*
Supranasals present; pterygoid bones separated anteriorly, palatal notch extending forward to level of centers of eyes 64

64. Prefrontals separated; 16–22 lamellae beneath 4th toe; dorsal scales feebly tricarinate or smooth .... *Mabuya aurata**
Prefrontals in contact; 12–16 lamellae beneath 4th toe; dorsal scales with 2–3 strong keels .... *Mabuya dissimilis*

65. Eyelids immovable; eye covered by spectacle .... *Ophisops jerdoni*
Eyelids movable 66

66. Nostril between 2 nasals and 1st upper labial .... *Acanthodactylus cantoris* subspecies
Nostril not in contact with 1st upper labial 67

67. Femoral pores absent .... *Eremias aporosceles*
Femoral pores present 68

68. Ventral plates in straight longitudinal series; lower nasal resting on 1st upper labial only; occipital shield in contact with interparietal .... *Eremias guttulata watsonana*
Ventral plates in oblique longitudinal series; lower nasal resting on 2–3 upper labials; occipital shield usually absent 69

69. Subocular bordering mouth 70
Subocular not bordering mouth 75

70. Lateral scales of 4th toe in complete row length of toe, forming distinct fringe 71
Lateral scales of 4th toe not forming distinct fringe 72

71. Broad dark dorsolateral stripe from nostril through eye, along body and side of tail on each side, 1–2 additional narrower dark stripes medial to these on each side, remainder of dorsal dark stripes interrupted and anastomosing to form reticulate pattern, evident even in very young specimens; 4th toe with 2 complete rows of subdigital scales, i.e. total of 4 scales counted around toe (except that extra scale may be present at a joint) .... *Eremias scripta*
Dorsal pattern consisting of 7 dark stripes, outer dorsolateral stripes broadest, persisting unbroken in both adults and juveniles; 4th toe with single row of subdigital scales, i.e. total of 3 scales counted around toe (except that extra scale may be present at a joint) .... *Eremias lineolata*

72. Back with dark stripes broader than interspaces in young and adults; no light ocelli on flanks nor spots contained within dark stripes, nor any tendency for flank stripes to break up 73
Back with dark stripes, breaking up into spots in adults; dark dorsolateral stripe containing white spots, or lateral and/or dorsolateral stripes breaking up into dark-margined ocelli 74

73. 4th toe with 2 complete rows of subdigital scales and complete row of sharply pointed lateral scales, i.e. total of 4 scales counted around penultimate phalanx; collar scales small, usually only single median collar scale distinctly larger than adjacent gular scales anterior to collar .... *Eremias fasciata*
4th toe with single complete row of subdigital scales and complete row of lateral to ventrolateral scales, i.e. total of 3 scales counted around penultimate phalanx; usually several collar scales distinctly larger than adjacent gular scales anterior to collar .... *Eremias regeli*

74. Adults usually with black dorsolateral stripe, more or less continuous for at least

major portion of its length, containing white spots, black stripe contrasting strongly with dorsal color pattern; juvenile with 4 dark stripes on dorsum between dorsolateral white-spotted stripes, vertebral stripe being white (dark stripes breaking up into 4 more or less regular rows of dark spots with age) .... *Eremias velox persica*

Adults with dark interrupted dorsolateral black stripe forming ocelli with white spots, this dorsolateral pattern not contrasting strongly with interrupted dark stripes and spots of dorsum; juveniles with 3 dark stripes on dorsum between white-spotted dorsolateral stripes, vertebral stripe being black, bifurcated on neck (dark stripes breaking up into several irregular rows of dark spots with age) .... *Eremias velox velox*

75\. 4th toe with distinct fringe on both lateral and medial sides, formed by complete row of sharply pointed lateral scales and complete row of similar medial scales; ungual lamellae of fingers and toes with prominent, flat, lateral expansions 76

4th toe without distinct fringe; ungual lamellae without prominent lateral expansion 77

76\. Scales of flanks distinctly larger than those of back; largest series of scales on lower surface of tibia only slightly broader than adjacent scales .... *Eremias grammica*

Scales of flanks not larger than those of back; series of broad plates on lower surface of tibia, more than twice as broad as adjacent scales .... *Eremias acutirostris*

77\. 2 series of femoral pores narrowly separated, space between series not exceeding ¼ length of each .... *Eremias aria*

2 series of femoral pores widely separated, space between series at least ⅓ length of each 78

78\. 4th toe with single row of subdigital scales; usually distinct tympanic shield; 4th supraocular usually distinct .... *Eremias intermedia*

4th toe with 2 rows of subdigital scales, internal much larger; tympanic scale usually small or indistinct; 4th supraocular usually indistinct .... *Eremias nigrocellata*

79\. Ventral scutes not enlarged, same size as adjacent scales; eyes small, covered by scales 80

Ventral scutes transversely enlarged; eyes well developed 81

80\. Scales in 22–24 rows around body .... *Typhlops vermicularis*

Scales in 14 rows around body .... *Leptotyphlops blanfordi*

81\. Ventral scutes narrower than full width of body; dorsal scale rows in more than 35 longitudinal rows at midbody .... (Genus *Eryx*[1]) 82

Ventral scutes as broad as full width of body; dorsal scales in 37 or less longitudinal rows 86

82\. Longitudinal dorsal scale rows less than 43 .... *Eryx elegans*

Longitudinal dorsal scale rows 43 or more 83

83\. Width of interorbital space considerably greater than distance from posterior edge of eye to corner of mouth; front and upper surface of snout slightly convex; 2nd upper labial usually higher than 3rd; ventrals without spots, or with widely separated dark spots .... *Eryx jaculus**

Width of interorbital space equal, less than, or slightly greater than distance from posterior edge of eye to corner of mouth; front and upper surface of snout not

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[1] Six currently recognized species of *Eryx* have been reported by various authors from Southwest Asia. Of these five have been at one time or another suggested as occurring in Afghanistan. A revision of the genus *Eryx* is long overdue. In lieu of such a revision we have included the five nominal species in our key; however we doubt that either *E. jaculus* or *E. miliaris* occurs in Afghanistan. See checklist for further comments.

convex; 2nd upper labial may be lower or higher than 3rd; ventrals as a rule with dark, confluent spots 84

84. Width of interorbital space considerably less than distance from posterior edge of eye to corner of mouth; eyes directed upward; scales on tail smooth or with scarcely detectable keels; 2nd upper labial usually lower than 3rd .... *Eryx miliaris**

Width of interorbital space equal, slightly less than, or slightly greater than distance from posterior edge of eye to corner of mouth; eyes directed laterally; scales on tail with prominent keels, at least in adults 85

85. Scales on body smooth, those on tail and on sides near anal region keeled; end of tail much narrower than head; no distinct bands on body or tail, but dark blotches and irregular markings present .... *Eryx tataricus*

Scales of body and tail more or less distinctly keeled; tail extremely blunt, often as wide as head; unicolored or with series of distinct dark bands on tail, sometimes on body, especially evident posteriorly .... *Eryx johnii*

86. Top of head covered by numerous small scales, none arranged to form regular large plates; enlarged fangs present 87

Top of head covered by 8–9 large plates disposed in regular pattern; enlarged fangs present or absent 90

87. Lateral scales in oblique series 88

Lateral scales in straight longitudinal series 89

88. Subcaudals single; keels of lateral scales serrated; ventrals without strong lateral keel .... *Echis carinatus*

Subcaudals paired; keels of scales not serrated; ventrals with strong lateral keel .... *Eristicophis macmahoni*

89. Supraocular "horn" present, surrounded by small scales; supranasal sac present, opening into upper part of nostril .... *Pseudocerastes persicus**

Supraocular "horn" absent; no supranasal sac .... *Vipera lebetina*

90. Facial pit present between nostril and eye 91

No facial pit present 92

91. Temporals, posterior upper labials fused .... *Agkistrodon himalayanus*

Temporals, posterior upper labials not fused .... *Agkistrodon halys*

92. Loreal absent, nasal shield in contact with preocular; dorsal scales in 19–25 longitudinal rows .... *Naja oxiana*

Loreal present, nasal shield not in contact with preocular; if loreal absent, dorsal scales in less than 17 longitudinal rows 93

93. Series of subocular scales separating labials from eye border; scales in 27–33 longitudinal rows at midbody; 10–13 upper labials .... *Spalerosophis diadema*

One or more upper labials bordering eye, or if subocular scales present excluding labials from eye border, then scales in less than 23 longitudinal rows 94

94. Scales in 15 longitudinal rows at midbody 95

Scales in 17 or more longitudinal rows at midbody 96

95. Loreal usually absent; temporals 1+1; subcaudals more than 60; head, nape with black crossbars or entirely black above .... *Eirenis persica**

Loreal present; temporals 1+2; subcaudals less than 60; brown crossbars on head chevron-shaped .... *Oligodon taeniolatus**

96. Dorsal scales keeled (except outer row usually smooth), in 19 longitudinal rows at midbody; ventrals less than 180; 1–2 anterior temporals 97

Dorsal scales smooth, or if keeled, then ventrals more than 180, 2–3 anterior temporals 98

97. 1 anterior temporal .... *Natrix tessellata*
 2 anterior temporals .... *Xenochrophis piscator*
98. Scales in 17 longitudinal rows at midbody 99
 Scales in 19–25 longitudinal rows at midbody 103
99. Pupil of eye vertically elliptical; black above with white or yellowish crossbars .... *Lycodon striatus bicolor**
 Pupil of eye round; color not as described above 100
100. Anal single; 1 anterior temporal; 8 upper labials .... *Psammophis leithi**
 Anal divided; 2 anterior temporals; 9 upper labials 101
101. No longitudinal stripes on body and tail; no longitudinal stripe through eye; maxillary teeth 20–38, posteriormost not grooved .... *Ptyas mucosus*
 Color pattern consisting of longitudinal stripes (sometimes indistinct); longitudinal dark stripe through eye; maxillary teeth 10–13, posteriormost enlarged, grooved 102
102. Caudals 72–115; 3 labials entering eye (4th to 6th); well defined longitudinal markings on top of head .... *Psammophis lineolatus*
 Caudals 118–134; 2 labials entering eye (5th and 6th); markings on top of head broken up into smaller blotches and spots .... *Psammophis schokari*
103. Scales in 19 longitudinal rows at midbody 104
 Scales in 21–25 longitudinal rows at midbody 108
104. Pupil vertically elliptical, or if pupil *wide open* and rounded, then rostral projecting 105
 Pupil round; rostral broadly rounded 106
105. Usually 1 prefrontal; anal single; at most 1 upper labial bordering eye .... *Lytorhynchus ridgewayi*
 2 prefrontals; anal divided; upper labials not bordering eye .... *Lytorhynchus maynardi*
106. Subocular present; 1 upper labial bordering eye .... *Coluber karelinii*
 No suboculars; 2 upper labials or more bordering eye 107
107. Scale rows 11–13 just anterior to vent; ventrals 205–244; subcaudals 124–136 .... *Coluber rhodorhachis*
 Scale rows 13–15 just anterior to vent; ventrals 199–211; subcaudals 82–119 .... *Coluber ventromaculatus**
108. Pupil vertically elliptical; anal single .... *Boiga trigonata melanocephalus*
 Pupil round; anal divided 109
109. 2 preoculars, 1 subocular; 21–23 scale rows at midbody; 9 (rarely 8 or 10) supralabials; posterior maxillary teeth longest; frontal with crescentic lateral margins .... *Coluber ravergieri*
 1 preocular, 1 small subocular; 23–25 scale rows at midbody; 8 (rarely 9) supralabials; anterior maxillary teeth longest; frontal with straight lateral margins .... *Elaphe dione*

CHECKLIST OF THE AMPHIBIANS AND REPTILES OF AFGHANISTAN

In the following list, species are arranged alphabetically within genera, genera within families, etc., and no systematic relationships are implied by the arrangement.

Class AMPHIBIA

Order CAUDATA

Family Hynobiidae

Genus **Batrachuperus** Boulenger

Batrachuperus Boulenger, 1878, Bull. Soc. Zool. France, vol. 3, pp. 71–72 (type species: *Salamandrella sinensis* Sauvage, by monotypy).

Batrachuperus mustersi Smith.

Batrachyperus mustersi Smith, 1940, Ann. Mag. Nat. Hist., ser. 11, vol. 5, pp. 382–383 (type locality: mountain streams of Paghman Range, above Paghman, Afghanistan, 9000–10,000 feet elevation; holotype: British Museum no. 1940.3.1.1).

Distribution. Known only from the type locality.

Order SALIENTIA

Family Bufonidae

Genus **Bufo** Laurenti[2]

Bufo Laurenti, 1768. Synops. Rept., p. 25 (type species: *Bufo viridis* Laurenti, 1768, by subsequent designation by Fitzinger, 1843).

Bufo andersonii Boulenger.

Bufo andersonii Boulenger, 1883, Ann. Mag. Nat. Hist., ser. 5, vol. 12, p. 161 (type locality: Ajmere, Rajputana [restricted by Leviton, Myers, and Swan, 1956, Occ. Pap. Nat. Hist. Mus. Stanford Univ. no. 1, p. 4]; 3 syntypes in British Museum).

Distribution. All of northern India at low elevations, from the Ganges Basin through Rajputana, Punjab, and Sind, to southern Afghanistan, north to Kashmir and Nepal; southern and eastern Arabia. In Afghanistan it is known from south of the Hindu Kush in the southeastern part of the country and along the Helmand River, west to the Seistan Basin. To 4500 feet elevation at Kandahar and Khost.

Bufo viridis Laurenti.

Bufo viridis Laurenti, 1768, Synops. Rept., p. 27, pl. 1, fig. 1 (type locality: Vienna, Austria).

Distribution. From southern Sweden and eastern France over all of Europe (except Iberian Peninsula) eastward to Mongolia, south in Central Asia to

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[2] Clarification of the type species of the nominal genus *Bufo*:

Bufo vulgaris Laurenti is cited as type species of the nominal genus *Bufo* by Stejneger (1907) and subsequent authors. This is in error. *Bufo vulgaris* was described by Laurenti. There is no indication that it is proposed as a substitute name for *Rana bufo* Linnaeus to avoid tautonomy, though this is not unlikely. Nevertheless it is subjective, there being no objective basis for this assumption. Also, inasmuch as *B. vulgaris* is not accompanied by a synonymy in which the Linnaean name is cited, nor are the figure references cited by Laurenti the same as those cited by Linnaeus, it is not possible to claim that *B. vulgaris* is a junior objective synonym of *R. bufo* Linnaeus, there being no indication that the two are based on the same type. Therefore, *Bufo vulgaris* Laurenti is type species of the genus *Bufo* only by reason of the fact that Stejneger so designated it in 1907. However, Stejneger was preceded by Fitzinger who, in 1843, designated the type species of Laurenti's genus as *Bufo viridis* Laurenti. To the best of our knowledge this constitutes the first acceptable designation of the type species of this nominal genus.

Tibet and the Himalayas, throughout Southwest Asia, parts of Arabia, and the northern Sahara as far west as Morocco. Throughout almost the whole of the Euro-Siberian, Irano-Turanian and Mediterranean regions. To 15,000 feet in the Himalayas.

Family RANIDAE

Genus **Rana** Linnaeus

Rana LINNAEUS, 1758, Syst. Nat., ed. 10, vol. 1, p. 210 (type species: *Rana temporaria* Linnaeus, 1758, by subsequent designation by Fitzinger, 1843).

Rana cyanophlyctis Schneider.

Rana cyanophlyctis SCHNEIDER, 1799, Hist. amph., vol. 1, p. 137 (type locality: eastern India).

DISTRIBUTION. From Thailand to Nepal and Ceylon, north to Kashmir and the Himalayas, and west through southern Afghanistan and Baluchistan to eastern Iran. It is also recorded from southern Arabia. In Afghanistan it occurs south of the Hindu Kush to elevations of about 4500 feet. It has been taken west of Dilaram and is known from the Iranian portion of the Seistan Basin.

Rana ridibunda ridibunda Pallas.

Rana ridibunda PALLAS, 1771, Reise versch. Prov. russ. Reich, vol. 1, p. 458 [not seen] (type locality: Gurjew [Gurev], USSR, north coast of Caspian Sea [restricted by MERTENS and MÜLLER, 1928, Abh. Senckenberg. Naturf. Ges., vol. 41, p. 20]).

Rana ridibunda ridibunda MERTENS, 1925, Abh. Senckenberg. Naturf. Ges., no. 39, p. 55.

DISTRIBUTION. The whole of Europe to 60° N. except northwest and central Italy; western Asia as far east as northern West Pakistan, Afghanistan, and eastern Turkestan; North Africa and Arabia as far south as the Hejaz. In Afghanistan it is known from the region north of the Hindu Kush, penetrating at least as far south and east as Paghman. It has been recorded from Iranian Seistan, however.

Rana sternosignata Murray.

Rana sternosignata MURRAY, 1885, Ann. Mag. Nat. Hist., ser. 5, vol. 16, pp. 120–121 (type locality: Quetta, West Pakistan).

DISTRIBUTION. The Quetta Plateau in Baluchistan, north at least to Kabul in Afghanistan, and Kashmir. Known localities in Afghanistan lie between 4500 and 8000 feet elevation.

Class REPTILIA

Order CHELONIA

Family TESTUDINIDAE

Genus **Testudo** Linnaeus

Testudo LINNAEUS, 1758, Syst. Nat., ed. 10, vol. 1, p. 197 (type species: *Testudo graeca* Linnaeus, 1758, by subsequent designation by Fitzinger, 1843, Syst. Tept., p. 29).

Testudo horsfieldii Gray.

Testudo horsfieldii GRAY, 1844, Cat. tort. croc. amphisb. British Mus., p. 7 (type locality: Afghanistan; holotype in British Museum).

DISTRIBUTION. From the northeast shores of the Caspian Sea eastward across Kazakhstan to Lake Zaysan and thence southwestward to Afghanistan, Waziristan, Baluchistan, and eastern Iran. To at least 8000 feet elevation in Afghanistan.

Order SQUAMATA
Suborder SAURIA
Family AGAMIDAE
Genus **Agama** Daudin

Agama DAUDIN, 1802, Hist. nat. Rept., vol. 3, p. 333 (type species: *Lacerta agama* Linnaeus, 1758, by absolute tautonomy).

Agama agilis Olivier.

Agama agilis OLIVIER, 1807, Voy. Emp. Otho., vol. 4, p. 394, and atlas, pl. 29, fig. 2 [not seen] (type locality: neighborhood of Baghdad, Iraq; syntypes: Paris Museum no. 5708 [2]).

DISTRIBUTION. Western Punjab; West Pakistan; Afghanistan; Iran; Asian steppes of the USSR (coasts of the Caspian Sea, east to the Tarbagatai, and north to the steppes of the lower reaches of Irgiz); Iraq. To about 7500 feet elevation in Afghanistan.

Agama agrorensis (Stoliczka).

Stellio agrorensis STOLICZKA, 1872, Proc. Asiatic Soc. Bengal, pp. 128–129 (type locality: Sussel Pass, at the entrance to the Agror Valley, Hazara District, NW. Punjab, West Pakistan; 9 syntypes in British Museum).

Agama agrorensis, BOULENGER, 1885, Cat. liz. British Mus., vol. 1, p. 363.

DISTRIBUTION. Punjab (Agror, or Oghi Valley); Kashmir (Jhelum Valley, Chilas); Chitral (Arandu); Afghanistan (valley of the Kabul River). To at least 6000 feet elevation.

Agama badakhshana Anderson and Leviton.

Agama badakhshana ANDERSON and LEVITON, Proc. California Acad. Sci., ser. 4, vol. 37, pp. 32–35, figs. 6–7 (type locality: Mazar-i-Sharif, Afghanistan; holotype: Field Museum of Natural History no. 161108).

DISTRIBUTION. Known from three localities, all in Afghanistan: Mazar-i-Sharif, and 64 miles east of Faizabad, both on the northern side of the Hindu Kush, and Paghman, on the southern side.

Agama caucasica (Eichwald).

Stellio caucasicus EICHWALD, 1831, Zool. spec. Ross. Polon., vol. 3, p. 187 (type locality: Tiflis and Baku, Caucasus, USSR).

Agama caucasica, BOULENGER, 1885, Cat. liz. British Mus., vol. 1, p. 367.

Distribution. Southeastern Caucasus and northeastern Turkey, east through the northern and mountainous regions of Iran, Transcaspian provinces of the USSR to Chubek, Tajikistan in the east, Afghanistan, and Waziristan and Baluchistan, West Pakistan. To 9000 feet in Afghanistan.

Agama erythrogastra (Nikolsky).

Stellio erythrogaster Nikolsky, 1896, Ann. Mus. Zool. Acad. Imp. Sci. St. Pétersbourg, vol. 1, pp. 370-371 (type locality: Kalender Abad and Ferimun eastern Iran; syntypes: Zoological Institute Leningrad nos. 8759, 8760).

Agama erythrogastra, Nikolsky, 1915, Faun. Russie, vol. 1, pp. 119–121.

Distribution. Northeastern Iran, in the vicinity of Mashhad, southeastern Turkmen, northern Afghanistan, south through the mountain passes to Paghman; 3000-8000 feet elevation.

Agama himalayana himalayana (Steindachner).

Stellio himalayanus Steindachner, 1867, Reise österr. Fregatte Novara., Zool. Teil., Rept., vol. 1, p. 22, pl. 1, fig. 8 (type locality: Leh and Kargil, Ladakh frontier district, Kashmir; syntypes in Vienna Museum).

Agama himalayana, Boulenger, 1885, Cat. liz. British Mus., vol. 1, p. 362.

Distribution. Himalayas, Trans-Himalayas, southern Tibet, Hindu Kush, the ridge system of Pamiro-Alai west up to the Pamir inclusive, and southern part of Tien Shan; not known north of the Fergana Valley; Chitral, Kashmir, and Ladakh; known from Afghanistan only in the northeast.

Agama lehmanni (Nikolsky).

Stellio lehmanni Nikolsky, 1896, Ann. Mus. Zool. Acad. Imp. Sci., St. Pétersbourg, vol. 1, p. xiv (type locality: Fergana and Bokhara, USSR; syntypes in Zoological Institute, Academy of Sciences, Leningrad).

Agama lehmanni, Bedriaga, 1907, Wissenschaft. Result. N. M. Przewalski Central Asien Reisen, vol. 3, Amphib. u. Rept., p. 126, pl. 2, fig. 2.

Distribution. The mountains of the southeastern part of Central Asia north to the Fergana Valley, west to the Nura Tau and Kugitang ridges, east to the Darvaz Ridge, south to northern Afghanistan (Terentjev and Chernov, 1949, p. 148). Mazar-i-Sharif, at about 1500 feet elevation, appears to be the only documented record for Afghanistan. In the USSR it is found up to 11,000 feet elevation.

Agama nupta De Filippi.

Agama nupta De Filippi, 1843, Giorn. Inst. Lomb. e Bib. Ital., vol. 6, p. 407 (type locality: Persepolis, Iran; holotype in Milan) [not seen].

Distribution. West Pakistan; Afghanistan; Iran; Iraq. It appears to be confined for the most part to the southern margins of the Iranian Plateau, ranging from 1000–8000 feet elevation in Iran. In Afghanistan it is known only from the areas south of the Hindu Kush, up to 5000 feet elevation.

Agama nuristanica Anderson and Leviton.

Agama nuristanica Anderson and Leviton, Proc. California Acad. Sci., ser. 4, vol. 37, pp. 39–42, fig. 8 (type locality: Kamdesh, Nuristan, Afghanistan; holotype: Field Museum of Natural History, no. 161136).

Distribution. Known only from the type locality in Nuristan, eastern Afghanistan, on the southern side of the Hindu Kush at 1342 meters elevation. Smith's (1935, pp. 214–216) record of *A. tuberculata* for Kabul may refer to this species.

Agama ruderata Olivier.

Agama ruderata Olivier, 1807, Voy. Emp. Otho., vol. 2, p. 429, pl. 29, fig. 3 (syntypes from Persia and northern Arabia; syntype: Paris Museum no. 2610) [not seen].

Trapelus megalonyx Günther, 1864, Rept. British India, p. 159, pl. 14, fig. C (type locality: probably Afghanistan; holotype: ♀ in British Museum).

Distribution. North Arabian Desert (Syria, Jordan, Turkey, Iraq, but probably not Saudi Arabia), Iran, southern Afghanistan, and northwestern West Pakistan. Northward it reaches the southern shore of the Caspian Sea and the southeastern Transcaucasian region of the USSR; to about 7500 feet elevation in Afghanistan.

Elsewhere (Clark, Clark, Anderson, and Leviton, 1969, pp. 292–294) we have commented upon the problems surrounding the proper allocation of the Afghan specimens. For the present, both *A. megalonyx* and *A. r. baluchiana* are considered synonyms of *A. ruderata*.

Agama tuberculata Gray.

Agama tuberculata Gray, 1827, Zool. Jour., vol. 3, p. 218 (type locality: "Bengal"; holotype in British Museum).

Distribution. The western Himalayas from Chitral and Kashmir through the Alpine Punjab to Katmandu District in Nepal. Smith's (1935, pp. 214–216) record for Kabul is the only documented Afghan occurrence, and this record may refer to *A. nuristanica* Anderson and Leviton.

Genus **Calotes** Cuvier

Calotes Cuvier, 1817, Règne Anim., vol. 2, p. 35 (type species: *Lacerta calotes* Linnaeus, 1758, by absolute tautonomy).

Calotes versicolor (Daudin).

Agama versicolor Daudin, 1802, Hist. nat. Rept., vol. 3, p. 395, pl. 44 (type locality: Pondicherry, India [restricted by Smith, 1935, Fauna British India, vol. 2, p. 192]; holotype in Paris Museum).

Calotes versicolor, Gray, 1845, Cat. spec. liz. British Mus., p. 243.

Distribution. The entire Indian and Indo-Chinese subregions; southeastern Afghanistan; extreme eastern Iran; Pakistan; the entire Indian Peninsula;

Nepal; Ceylon; Andaman Islands; Pulo Condore; Hainan; Hong Kong; southern China; the northern part of the Malay Peninsula; Sumatra; in West Pakistan it ranges north to Swat; locally distributed in Baluchistan. Only two documented localities for Afghanistan, both in the eastern part of the country, south of the Hindu Kush, the highest at 7400 feet elevation.

Genus **Phrynocephalus** Kaup

Phrynocephalus KAUP, 1825, Isis von Oken, vol. 1, p. 591 (type species: *Lacerta guttata* Gmelin, 1789, by subsequent designation by FITZINGER, 1843, Syst. Rept., pp. 18 and 88) [ICZN, 1964: 69a, iv].

Phrynocephalus clarkorum Anderson and Leviton.

Phrynocephalus ornatus BOULENGER (in part), 1887, Cat. liz. British Mus., vol. 3, pp. 496–497.

Phrynocephalus clarkorum ANDERSON and LEVITON, 1967, Proc. California Acad. Sci., ser. 4, vol. 35, pp. 228–231, fig. 1 (type locality: southeast of Kandahar, Afghanistan, 31°20′ N., 65°50′ E.; holotype: California Academy of Sciences no. 97989).

DISTRIBUTION. The Helmand River basin of Afghanistan and West Pakistan.

Phrynocephalus euptilopus Alcock and Finn.

Phrynocephalus euptilopus ALCOCK and FINN, 1896, Jour. Asiatic Soc. Bengal, vol. 65, pt. 2, p. 556, pl. 12 (type locality: West Pakistan near Darband [elev. 3000 feet], Baluchistan; syntypes in Indian Museum, Calcutta; British Museum; Museum of Comparative Zoology, Harvard [MCZ 7227 ♀]).

DISTRIBUTION. Known from the six syntypes which were collected near Darband, West Pakistan, 3000 feet elevation, a small hollow in the Baluchistan desert basin region at the Afghan frontier, and from recently collected specimens from southeast of Darweshan, in the Helmand basin, Afghanistan (California Academy of Sciences nos. 120205–120207).

Phrynocephalus interscapularis Lichtenstein.

Phrynocephalus interscapularis LICHTENSTEIN, 1856, Nomen. Rept. Amphib. Mus. Zool. Berol., p. 12 (type locality: Bokhara, USSR).

DISTRIBUTION. Central Asian republics of USSR, north to the southeastern Ust Urt, Aral Sea, and Aral Kara Kums, east to the valley of the Syr Darya River, the Kara-tau Ridge, spurs of the Tien Shan and Pamiro-Alai; along the valley of the Pyandzh River it penetrates east to the Vakhsh Valley. It is known in lowland northern Afghanistan from the area between Andkhui and Mazar-i-Sharif, below 2000 feet elevation.

Phrynocephalus luteoguttatus Boulenger.

Phrynocephalus luteoguttatus BOULENGER, 1887, Cat. liz. British Mus., vol. 3, p. 497 (type locality: between Nushki and Helmand, along Afghan-Baluch border; Helmand, Afghanistan; syntypes in British Museum).

DISTRIBUTION. Afghanistan in the Helmand River basin, West Pakistan in the desert basins of the Nushki and Chagai districts and western Las Bela. It probably enters Seistan in Iran, but no reliable Iranian records exist; to about 4000 feet elevation.

Phrynocephalus maculatus Anderson.

Phrynocephalus maculatus John Anderson, 1872, Proc. Zool. Soc., London, p. 389 (type locality: Awada, Iran [corrected to Abadeh, north of Shiraz, by Blanford, 1876, Zool. E. Persia, vol. 2, p. 331]).

Distribution. The Afghan-Baluchistan border region, east as far as Nushki; the Central Plateau of Iran; northern and gulf coastal Arabia, and Iraq. The extent of its penetration into Afghanistan is not known, though it does reach Darweshan in the Helmand basin; it occurs in Iranian Seistan, on the Central Plateau in Iran, and may be expected throughout the low southern and western regions of Afghanistan.

Phrynocephalus mystaceus (Pallas).

Lacerta mystacea Pallas, 1776, Reise versch. Prov. russ. Reich., vol. 3, p. 702, pl. 5, fig. 1 (type locality: Naryn steppe on north coast of Caspian Sea, USSR [restricted by Mertens and Müller, 1928, Abh. Senckenberg. naturf. Ges., vol. 41, p. 26]).

Phrynocephalus mystaceus, Boulenger, 1885, Cat. liz. British Mus., vol. 1, pp. 379–380.

Distribution. Found in Central Asian USSR, southern Kazakhstan; Astrakhan District, eastern Ciscaucasia, northeastern and eastern Iran, and adjacent regions of Afghanistan; in Ciscaucasia south to the vicinity of Makhach-kala; the western limit of distribution passes between the Volga and the Don, the northern limit reaches 48–50° N in some places (Irgiz, Turgai), and in eastern Kazakhstan to the Balkhash and Ala-kul lakes. To the east the distribution is limited by the foothills of Tien Shan and Pamiro-Alai; it somewhat surpasses the Termez along the valley of the Amu Darya (Terentjev and Chernov, 1949, p. 159). In Afghanistan it occurs north of the central massif; it may extend south of the Hari Rud along the western border inasmuch as it has been recorded from northeastern Iran (Zirkuch region) near the Afghan border.

Phrynocephalus ornatus Boulenger.

Phrynocephalus ornatus Boulenger (in part), 1887, Cat. liz. British Mus., pp. 496–497 (type locality: between Nushki and Helmand, Afghan-Baluch border; lectotype: British Museum no. 1946.8.28.20 [Anderson and Leviton, 1967, Proc. California Acad. Sci., ser. 4, vol. 35, pp. 231–233]).

Distribution. The Helmand River basin of Afghanistan and the desert basins of Baluchistan, West Pakistan. Also recorded from the Zirkuch region of eastern Iran (Nikolsky, 1897, p. 324). Whether these latter specimens belong to *Phrynocephalus ornatus* or to *P. clarkorum*, or both, has not been determined.

Phrynocephalus reticulatus boettgeri Bedriaga.

Phrynocephalus raddei var. *boettgeri* Bedriaga, 1907, Wissenschaft Result. N. M. Prewalski Central Asien Reisen, vol. 3, p. 217 (type locality: Shirabad, Uzbekistan, USSR; holotype: Zoological Institute Leningrad no. 6117).

Phrynocephalus reticulatus boettgeri, Terentjev and Chernov, 1949, Diag. Rept. Amph., p. 154.

Distribution. Southwestern Tajikistan and adjacent regions of Uzbekistan; northern lowland Afghanistan.

Phrynocephalus scutellatus (Olivier).

Agama scutellata Olivier, 1807, Voy. Emp. Otho. (ed. 4), vol. 3, p. 110, Atlas, pl. 42, fig. 1 [not seen] (type locality: Mt. Sophia, near Isfahan, Iran; holotype: Paris Museum no. 6947).

Phrynocephalus tickelii Gray, 1845, Cat. liz. British Mus., p. 260 (type locality: Afghanistan; holotype in British Museum).

Phrynocephalus scutellatus, Smith, 1935, Fauna British India, vol. 2, Sauria, p. 229.

Distribution. The Central Plateau of Iran, southern Iran, southern Afghanistan, and northern Baluchistan, West Pakistan; to at least 7200 feet elevation in Afghanistan.

Genus **Uromastyx** Merrem

Uromastyx Merrem, 1820, Tent. Syst. Amph., p. 56 (type species: *Stellio spinipes* Daudin, 1802, by subsequent designation by Fitzinger, 1843, Syst. Rept., p. 18).

Uromastyx asmussi (Strauch).

Centrotrachelus asmussi Strauch, 1863, Bull. Acad. Imp. Sci. St. Pétersbourg, vol. 6, col. 479 (type locality: Sar-i-Tschah, Iran; holotype in Zoological Institute Leningrad).

Uromastix asmussi, Boulenger, 1885, Cat. liz. British Mus., vol. 1, p. 409.

Distribution. The eastern portion of the Central Plateau of Iran, and the adjacent areas of West Pakistan and Afghanistan; 1800–4000 feet elevation in Iran. The extent of its occurrence in Afghanistan is unknown, as there exists a single record for that country, on the Afghan-Baluch border.

Uromastyx hardwickii Gray.

Uromastix hardwickii Gray, 1827, Zool. Jour., vol. 3, p. 219 (type locality: Kanauj district, United Provinces, India; type in British Museum).

Distribution. India, from the United Provinces to Kathiawar and west to the Northwest Frontier Provinces and southeastern Baluchistan east of the Iranian Plateau and below 2000 feet elevation. Afghanistan along the Kabul River Valley.

Family Anguidae

Genus **Ophisaurus** Daudin

Ophisaurus Daudin, 1803, Bull. Soc. Phil., vol. 3, p. 188 (type species: *Anguis ventralis* Linnaeus, 1758, by monotypy).

Ophisaurus apodus (Pallas).

Lacerta apoda Pallas, 1775, Nov. Comment. Acad. Sci. Petropol., vol. 19, p. 435, pls. 9–10 [not seen] (type locality: Naryn steppe on the north coast of the Caspian Sea, USSR).

Ophisaurus apodus, Mertens and Müller, 1928, Abh. Senckenberg. naturf. Ges., vol. 41, p. 26.

Distribution. Balkan Peninsula (to Istria and southern Dobrudsha in the north); Crimean Peninsula; Turkey; Rhodes; Syria; northern and western Iran; Caucasus, Transcaspian, and Turkestan regions of USSR, and northern Afghanistan north of the Hindu Kush; to at least 8700 feet in Afghanistan.

Family GEKKONIDAE

Genus **Agamura** Blanford

Agamura Blanford, 1874, Ann. Mag. Nat. Hist., ser. 4, vol. 13, p. 455 (type species: *Gymnodactylus persicus* Duméril, 1856, by subsequent designation by Smith, 1935, Fauna British India, vol. 2, p. 61).

Agamura femoralis: See Addendum, pg. 205.

Agamura persica (Duméril).

Gymnodactylus persicus Duméril, 1856, Arch. Mus. Hist. Nat. Paris, vol. 8, p. 481 (type locality: Iran; syntypes: Paris Museum no. 6761 [3]).

Agamura persica, Blanford, 1874, Ann. Mag. Nat. Hist., ser. 4, vol. 13, p. 455.

Distribution. Iran, on the Central Plateau; West Pakistan, east to Cape Monze near Karachi and inland to Waziristan; Afghanistan in the areas south of the Hindu Kush and the low country west of the mountains, along the Iranian border; to 8500 feet elevation at Paghman.

Alsophylax pipiens: See Addendum, pg. 205.

Genus **Bunopus** Blanford

Bunopus Blanford, 1874, Ann. Mag. Nat. Hist., ser. 4, vol. 13, p. 454 (type species: *Bunopus tuberculatus* Blanford, 1874, by monotypy).

Bunopus tuberculatus Blanford.

Bunopus tuberculatus Blanford, 1874, Ann. Mag. Nat. Hist., ser. 4, vol. 13, p. 454 (syntypes from Iran: Bahu Kalat; Pishin; Isfandak; near Bampur; Rigan; Narmashir: Tunb Island; West Pakistan: Baluchistan: Mand; Saman; Dasht; syntypes: British Museum; Indian Museum, Calcutta; Museum of Comparative Zoology, Harvard no. 7128).

Distribution. Iraq; Iran; Afghanistan; West Pakistan. All Afghan records are for Seistan, the Helmand Basin, and the higher regions to the east (7000 feet elevation at Ghaomi Faringi).

Genus **Crossobamon** Boettger

Crossobamon Boettger, 1888, Zool. Jahrb. III, Syst., p. 880 (type species: *Gymnodactylus eversmanni* Wiegmann, 1834, by monotypy).

Crossobamon eversmanni (Wiegmann).

Gymnodactylus eversmanni Wiegmann, 1834, Herpet. Mexicana, p. 19, note 28 (type locality: "Asia media").

Crossobamon eversmanni, Boettger, 1888, Zool. Jahrb. III, Syst., p. 880.

Distribution. Central Asian republics of the USSR, northeastern and eastern Iran and neighboring regions of Afghanistan. In the north it ranges to the northern Chink (Precipice), Ust Urt, Irgiz River, Aral Kara Kum, and sands of Muyun Kum, east to the mountain system of Tien Shan and Pamiro-Alai (Terentjev and Chernov, 1949, p. 129).

Crossobamon lumsdeni (Boulenger).

Stenodactylus lumsdeni Boulenger, 1887, Cat. liz. British Mus., vol. 3, p. 479 (type locality: Afghan-Baluch border between Nushki and Helmand; holotype in British Museum).
Crossobamon lumsdeni, Kluge, 1967, Bull. American Mus. Nat. Hist., vol. 135, p. 23.

Distribution. Known from the holotype, which was taken somewhere between Nushki, West Pakistan, and the Helmand River, Afghanistan. Nikolsky (1899, p. 388) records it from Gurmuck, eastern Kerman, Iran.

Crossobamon maynardi (Smith).

Stenodactylus orientalis, Alcock and Finn, 1896 (*nec* Blanford, 1876), Jour. Asiatic Soc. Bengal, vol. 65, p. 554.
Stenodactylus maynardi Smith, 1933, Rec. Indian Mus., vol. 35, p. 18 (type locality: Baluchistan, near Afghan border; based on Alcock and Finn's specimens; syntypes: British Museum no. 1931.6.14.1 ♀, and Indian Museum, Calcutta, no. 13944 ♂).
Crossobamon maynardi, Kluge, 1967, Bull. American Mus. Nat. Hist., vol. 135, p. 23.

Distribution. The types were collected somewhere along the route followed by Maynard and McMahon during the travels of the Afghan-Baluch Boundary Commission of 1896. No definite locality was recorded. Minton (1966, p. 165) records specimens from the vicinity of Nushki, Chagai District, Baluchistan, West Pakistan. It is known from the Helmand Basin in Afghanistan.

Genus **Cyrtodactylus** Gray

Cyrtodactylus Gray, 1827, Phil. Mag., ser. 2, vol. 2, p. 55 (type species: *Cyrtodactylus pulchellus* Gray, 1827, by monotypy).

Cyrtodactylus caspius(Eichwald).

Gymnodactylus caspius Eichwald, 1831, Zool. Spec., vol. 3, p. 181 (type locality: Baku, on the Caspian Sea, USSR; syntypes: Zoological Institute Leningrad nos. 3181–3182 [?]).
Cyrtodactylus caspius, Underwood, 1954, Proc. Zool. Soc. London, vol. 124, p. 475.

Distribution. Eastern Azerbaidzhan SSR, northern and eastern Iran, northern Afghanistan, and Central Asian republics of the USSR, north to a line connecting the southeastern coast of the Kosomolets Gulf with the northern coast of the Aral Sea, and east to the mountains in the Kysyl Kums, the Nura Tau Ridge, and foothills of the Pamiro-Alai; along the valley of the Pyandzh River it reaches east to the surroundings of Chubek (Terentjev and Chernov, 1949, p. 137). In Afghanistan it occurs north of the Hindu Kush.

Cyrtodactylus fedtschenkoi (Strauch).

Gymnodactylus fedtschenkoi STRAUCH, 1887, Mém. Acad. Imp. Sci. St. Pétersbourg, ser. 7, vol. 35, pp. 46–47 (syntypes from USSR: Samarkand; Bokhara; Gissar; syntypes: Zoological Institute Leningrad nos. 3387[2], 5039[2], 6354, 5355[4], 6479, 7401[2]).

Cyrtodactylus fedtschenkoi, UNDERWOOD, 1954, Proc. Zool. Soc. London, vol. 124, p. 475.

DISTRIBUTION. Western Turkmen, Uzbekistan, Tajikistan, Afghanistan, eastern Iran, and western Baluchistan. In the USSR the westernmost localities are the valley of the Tedzhen River, surroundings of Mara, coast of the Aral Sea; the northeastern border of the range does not reach beyond the valley of the Syr Darya River. In Afghanistan it is known from north of the Hindu Kush and has been found at Paghman. It has been suggested that *Gymnodactylus longipes* Nikolsky of eastern Iran is a synonym (Clark, Clark, Anderson, and Leviton, 1969, p. 301).

Cyrtodactylus russowii (Strauch).

Gymnodactylus russowii STRAUCH, 1887, Mém. Acad. Imp. Sci. St. Pétersbourg, ser. 7, vol. 35, pp. 49–51, figs. 10–12 (syntypes from USSR: Novo-Alexandrovsk; Chodschent; Mangyschlak; Murza Robat; Mohol-tau; Tschimkent; Tschinaz; Golodnaja desert; Utsch-Kurgan at Naryn; Clark-Ukjur; syntypes: Zoological Institute Leningrad nos. 3658[2], 3659, 3660, 3700[3], 3701[2], 4192, 4193[6], 4194, 4195[5], 4310[2], 5037, 5197, 5218, 5224, 5800[2], California Academy of Sciences nos. 94050–94052).

Cyrtodactylus russowii, UNDERWOOD, 1954, Proc. Zool. Soc. London, vol. 124, p. 475.

DISTRIBUTION. Eastern Caucasus foreland (Starogladkowskaja) and from the east coast of the Caspian Sea to central Asia, including northern Iran and northern Afghanistan, according to Wermuth (1965, p. 66). We know of no documented records for either Iran or Afghanistan.

Cyrtodactylus scaber (Heyden).

Stenodactylus scaber HEYDEN, 1827, *in* RÜPPELL, Atlas Reise nördl. Afrika, Rept., p. 15, pl. 4, fig. 2 (type locality: Tor, Sinai Peninsula [see Anderson, J., 1898, Zool. Egypt, p. 55, for comment on probable source of Heyden's specimens]; lectotype: Senckenberg Museum Frankfurt no. 8180 ♂).

Cyrtodactylus scaber, UNDERWOOD, 1954, Proc. Zool. Soc. London, vol. 124, p. 475.

DISTRIBUTION. From Egypt south to Ethiopia, and east across Arabia and the arid regions of Southwest Asia to Afghanistan, West Pakistan, and northwestern India. In Afghanistan it is known from the low elevations of the south and southeast, up to about 5000 feet elevation. Our previous (Clark, Clark, Anderson, and Leviton, 1969, p. 302) identification of a small juvenile gecko from northwestern Afghanistan is in error. This specimen has been reidentified as *C. caspius*.

Cyrtodactylus watsoni (Murray).

Gymnodactylus watsoni MURRAY, 1892, Zool. Beloochistan and S. Afghanistan, pp. 68–69 (type locality: Quetta, West Pakistan).

Cyrtodactylus watsoni, MINTON, 1966, Bull. American Mus. Nat. Hist., vol. 134, p. 79.

Distribution. Northern Las Bela to Quetta, and northeastward to Swat and the northern Punjab in West Pakistan; westward up to the Kabul River Valley at least as far as Jalalabad in Afghanistan.

Cyrtodactylus species.

Cyrtodactylus fedtschenkoi, Clark, Clark, Anderson, and Leviton, 1969, Proc. California Acad. Sci., ser. 4, vol. 36, pp. 300–302 [but not including fig. 2]. Anderson and Leviton, 1969, Proc. California Acad. Sci., ser. 4, vol. 37, p. 45.

Distribution. A *Cyrtodactylus* closely allied to *C. fedtschenkoi* occurs in the Helmand Basin from Farah in the west to near Kandahar in the east. This appears to be an undescribed species, and questions regarding the systematics of these and related geckos are under study.

Genus **Eublepharis** Gray

Eublepharis Gray, 1827, Phil. Mag., ser. 2, vol. 2, p. 56 (type species: *Eublepharis hardwickii* Gray, 1827, by monotypy).

Eublepharis macularius (Blyth).

Cyrtodactylus macularius Blyth, 1854, Jour. Asiatic Soc. Bengal, vol. 23, pp. 737–738 (type locality: Salt Range, Punjab; holotype in Indian Museum, Calcutta).

Eublepharis macularius, John Anderson, 1871, Proc. Zool. Soc. London, p. 163.

Distribution. Southern Transcaspia, eastern Afghanistan south of the Hindu Kush, West Pakistan in Baluchistan, the Northwest Frontier Provinces, and south to Rajputana and the Khandesh District of India; to at least 5300 feet elevation in Afghanistan, 8000 feet in Baluchistan. As yet, specimens are unknown from the large area between southern Turkmen and eastern Afghanistan.

Genus **Hemidactylus** Oken

Hemidactylus Oken, 1817, Isis von Oken, col. 1183 (based on Cuvier's Hemidactyle, 1817, Règne Anim., vol. 2, p. 47; type species: *Gecko tuberculosus* Daudin).

Hemidactylus flaviviridis Rüppell.

Hemidactylus flaviviridis Rüppell, 1835, Neue Wirbelth. Faun. Abyss., Amph., p. 18, pl. 6, fig. 2 (type locality: Nassaua Island, Eritrea; lectotype: Senckenberg Museum Frankfurt no. 8772 ♂).

Distribution. Northern India west of Bengal and south to Bombay, through southern (coastal) Iran and Arabia to the African shores of the Red Sea. In Afghanistan it is known only from Paghman and Jalalabad. Much of its distribution, from the shores of the Red Sea and around the shores of the Arabian Peninsula and Iran, is due to its having been carried about by man, and its presence in Afghanistan may also be due to human agency.

Genus **Teratoscincus** Strauch

Teratoscincus Strauch, 1863, Bull. Acad. Imp. Sci. St. Pétersbourg, vol. 6, col. 480 (type species: *Teratoscincus keyserlingi* Strauch, 1863, by monotypy).

Teratoscincus bedriagai Nikolsky.

Teratoscincus bedriagai Nikolsky, 1899, Ann. Mus. Zool. Acad. Imp. Sci., St. Pétersbourg, vol. 4, pp. 146–147 (types from Seistan and Zirkuch, eastern Iran; syntypes: Zoological Institute Leningrad nos. 9157, 9158[2], 9159[3], 9160, 9161, 9162, 9163).

Distribution. Eastern Iran and the Helmand River basin of Afghanistan; to at least 4700 feet elevation.

Teratoscincus microlepis Nikolsky.

Ceramodactylus affinis, Alcock and Finn, 1896 (*nec* Murray, 1884), Jour. Asiatic Soc. Bengal, vol. 65, p. 554.

Teratoscincus microlepis Nikolsky, 1899, Ann. Mus. Zool. Acad. Imp. Sci., St. Pétersbourg, vol. 4, pp. 145–146 (type locality: Duz-Ab; holotype: Zoological Institute Leningrad no. 9164).

Distribution. Extreme eastern Iran and adjacent Baluchistan and Afghanistan along the Afghan-Baluchistan border.

Teratoscincus scincus (Schlegel).

Stenodactylus scincus Schlegel, 1858, Handl. Dierk., vol. 2, p. 16 (type locality: Ili River, Turkestan, USSR; holotype in Leiden Museum).

Teratoscincus scincus, Boulenger, 1885, Cat. liz. British Mus., vol. 1, pp. 12–13, pl. 2, fig. 3.

Distribution. Central Asia, in the north up to the Chink (Precipice) Ust Urt, Aral Kara Kum, and valleys of the rivers Chu and Ili, east to the foothills of the Tien Shan and Pamiro-Alai; one record for Sachow in the southern Gobi; the vicinity of Kokand in the Syr Darya Valley and Vakhsh Valley inclusive in the valleys of the river Pyandzh; northeastern and eastern Iran (Terentjev and Chernov, 1949, p. 128). To the west it reaches the eastern shore of the Caspian Sea. Its western limit in Iran is the steppe between Argavani and Marinjab, Tehran Province. In Baluchistan it is not known east of Nushki, nor south of Kharan (Minton, 1966, p. 76). It is known in Afghanistan from the low deserts along the western and southern borders; to 6000 feet elevation in Iran, at least 4700 feet in Afghanistan.

Family LACERTIDAE

Genus **Acanthodactylus** Fitzinger

Acanthodactylus Fitzinger, 1834, *in* Wiegmann, Herpet. Mexicana, p. 10 (type species: *Lacerta boskiana* Lichtenstein, 1823, by monotypy).

Acanthodactylus cantoris Günther.

Acanthodactylus cantoris Günther, 1864, Rept. British India, p. 73 (type locality: Ramnagar, Agra, India; holotype in British Museum).

Distribution. The species as a whole ranges from northwestern India through West Pakistan, southern Afghanistan, and lowland southern Iran and Arabia. In Afghanistan it occurs in the valley of the Kabul River and in the Helmand River basin. The status of these populations is under study.

Genus **Eremias** Fitzinger

Eremias Fitzinger, 1834, *in* Wiegmann, Herpet. Mexicana, p. 9 (type species: *Lacerta variabilis* Pallas, 1811, by subsequent designation by Fitzinger, 1843, Syst. Rept., p. 21).

Eremias acutirostris (Boulenger).

Scapteira acutirostris Boulenger, 1887, Cat. liz. British Mus., vol. 3, pp. 114–115 (type locality: between Nushki and Helmand, Afghan-Baluch border region; holotype in British Museum).

Eremias (Scapteira) acutirostris, Lantz, 1928, Bull. Mus. Georgie, vols. 4 and 5, pp. 41, 136.

Distribution. Desert basins of northwestern Baluchistan and adjoining Afghanistan.

Eremias aporosceles (Alcock and Finn).

Scapteira aporosceles Alcock and Finn, 1896, Jour. Asiatic Soc. Bengal, vol. 65, p. 559, pl. 13 (type locality: Afghan-Baluch border: "common west of Robat I" [restricted by Smith, 1935, Fauna British India, vol. 2, p. 388, to Baluchistan: near Nushki; Robat I lies some 120 miles to the west of Nushki, however]; syntypes in British Museum, and Indian Museum, Calcutta).

Eremias (Scapteira) aporosceles, Lantz, 1928, Bull. Mus. Georgie, vols. 4 and 5, pp. 41, 127-130, 136.

Distribution. Baluchistan, West Pakistan, and Afghanistan, along the Afghan-Baluch border.

Eremias aria Anderson and Leviton.

Eremias aria Anderson and Leviton, 1967, Occ. Pap. California Acad. Sci., no. 64, pp. 1–4, fig. 1 (type locality: 5–10 mi. ENE. Nimla on old Kabul-Jalalabad road, 10 mi. SW. Balabagh [34°19–21′ N, 70°10–15′ E]; holotype: California Academy of Sciences no. 96204 ♂).

Distribution. Known only from the vale of Jalalabad in eastern Afghanistan.

Eremias fasciata Blanford.

Eremias fasciata Blanford, 1874, Ann. Mag. Nat. Hist., ser. 4, vol. 14, p. 32 (type locality: Saidabad, southwest of Kerman, Iran; syntypes in British Museum).

Distribution. Eastern Iran, southern Afghanistan in the Helmand River basin, and Baluchistan, West Pakistan.

Eremias grammica (Lichtenstein).

Lacerta grammica Lichtenstein, 1823, *in* Eversmann, Reise nach Buchara, p. 140 (type locality: Karakum and Kizyl-Kum, USSR).

Eremias (Scapteira) grammica, Lantz, 1928, Bull. Mus. Georgie, vols. 4 and 5, pp. 41, 117–122, 136.

Distribution. Central Asian republics of the USSR, southern Kazakhstan, north to lower reaches of Irghiz and Turgai rivers and Lepsa River, east to Ala Tau mountains, northeastern and eastern Iran, and adjacent lowland regions of Afghanistan, north of the Hindu Kush.

Eremias guttulata watsonana Stoliczka.

Eremias (*Mesalina*) *watsonana* Stoliczka, 1872, Proc. Asiatic Soc. Bengal, pp. 86–87 (type locality: between Karachi and Sakhar, Sind, West Pakistan; syntypes: British Museum, and Indian Museum, Calcutta).

Eremias guttulata watsonana, Smith, 1935, Fauna British India, vol. 2, pp. 389–390.

Distribution. *Eremias guttulata* ranges from North Africa through Arabia and the desert regions of Southwest Asia, north to Turkman and east to Sind in West Pakistan. *E. g. watsonana* occurs throughout Iran and Afghanistan at elevations below 8000 feet. According to Minton (1966, p. 110), it is found throughout the arid parts of West Pakistan but often rather spottily, common in Las Bela and along the edge of the Thar Desert, but rare in the intervening area.

Eremias intermedia (Strauch).

Podarces (*Eremias*) *intermedia* Strauch, 1876, Voy. Przewalski, Rept., p. 28 (type locality: Kizil Kum, Aralo-Caspian desert, USSR).

Eremias intermedia, Boulenger, 1887, Cat. liz. British Mus., vol. 3, pp. 100–101.

Distribution. Soviet Central Asia and southern regions of Kazakhstan; north to Mangyshlak, sands of the Bol'shie Barsuki, Aral Kara Kums, valley of Chu River and Balkhash Lake; east to Tien Shan and Pamiro-Alai; reaching the sands of the Vakhsh lowlands along the valley of the Amu Darya River. It has been taken in the valley of the Tajan River at the point where the borders of Iran, Afghanistan, and Turkmen meet, and undoubtedly occurs within the borders of Iran and Afghanistan, although no records exist to the south of this point.

Eremias lineolata (Nikolsky).

Scapteira lineolata Nikolsky, 1896, Ann. Mus. Zool. Acad. Imp. Sci., St. Pétersbourg, vol. 1, p. 371 (type locality: between Faizabad and Nusi, eastern Iran; syntypes: Zoological Institute Leningrad no. 8801[6]; British Museum).

Eremias lineolata, Lantz, 1928, Bull. Mus. Georgie, vols. 4 and 5, pp. 39, 79–84, 134.

Distribution. Turkmen, Uzbekistan, southern Kazakhstan, southwestern Tajikistan, USSR. It occurs in eastern Iran and northern lowland Afghanistan. In the north it ranges up to the Chink (Precipice) Ust Urt, Aral Sea, middle and lower course of the Chu River and lower coast of Balkhash Lake, east to the Tien Shan and Pamiro-Alai mountain system. To the east it reaches the lower extent of the Vakhsh River inclusive along the Amu Darya Valley.

Eremias nigrocellata Nikolsky.

Eremias nigrocellata Nikolsky, 1896, Ann. Mus. Zool. Acad. Imp. Sci. St. Pétersbourg, vol. 1, p. 371 (types from between Feizabad and Mondechi, and Seistan, eastern Iran; syntypes: Zoological Institute Leningrad nos. 8798[3], 8779[2], 8800).

Distribution. Southwestern Tajikistan, southern Uzbekistan (vicinity of Shirabad) in the USSR; eastern Iran; northern lowland Afghanistan. It occurs between 4000 and 5000 feet elevation in Iran; known Afghan localities are below 2000 feet.

Eremias regeli Bedriaga.

Eremias regeli Bedriaga, 1907, Ann. Zool. Mus. Acad. Imp. Sci. St. Pétersbourg, vol. 10 (1905), p. 236 (type locality: Shirabad, Uzbekistan, USSR; syntype: Zoological Institute Leningrad no. 6115).

Distribution. Found in the USSR in the valleys of the upper reaches of the Amu Darya River and lower course of the Pyandzh River and their tributaries, and adjacent foothills. In the west it is known up to the vicinity of Kelif, east of Kulyab, north to the Gissar Ridge (Terentjev and Chernov, 1949, p. 199). The only Afghan record is in the valley of the Kabul River, to the south of the Hindu Kush, an unexpected occurrence suggesting serious unsolved systematic and zoogeographic problems.

Eremias scripta (Strauch).

Podarces (Scapteira) scripta Strauch, 1867, Mel. Biol. Acad. St. Pétersbourg, vol. 6, p. 424 (type locality: Aralo-Caspian desert, USSR; no specimens listed, nor type designated).

Eremias (Rhabderemias) scripta, Lantz, 1928, Bull. Mus. Georgie, vols. 4 and 5, pp. 38, 73–79, 133.

Distribution. Soviet Central Asia and southern Kazakhstan; in the north to Mangyshlak, southern Ust Urt Precipice, sands of Bol'shie Barsuki, valley of Chu River, coast lines of Lake Balkhash, and valley of the Lepsa River, east to the Tien Shan and Pamiro-Alai mountain ranges; along the Amu Darya Valley it reaches the lowlands of the Vakhsh River. Terentjev and Chernov (1949, p. 204) state that it is found in eastern Iran and adjacent regions of Afghanistan and Baluchistan. We find no records for Iran; in Afghanistan it occurs in the southern desert region, and in Baluchistan it is known from the Chagai District. If this southern population is, indeed, the same species as that inhabiting the USSR, it is to be expected along the Afghan-Iranian border.

Eremias velox persica Blanford.

Eremias persica Blanford, 1874, Ann. Mag. Nat. Hist., ser. 4, vol. 14, p. 31 (type locality: near Isfahan, Iran; syntypes in British Museum).

Eremias velox var. *persica*, Boulenger, 1921, Monogr. Lacert., vol. 2, pp. 312–314.

Distribution. The Central Plateau of Iran, southern Turkmen (vicinity of Kushka and Kopet Dagh), southern Afghanistan, and Baluchistan and Waziristan, West Pakistan. To at least 8000 feet in Afghanistan.

Eremias velox velox (Pallas).

Lacerta velox Pallas, 1771, Reise Russ. Reich, vol. 1, p. 457 (type locality: Inderskija Gory, region of lower Ural River, USSR).

Eremias velox, Wiegmann, 1834, Herpet. Mexicana, p. 9.

Eremias velox velox, Lantz, 1918, Proc. Zool. Soc. London, p. 14.

Distribution. From the Volga to western Mongolia and into Sinkiang. In the southeast it is limited by the Tien Shan Mountains, and in the southwest by the Elburz Mountains and the south coastal region of the Caspian Sea. The Kopet Dagh forms its southern limit, except where it may penetrate the northeastern border of Iran, extending also into northwestern Afghanistan, perhaps south along the Iran-Afghan border to the Seistan Basin. The only published records for Afghanistan are the River Tajan just at the Afghan-Iran-Transcaspian border, and New Gulran in northwestern Afghanistan.

Genus **Ophisops** Ménétries

Ophisops MÉNÉTRIES, 1832, Cat. rais. Obj. Zool. Caucas., p. 63 (type species: *Ophisops elegans* Ménétries, 1832, by monotypy).

Ophisops jerdoni Blyth.

Ophisops jerdoni BLYTH, 1853, Jour. Asiat. Soc. Bengal, vol. 22, p. 653 (type locality: Mhow, Indore, Central India; holotype lost [*fide* SMITH, 1935, Fauna British India, vol. 2, p. 377]).

DISTRIBUTION. From the Kabul River Valley of eastern Afghanistan through the Northwest Frontier Provinces and northern Punjab of West Pakistan south to Rewa State and Bellary in western India.

Family SCINCIDAE

Genus **Ablepharus** Fitzinger

Ablepharus FITZINGER, 1823, *in* LICHTENSTEIN, Ver. Doub. Zool. Mus. Berlin, p. 103 (type species: *Ablepharus pannonicus* Lichtenstein, 1823, by monotypy).

Ablepharus bivittatus lindbergi Wettstein.

Ablepharus bivattatus lindbergi WETTSTEIN, 1960, Zool. Anz., vol. 165, pp. 61–62 (type locality: steppe a few km. west of Obeh, east of Herat, northwestern Afghanistan; holotype: Vienna Museum no. 15877).

DISTRIBUTION. *Ablepharus bivittatus* ranges from the Caucasus and Talysh mountains in southeastern Transcaucasia, USSR, northern Iran (to 11,000 feet elevation) and the Zagros Mountains of western Iran, through southern Turkmen in the Kopet Dagh, to Afghanistan and the Punjab. *Ablepharus b. lindbergi* is known from upland Afghanistan (to at least 9600 feet elevation), and a single record from the Punjab.

*__Ablepharus grayanus__ (Stoliczka).

Blepharosteres grayanus STOLICZKA, 1872, Proc. Asiat. Soc. Bengal, pp. 74–75 (type locality: Waggur District, northeastern Kachh, West Pakistan; holotype in Indian Museum, Calcutta).

Ablepharus grayanus, BOULENGER, 1887, Cat. liz. British Mus., vol. 3, p. 352.

DISTRIBUTION. In West Pakistan it is known from Kutch, Sind, mostly west of the Indus, eastern Baluchistan, and the Punjab and Northwest Frontier Provinces at low elevations (Minton, 1966, p. 104). It is recorded from the eastern and southeastern margins of the Central Plateau in Iran, and in the USSR from a single locality, Nimichi-Bol', in southern Tajikistan. There appear to be no documented records for Afghanistan, although Terentjev and Chernov (1949, p. 171) state that it occurs there.

Ablepharus pannonicus Lichtenstein.

Ablepharus pannonicus Lichtenstein, 1823, *in* Eversmann, Reise nach Buchara, p. 145 (type locality: Buchara, USSR).

Distribution. Iraq; northern and western Iran; in the USSR it is found in the Kopet Dagh, mountains of the Pamiro-Alai systems and their foothill lowlands, north to the vicinity of Leninabad, east to Darvaz, inclusive; probably throughout most of Afghanistan to at least 7600 feet elevation; in West Pakistan it occurs in the mountainous northern sections from Quetta to Chitral; northern Punjab.

Genus **Eumeces** Wiegmann

Eumeces Wiegmann, 1834, Herpet. Mexicana, p. 36 (type species: *Scincus pavimentatus* Geoffroy-St. Hillaire, 1827, by subsequent designation by Taylor, 1935, Univ. Kansas Sci. Bull., vol. 23, p. 29).

*__Eumeces blythianus__ (Anderson).

Mabouia blythiana John Anderson, 1871, Proc. Asiat. Soc. Bengal, p. 186 (type locality: Amritzar, Punjab).
Eumeces blythianus, Boulenger, 1887, Cat. liz. British Mus., vol. 3, p. 385.

Distribution. Not yet recorded from within the political boundaries of Afghanistan, but known from the Afridi country along the Afghan border near the Khyber Pass. Minton (1966, p. 102) found it south to the coastal plain at Karachi. The type, said to come from Amritsar in the Punjab, was purchased from a merchant.

Eumeces schneideri (Daudin).

Scincus schneideri Daudin, 1802, Hist. nat. Rept., vol. 4, p. 291 (no type locality given).
Eumeces schneideri, Boulenger, 1887, Cat. liz. British Mus., vol. 3, pp. 383–384.

Distribution. *Eumeces schneideri* (*sensu lata*), is found across North Africa north of the Sahara; Southwest Asia, from the Mediterranean to West Pakistan, and from the Transcaucasian and Transcaspian provinces of the USSR to northern Saudi Arabia and the Persian Gulf. In Afghanistan it is known from the Helmand Basin and from northern Afghanistan in the low country north of the Hindu Kush.

We have examined none of the specimens from Afghanistan. Terentjev and Chernov (1949, p. 169) state that *Eumeces s. princeps*, the subspecies which occurs in the USSR, is also found in Afghanistan. *Eumeces s. zarudnyi* is the form from eastern Iran. Both may occur in Afghanistan. Some recent workers regard *E. blythianus* as a subspecies of *E. schneideri*, and a record from the Helmand may refer to this form. We have not seen enough material to express an opinion regarding the relationships of the several nominal forms.

Eumeces taeniolatus (Blyth).

Eurylepis taeniolatus BLYTH, 1854, Jour. Asiat. Soc. Bengal, vol. 23, pp. 739–740 (type locality: Salt Range, Punjab; holotype in Indian Museum, Calcutta).
Eumeces taeniolatus, STOLICZKA, 1872, Proc. Asiat. Soc. Bengal, pp. 75–76.

DISTRIBUTION. Southern Turkmen, USSR; eastern Iran; Afghanistan; West Pakistan; Kashmir; Arabia (two records exist for the Arabian peninsula, that of Taylor (1935), pp. 111–119) citing a specimen in the British Museum from El Kubar, southwestern Arabia, and Haas (1957, pp. 74–75, fig. 9) for a specimen from 23 miles north of Hail, Saudi Arabia, and citing a British Museum specimen from Muscat). While Terentjev and Chernov (1949, p. 170) state that it is found in northern and northeastern Iran, the only record we find is that of the River Tajan on the Afghan-Iran-Turkmen border. In Afghanistan, the only known locality other than the River Tajan is Pandjvai near Kandahar.

Genus **Mabuya** Fitzinger

Mabuya FITZINGER, 1826, Neue Class. Rept., pp. 23 and 52 (type species: *Lacerta mabouya* Lacépède, 1788, by tautonomy).

***Mabuya aurata** (Linnaeus).

Lacerta aurata LINNAEUS, 1758 (in part), Syst. Nat., ed. 10, p. 209 (type locality: Cyprus).
Mabuya aurata, ANDERSSON, 1900, Kungl. Sv. Vet.-Akad. Handl. Stockholm, vol. 26, pt. 4, p. 14.

DISTRIBUTION. Ethiopia; Eritrea; Cyprus; Syria; Turkey; Iraq; northern and western Iran; Muscat; Armenian SSR, Nakhichevan ASSR, southern Turkmen and Uzbekistan, north to Dzhizak and Chinaz. A record for Sind is in considerable doubt (Minton, 1966, p. 99), and it has not been recorded from the eastern part of the Plateau of Iran. The only possible Afghan record is for the River Tajan at the Iran-Afghanistan-Turkmen borders.

Mabuya dissimilis (Hallowell).

Euprepes dissimilis HALLOWELL, 1860, Trans. American Phil. Soc., vol. 11, p. 78 (type locality: Bengal).
Mabuya dissimilis, BOULENGER, 1887, Cat. liz. British Mus., vol. 3, p. 175.

DISTRIBUTION. From West Bengal and Bihar across the plains of northern and central India. In West Pakistan it ranges from the delta of the Indus north to Rawalpindi and Campbellpore, but not westward onto the Plateau of Iran (Minton, 1966, p. 101). In Afghanistan it is known only from the valley of the Kabul River, to 3500 feet elevation.

Genus **Ophiomorus** Duméril and Bibron

Ophiomorus Duméril and Bibron, 1839, Erp. Gen., vol. 5, p. 799 (type species: *Ophiomorus miliaris* Duméril and Bibron, 1839, by monotypy).

Leviton's (1959, p. 461) inclusion of *O. brevipes* in the list of species known from Afghanistan was based on the speculation by Terentjev and Chernov (1949, p. 175) that it occurs in Afghanistan.

Ophiomorus tridactylus (Blyth).

Sphenocephalus tridactylus Blyth, 1855, Jour. Asiatic Soc. Bengal, vol. 22, p. 654 (type locality: Afghanistan; holotype in Indian Museum, Calcutta).

Ophiomorus tridactylus, Boulenger, 1887 (in part), Cat. liz. British Mus., vol. 3, pp. 394–395.

Distribution. The sandy areas of the Helmand Basin and adjacent regions of eastern Iran, southern Afghanistan, and northern Baluchistan, West Pakistan.

Genus **Scincella** Mittleman

Scincella Mittleman, 1950, Herpetologica, vol. 6, p. 19 (type species: *Scincus lateralis* Say, 1823, by original designation).

Scincella himalayana (Günther).

Eumeces himalayanus Günther, 1864, Rept. British India, p. 86 (type locality: Western Himalayas; holotype in British Museum).

Scincella himalayana, Mittleman, 1950, Herpetologica, vol. 6, p. 19.

Distribution. Mountainous regions from Nepal west to southern Turkmen; known from Chitral and the Hazara District of West Pakistan; Kashmir; Nuristan in eastern Afghanistan (based on two specimens in the Universitetets Zoologiske Museum from Pashki, identified as this species, but not seen by us).

Family VARANIDAE

Genus **Varanus** Merrem

Varanus Merrem, 1820, Tent. Syst. Amph., p. 58 (type species: *Lacerta varia* Shaw, 1790, by subsequent designation of Gray, 1827, Phil. Mag., ser. 2, vol. 3, p. 55).

Varanus bengalensis bengalensis (Daudin).

Tupinambis bengalensis Daudin, 1802, Hist. nat. Rept., vol. 3, p. 67 (type locality: Bengal; holotype: Paris Museum no. 2179).

Varanus bengalensis, Duméril and Bibron, 1836, Erp. Gen., vol. 3, p. 480.

Varanus (*Indovaranus*) *bengalensis bengalensis*, Mertens, 1942, Abh. Senckenberg. Naturf. Ges., no. 466, p. 334.

Distribution. From southeastern Iran through West Pakistan and India to Assam and Burma, south to Tharawaddy and the Henzada District, north to Nepal, Bigrani (western Himalayas) and Darjeeling (eastern Himalayas). In

Afghanistan it is known only from the valley of the Kabul River, to elevations of 8600 feet to the north of Jalalabad.

Varanus griseus caspius (Eichwald).

Psammosaurus caspius EICHWALD, 1831, Zool. Spec., vol. 3, p. 190 (type locality: Dardsha Peninsula, east coast of Caspian Sea, USSR).

Varanus (*Psammosaurus*) *griseus caspius*, MERTENS, 1954, Senckenberg. Biol., vol. 35, p. 355.

DISTRIBUTION. The species ranges from North Africa through Southwest Asia to northern India. It reaches Rio de Oro in the west and Ambala, Agra, and Narsingarh in the east; northward it extends to the Transcaspian provinces of the USSR. *Varanus g. caspius* ranges from the eastern coast of the Caspian Sea through Central Asian republics of the USSR and southern Kazakhstan, where it is known up to the southern Ust Urt Precipice, coasts and islands of the Aral Sea, east to the Syr Darya Valley and mountains of the Tien Shan and Pamiro-Alai systems. It reaches east to Chubek along the valleys of the Amu Darya and Pyandzh rivers and is found throughout the Plateau of Iran, west to the Zagros Mountains, and southeast to northern Baluchistan. The area west of the Plateau of Iran is occupied by *V. g. griseus*, while *V. g. koniecznyi* is the form to the east. In Afghanistan the known localities are in the Helmand Basin in the southern part of the country, and the valley of the Hari-Rud in the north. It undoubtedly occurs in the lower elevations throughout Afghanistan.

Suborder SERPENTES

Family BOIDAE

Genus **Eryx** Daudin

Eryx DAUDIN, 1803, Hist. nat. Rept., vol. 7, p. 251 (type species: *Boa turcica* Olivier, 1801, by subsequent designation by FITZINGER, 1843, Syst. Rept., p. 24).

Eryx elegans (Gray).

Cursoria elegans GRAY, 1849, Cat. sn. British Mus., p. 107 (type locality: Afghanistan; holotype in British Museum).

Eryx elegans, BLANFORD, 1876, Zool. E. Persia, vol. 2, p. 402.

DISTRIBUTION. Known from Paghman in Afghanistan. According to Terentjev and Chernov (1949, pp. 229-230), *Eryx jaculus czarewskii* Nikolsky, 1916, is a synonym (see also Anderson and Leviton, 1969, p. 51). Stull (1935, p. 407) regarded *E. j. czarewskii* as a synonym of *E. miliaris* (Pallas).

This species is known from the Kopet Dagh in southern Turkmen, USSR, and adjacent northern Iran.

Eryx johnii (Russell).

Boa johnii RUSSELL, 1801, Indian Serp., vol. 2, pp. 18 and 20, pls. 16–17, fig. 1 [pl. 17] (type locality: Tranquebar, India).

Eryx johnii, DUMÉRIL and BIBRON, 1844, Erp. Gen., vol. 6, p. 458.

Distribution. Known definitely from the coastal plain of West Pakistan from the Hab River Valley eastward into the Thar Desert and northward in the Indus Valley to central Sind at elevations below 500 feet (Minton, 1966, p. 119). According to Smith (1943, p. 114), it occurs also in Rajputana, Punjab, United Provinces, Baluchistan, and the Northwest Frontier Provinces (West Pakistan). It must be pointed out that the type of *Eryx persicus* Nikolsky, 1907, regarded by Stull (1935, p. 407) and Smith (*loc. cit.*) as a subspecies of *E. johnii*, is from Aguljaschker, Arabistan [=Khuzestan], Iran. There are no further records of the occurrence of either nominal form in the intervening areas of Iran. The single record of *E. johnii* for Afghanistan is that of Murray (1892, p. 71) for Mundi, Hissar, south of Kandahar.

Eryx tataricus (Lichtenstein).

Boa tatarica Lichtenstein, 1823, *in* Eversmann, Reise nach Buchara, p. 146 (type locality: Aral Sea, USSR).

Eryx tataricus, Terentjev and Chernov, 1949, Diag. Rept. Amph., p. 230.

Distribution. Kazakhstan, Uzbekistan, Turkmen, Tajikistan, western China, Mongolia, Iran, and Afghanistan; from the Aral Sea east to the Altai Mountains, and south to northwestern Baluchistan. It is known from northern Afghanistan, Paghman, and the southern desert region of Afghanistan. Boulenger's records (1889, p. 101) of *E. jaculus* from northwestern Afghanistan probably should be referred to *E. tataricus*.

Family Colubridae

Genus **Boiga** Fitzinger

Boiga Fitzinger, 1826, Neue Class. Rept., pp. 29, 31, 60 (type species: *Coluber irregularis* Merrem, 1820, by original designation).

Boiga trigonata melanocephalus Annandale.

Boiga trigonata var. *melanocephalus* Annandale, 1904, Jour. Asiat. Soc. Bengal, vol. 73, p. 209, pl. 9, figs. 3–4 (type locality: Preso-Baluchistan frontier; 3 syntypes in Indian Museum, Calcutta).

Distribution. From western Baluchistan through eastern Iran, southern and western lowland Afghanistan to Uzbekistan and Tajikistan; north in the USSR to the Repetek Station, east to the vicinity of Kurgan-Tyube (Tajikistan).

Genus **Coluber** Linnaeus

Coluber Linnaeus, 1758 (in part), Syst. Nat., ed. 10, vol. 1, p. 216 (type species: *Coluber constrictor* Linnaeus, 1758, by subsequent designation by Fitzinger, 1843, Syst. Rept., p. 26).

Coluber karelinii Brandt.

Coluber karelinii Brandt, 1838, Bull. Acad. Imp. Sci. St. Pétersbourg, vol. 3, p. 243 (type locality: borders of Caspian Sea; syntypes: Zoological Institute Leningrad nos. 1695–1700).

Distribution. Eastern Iran, Baluchistan in the Quetta-Pishin area, southern lowland Afghanistan, north along the western margin to Turkmen, Uzbekistan, Kirghizia, Tajikistan (east to the Vakhsh Valley and Leninabad), southwestern Kazakhstan. Kaidak Gulf and southern coast of Aral Sea are northernmost known localities (Terentjev and Chernov, 1949, p. 243).

Coluber ravergieri Ménétries.

Coluber ravergieri Ménétries, 1832, Cat. rais. Obj. Zool., p. 69 [not seen] (type locality: Baku, Georgia, USSR; holotype in Leningrad).

Distribution. Extreme northeastern Africa, through the eastern Mediterranean, including Israel, Lebanon, Syria, Turkey, to Jordan, Iraq, Iran, Georgia, Armenia, Azerbaidzhan, Dagestan, USSR, east through Turkmen and Afghanistan to the mountainous areas of the northern part of Kalat District to Chitral, West Pakistan. In Soviet Central Asia it reaches as far north as the Emba River and the lower reaches of the Syr Darya River; in the northeast it reaches western Mongolia. Afghan localities are in the north and east of the country at elevations of 2000–8000 feet.

Coluber rhodorachis (Jan).

Zamenis rhodorachis Jan, 1863, vol. 1, p. 356 (type locality: Schiraz, Persia).
Coluber rhodorachis, Parker, 1931, Ann. Mag. Nat. Hist., ser. 10, vol. 8, p. 516.

Distribution. Egypt south to Somalia, east through Arabia, Israel, Jordan, Syria, Iraq, Iran, Afghanistan, West Pakistan except Thar Desert and upper Indus basin, north to southern Turkmen, southern Uzbekistan, and western Tajikistan, USSR, no further north than 40° N. According to Terentjev and Chernov (1949, p. 242) the most eastern and northeastern localities are: vicinity of Samarkand and Tashkent, Zeravshan Ridge, surroundings of Stalinabad and Darvaz Ridge. In Afghanistan it is known from lower elevations on both the north and south side of the Hindu Kush.

***Coluber ventromaculatus** Gray and Hardwicke.

Coluber ventromaculatus Gray and Hardwicke, 1834, Illust. Indian Zool., vol. 2, pl. 80, fig. 1 (type locality not stated).

Distribution. From Almora, United Provinces south to the Khandesh District near Bombay, India, west through West Pakistan, Iran, Iraq, northern Arabia, and Jordan to Israel. Boulenger (1890, pp. 325–326) includes Afghanistan in the distribution, although we find no documented records. Terentjev and Chernov (1949, p. 242) say that records for this species in the USSR refer to *C. rhodorachis*. Various authors have considered both *C. karelinii* and *C. rhodorachis* as synonyms of *C. ventromaculatus*, and the separation of these forms is far from clear (Leviton, 1959, pp. 454–456).

Genus **Eirenis** Jan

Eirenis Jan, 1863, Arch. Zool., vol. 2, p. 256 (type species: *Coluber collaris* Ménétries, by subsequent designation by Smith, 1943, Fauna British India, Serp., p. 187).

*Eirenis persica (Anderson).

Cyclophis persicus John Anderson, 1872, Proc. Zool. Soc. London, p. 392 (type locality: Bushire, Iran; holotype in British Museum).
Eirenis persica, Stickel, 1951, Herpetologica, vol. 7, p. 128.

Distribution. The Iranian Plateau, from Jarmo, eastern Iraq, through Iran to the Kopet Dagh in southern Turkmen, east to Swat, Punjab, and western Sind, West Pakistan. As yet there are no Afghan records; it is included here on the basis of its occurrence to the west, south, and east of that country.

Genus **Elaphe** Fitzinger

Elaphe Fitzinger, 1833, *in* Wagler, J., Descr. Icon. Amphib., vol. 3, text to pl. 27 (type species *E. parreysii* Fitzinger).

Elaphe dione (Pallas).

Coluber dione Pallas, 1773, Reise russ. Reichs, vol. 2, p. 717 (type locality: "Salt steppes toward the Caspian Sea").
Elaphe dione, Duméril, Bibron, and Duméril, 1854, Erp. Gen., vol. 7, p. 248.

Distribution. From the valley of the Volga River, in southeastern Russia through temperate Asia to the Amur country in the north and south through eastern China to Kuikiang (Stejneger, 1907, p. 318). In Afghanistan known from one unpublished record from Bolla-Kuchi village, 6.5 miles southeast of Kunduz, Kunduz Province (USNM 166774–166775).

Genus **Lycodon** Boie

Lycodon H. Boie, 1826, Ferussac's Bull. Sci. Nat., vol. 9, p. 238 (type species: *Coluber aulicus* Linnaeus, 1758, by subsequent designation by Fitzinger, 1826, Neue Class. Rept., p. 30).

*Lycodon striatus bicolor (Nikolsky).

Contia bicolor Nikolsky, 1903, Ann. Mus. Zool. Acad. Imp. Sci. St. Pétersbourg, vol. 8, pp. 96–97 (syntypes from eastern Iran, and Kulkulab, Transcaspia, USSR; syntypes: Zoological Institute Leningrad nos. 10006, 10013).
Lycodon striatus bicolor, Chernov, 1935, Compt. Rendu Acad. Sci. URSS, n. ser., vol. 3, p. 189.

Distribution. Eastern and northeastern Iran, southern Turkmen, Uzbekistan (exclusive of the Kara-Kalpak ASSR), and western Tajikistan; north to the Chirchik River hydroelectric plant (Terentjev and Chernov, 1949, p. 238). Minton (1966, p. 132) referred a specimen from the vicinity of Quetta, Baluchistan to this subspecies. Thus far there are no Afghan records for this species; it has been taken in the Iranian part of the Seistan Basin, however.

Genus **Lytorhynchus** Peters

Lytorhynchus Peters, 1862, Monat. Acad. Berlin, p. 273 (type species: *Heterodon diadema* Duméril, Bibron and Duméril, 1854, by monotypy).

Lytorhynchus maynardi Alcock and Finn.

Lytorhynchus maynardi Alcock and Finn, 1896, Jour. Asiat. Soc. Bengal, vol. 65, p. 562, pl. 14 (type locality: Koh-Malik-do-Khand, Afghan-Baluchistan frontier; syntypes in the Indian Museum, Calcutta, and British Museum).

Distribution. Desert basins of southern Afghanistan and northern Baluchistan, West Pakistan (from Nushki to the Iranian border).

Lytorhynchus ridgewayi Boulenger.

Lytorhynchus ridgewayi Boulenger, 1887, Ann. Mag. Nat. Hist., ser. 5, vol. 20, p. 413 (type locality: Chinkilok, Afghanistan; holotype in British Museum).

Distribution. From southern and central Iran and Turkmen, USSR (east to the Repetek Station) east through northwestern and southern Afghanistan and northern Baluchistan.

Genus **Natrix** Laurenti

Natrix Laurenti, 1768, Syn. Rept., p. 73 (type species: *Natrix torquatus*, by subsequent designation of Fleming, 1822).

Natrix tessellata tessellata (Laurenti).

Coronella tessellata Laurenti, 1768, Syn. Rept., p. 87 (type locality: "in Japidia, volgo Cars").
Natrix tessellata, Bonaparte, 1834, Icon. Faun. Ital., vol. 2, pl.
Natrix tessellata tessellata, Sochurek, 1956, Burgenl. Heimatbl. Eisenstadt, vol. 18, p. 89.

Distribution. From southern and middle Europe, eastward through the Balkans, Southwest Asia, southern USSR (southern Ukraine, Crimea, Transcaucasian republics, Turkmen, Uzbekistan, Tajikistan, Khirgiz, and Kazakhstan; reaching the lower Usa River along the Volga Valley, and north as far as 53–54° N.) to northern and eastern Afghanistan and Chitral, West Pakistan.

Genus **Oligodon** Boie

Oligodon Boie, 1827, Isis von Oken, p. 519 (type species: *Coluber bitorquatus* Reinwardt, by monotypy).

***Oligodon taeniolatus** (Jerdon).

Coronella taeniolata Jerdon, 1853, Jour. Asiat. Soc. Bengal, vol. 22, p. 528 (type locality: Vizagapatam; based on Russell, 1796, Indian Serp., vol. 1, p. 24, pl. 19).
Oligodon taeniolatus, Wall, 1921, Sn. Ceylon, p. 239.

Distribution. From Bihar, India, to southeastern Baluchistan, south through peninsular India to Ceylon. It is found in West Pakistan in the lowlands, from the Indus delta north to Rawalpindi, west to Bela (Minton, 1966,

p. 134). It is known in southern Turkmen from a single specimen from the Kopet Dagh (Terentjev and Chernov, 1949, p. 258). No records exist for Afghanistan, but its known distribution suggests that it occurs there in the low deserts of the south and west.

Genus **Psammophis** Fitzinger

Psammophis Fitzinger, 1826, Neue Class. Rept., pp. 29–30 (type species: *Coluber sibilans* Linnaeus, 1758, by original designation).

*Psammophis leithii Günther.

Psammophis leithii Günther, 1769, Proc. Zool. Soc. London, p. 505, pl. 39 (type locality: Sind; holotype in British Museum).

Distribution. From Fyzabad, in the United Provinces to Poona and west to Waziristan and southeastern Baluchistan. In West Pakistan it is known from Azad Kashmir to the southern Thar and west to Waziristan and southern Kalat District (Minton, 1966, p. 141). No verifiable records exist for Afghanistan; Boulenger's (1889, p. 103) records for Helmand and Hamun to Khusan refer to *Psammophis schokari* (Boulenger, 1896, pp. 157–158).

Psammophis lineolatus (Brandt).

Coluber (*Taphrometopon*) *lineolatus* Brandt, 1838, Bull. Acad. Imp. Sci. St. Pétersbourg, vol. 3, p. 243 (type locality: Transcaspia).

Psammophis lineolatus, Smith, 1943, Fauna British India, vol. 3, p. 367.

Distribution. Turkmen, Uzbekistan, Tajikistan, Khirgiz, Kazakhstan, USSR, to about 49° N., through Mongolia to Kansu and Ala Shan inclusive; south through eastern Iran (west as far as Yezd-i-Khast) and Afghanistan to the Quetta Plateau, Baluchistan, West Pakistan.

Psammophis schokari (Forskål).

Coluber schokari Forskål, 1775, Descr. Anim., p. 14 (type locality: Yemen).

Psammophis schokari, Boulenger, 1896, Cat. sn. British Mus., vol. 3, pp. 157–158.

Distribution. From Morocco across North Africa (south to Somalia) and the entire Arabian peninsula (at least the coastal regions) through Israel, Lebanon, Syria, Jordan, Iraq, Iran, southern Turkmen, southern Afghanistan, and West Pakistan, east to Kashmir, and south to Kutch.

Genus **Ptyas** Fitzinger

Ptyas Fitzinger, 1843, Syst. Rept., p. 26 (type species: *Coluber blumenbachii* Merrem, 1820, by original designation).

Ptyas mucosus (Linnaeus).

Coluber mucosus Linnaeus, 1758, Syst. Nat., vol. 1, p. 226 (type locality: India; type in Stockholm).

Ptyas mucosus, Cope, 1860, Proc. Acad. Philadelphia, p. 563.

Distribution. From the Murgab basin in southern Turkmen, probably locally in eastern Iran, southern Afghanistan (existing records are all in the southeastern portion, including the Kabul River Valley, and between Kabul and Kandahar), West Pakistan, from the lower Indus west to Baluchistan and north to Chitral, throughout India and Ceylon and eastward to southern China and Viet Nam; Formosa; Java, Sumatra, and the Andaman Islands.

Genus **Spalerosophis** Jan

Spalerosophis Jan, 1865, *in* De Filippi, Viag. in Persia, vol. 1, p. 356 (type species: *Spalerosophis microlepis* Jan 1865, by monotypy).

Spalerosophis diadema schirazana (Jan).

Periops parallelus var. *schirazana* Jan, 1865, *in* De Filippi, Viag. in Persia, vol. 1, p. 356 (type locality: Persia).

Spalerosophis diadema schirazianus, Mertens, 1956, Jh. Ver. Naturk. Württemberg, vol. 111, p. 96.

Distribution. From the Zagros Mountains of western Iran east through southern Turkmen, Uzbekistan, and western Tajikistan, USSR (extreme locality records being: Vakhsh River; vicinity of Osh; coastline of Kenderli Gulf; and Kyzyl Kum, north of Khoresm oasis [Terentjev and Chernov, 1949, p. 245]), northern lowland Afghanistan, the southern Afghan desert region, north at least to Paghman, and south to Quetta and western Las Bela in Baluchistan.

Xenochrophis piscator: See Addendum, pg. 206.

Family Elapidae

Genus **Naja** Laurenti

Naja Laurenti, 1768, Synops. Rept., p. 90 (type species: *Naja lutescens* Laurenti, 1768, by subsequent designation by Leviton, 1967, *in* Bücherl, W., Venomous Animals and their Venoms, p. 547).

Naja oxiana (Eichwald).

Tomyris oxiana Eichwald, 1831, Zool. Spec., p. 171 (type locality: Transcaspia, USSR).

Naja oxiana, Strauch, 1869, Bull. Acad. Imp. Sci. St. Pétersbourg, vol. 13, cols. 81–94.

Distribution. Southern Turkmen, Uzbekistan (north to Samarkand and Aristan-Bel-tau mountains), southwestern Tajikistan, USSR; northeastern Iran; Afghanistan (documented records are in the northwest, south, and south of the Hindu Kush); northeastern Baluchistan, Northwest Frontier Provinces, and Kashmir, West Pakistan.

Family Leptotyphlopidae

Genus **Leptotyphlops** Fitzinger

Leptotyphlops Fitzinger, 1843, Syst. Rept., p. 24 (type species: *Typhlops nigricans* Schlegel, 1844, by original designation).

Leptotyphlops blandfordi (Boulenger).

Glauconia blanfordii Boulenger, 1890, Fauna British India, p. 243 (type locality: Sind; holotype in British Museum).

Leptotyphlops blanfordi, Werner, 1936, Festschr. Strand, vol. 2, p. 201.

Distribution. Known from the Indus delta north through southern Punjab to Sibi and the Northwest Frontier Provinces (Minton, 1966, p. 117). In Afghanistan it occurs in the valley of the Kabul River. Specimens recorded from Kuh-i-Malik Siah, at 5000 feet elevation at the point where the Iranian, West Pakistan, and Afghan borders meet (Alcock and Finn, 1896, p. 561) have not been reexamined by subsequent workers.

Family Typhlopidae

Genus **Typhlops** Oppel

Typhlops Oppel, 1811, Ordn. Fam. Gatt. Rept., p. 54 (type species: *Anguis lumbricalis* Linnaeus, 1766 [*fide* Smith, 1943, p. 43]).

Typhlops vermicularis Merrem.

Typhlops vermicularis Merrem, 1820, Tent. Syst. Amph., p. 158 (type locality: Greek islands; restricted by Mertens and Müller, 1928, Abh. Senckenb. Naturf. Ges., vol. 41, p. 45).

Distribution. Southern Yugoslavia, Albania, southern Bulgaria, Greece, Noxos in the Cyclades, Rhodes, Turkey, Syria, lower Egypt, Israel, Transcaucasian republics of the USSR, Dagestan, southern Turkmen, southern Uzbekistan, southern and western Tajikistan, Iran, and Afghanistan (the only known record being for north of Herat, in the northwest).

Family Viperidae

Genus **Agkistrodon** Beauvois

Agkistrodon Beauvois, 1799, Trans. American Philos. Soc., vol. 4, p. 381 (type species: *Agkistrodon mokasen* Beauvois, 1799, by monotypy).

Agkistrodon halys (Pallas).

Coluber halys Pallas, 1776, Reise versch. Prov. Russ. Reich, vol. 3, p. 403 (type locality: eastern Naryn Steppe).

Ancistrodon halys, Boulenger, 1896, Cat. sn. British Mus., vol. 3, pp. 524–525.

Distribution. From Azerbaidzhan, northern Iran, and the Trans-Volga region through central Asia and southern Siberia (to about 55–56° N.), to the Pacific. Our inclusion of this species in the Afghan fauna is based on a specimen in the Universitetets Zoologiske Museum, Copenhagen (not seen by us) labeled "Ancistrodon" from the Sauzak Pass near Herat, northwestern Afghanistan.

Agkistrodon himalayanus (Günther).

Halys himalayanus Günther, 1864, Rept. British India, p. 393, pl. 24, fig. A (type locality: Garwal, western Himalayas; 2 syntypes in British Museum).

Ancistrodon himalayanus, Boulenger, 1890, Fauna British India, p. 424, fig. 125.

Distribution. The western Himalayas, from Sikkim to Chitral, West Pakistan. A specimen labeled "Ancistrodon" (not seen by us) in the Universitetets Zoologiske Museum, Copenhagen, collected at Wama, Nuristan, in eastern Afghanistan, prompt our inclusion of this species in the checklist.

Genus **Echis** Merrem

Echis Merrem, 1820, Tent. Syst. Amph., p. 149 (type species: *Pseudoboa carinata* Schneider, 1801, by subsequent designation by Fitzinger, 1843, Syst. Rept., p. 28).

Echis carinatus (Schneider).

Pseudoboa carinata Schneider, 1801, Hist. Amph., vol. 2, p. 285 (type locality: Arni; based on Russell, 1796, Indian Serp., vol. 1, pl. 2).
Echis carinata, Wagler, 1830, Syst. Amph., p. 177.

Distribution. Northern Africa south to Ghana in the west, Kenya in the east, through Arabia and Southwest Asia north to Turkmen, southern Uzbekistan (north to Samarkand), and northwestern Tajikistan, east to the Vakhsh Valley inclusive in the USSR, south through Afghanistan and all of West Pakistan exclusive of the Himalayan region, east to the Ganges Valley, and south through drier regions of India, to northern Ceylon. In Afghanistan it occurs in the lower elevations both north and south of the Hindu Kush.

Genus **Eristicophis** Alcock and Finn

Eristicophis Alcock and Finn, 1896, Jour. Asiatic Soc. Bengal, vol. 65, p. 564 (type species: *Eristicophis macmahoni* Alcock and Finn, by monotypy).

Eristicophis macmahoni Alcock and Finn.

Eristicophis macmahoni Alcock and Finn, 1896, Jour. Asiatic Soc. Bengal, vol. 65, pp. 564–565, pl. 15, figs. 1, 1a (types from Amirchah; Zeh; Drana Koh; Robat I, Afghan-Baluch border).

Distribution. The desert basin region of northwestern Baluchistan, West Pakistan, from Nushki westward to the border, and south to Kharan; the southern desert of Afghanistan in Registan and the Dasht-i-Margo; Seistan, eastern Iran; below 4000 feet elevation.

Genus **Pseudocerastes** Boulenger

Pseudocerastes Boulenger, 1896, Cat. sn. British Mus., vol. 3, p. 501 (type species: *Cerastes persicus* Duméril, Bibron and Duméril, 1854, by monotypy).

***Pseudocerastes persicus persicus** (Duméril, Bibron, and Duméril).

Cerastes persicus Duméril (AHA), 1853, Mém. Acad. Sci. Inst. France, vol. 23, p. 532 (*nomen nudum*); Duméril, Bibron, and Duméril, 1854, Erp. Gen., vol. 7, p. 1443, pl. 78b, fig. 5 (type locality: Persia).
Pseudocerastes persicus, Boulenger, 1896, Cat. sn. British Mus., vol. 3, p. 501.

Distribution. *Pseudocerastes persicus* ranges from the central Sinai peninsula through the Negev in Israel, Jordan, northern Saudi Arabia, Iraq, Iran, and

West Pakistan as far east as Manguli in southwestern Kalat. There is a fragmentary specimen (*P. bicornis* Wall) from Khajieri Kach above Gwaleri Kolal in the Gomal Pass, Waziristan, West Pakistan. This latter record is close to the Afghan border, but while Afghanistan has been included in the distribution of this species by previous authors, we find no documented records.

Genus **Vipera** Laurenti

Vipera Laurenti, 1768, Synops. Rept., p. 99 (type species: *Vipera redi*, Latreille, by subsequent designation by Fitzinger, 1843, Syst. Rept., p. 28).

Vipera lebetina (Linnaeus).

Coluber lebetinus Linnaeus, 1758, Syst. Nat., ed. 10, vol. 1, p. 216 (type locality: Cyprus; restricted by Mertens and Müller, 1928, Abh. Senckenberg. Naturf. Ges., vol. 41, p. 52).
Vipera lebetina, Daudin, 1803, Hist. nat. Rept., vol. 6, p. 137.

Distribution. North Africa from Morocco to Tripoli; Cyprus and the Cyclades Islands of the eastern Mediterranean, Turkey, Syria, Lebanon, Israel, Jordan, Iraq, Iran, Transcaucasian republics of the USSR, Dagestan, southern part of Central Asian republics, east to Khorog and northeast to the vicinity of Leninabad, USSR; Afghanistan, West Pakistan (from Waziristan south to the Quetta Plateau), and east to Kashmir. Apart from a recently collected specimen from Jalalabad, in the valley of the Kabul River, eastern Afghanistan, all Afghan records for this species are from the northwestern part of the country.

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ADDENDUM

***Agamura femoralis** Smith.

Agamura femoralis Smith, 1933, Rec. Indian Mus., vol. 35, p. 17 (type locality: Kharan, Baluchistan, West Pakistan).

Distribution. Northwestern Baluchistan, West Pakistan.

Genus **Alsophylax** Fitzinger

Alsophylax Fitzinger, 1843, Syst. Rept., p. 18 (type species *Gymnodactylus pipiens* Eichwald, by original designation).

Alsophylax cf. **pipiens** (Pallas).

Lacerta pipiens Pallas, 1811, Zoogr. Ross-asiatica, p. 27 (type locality: Mt. Bogdo, near the Volga River, USSR).

Alsophylax pipiens Fitzinger, 1843, Syst. Rept., pp. 18, 90.

Distribution. From the lower Volga and Transcaspia region of the USSR to central Mongolia and the Ala-Schan mountains, south to northern Iran and Afghanistan. In Afghanistan we have seen material only from the vicinity of Kabul (see: Clark, Clark, Anderson and Leviton, 1969). Mertens (1965, p. 2) reports one specimen from Oukak.

Genus **Xenochrophis** Günther

Xenochrophis Günther, 1864, Rept. British India, p. 273 (type species: *Psammophis cerasogaster* Cantor, by monotypy).

Xenochrophis piscator (Schneider).

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Natrix piscator Smith, 1943, Fauna British India, Serp., p. 293.

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Distribution. From Baluchistan, West Pakistan, throughout all of India, Ceylon, central Nepal to 5000 feet, and east throughout the whole of the Indochinese Subregion, Southern China, Malaya and western Indonesia. In Afghanistan, collected 40 km. southwest of Jalalabad.

NOTE. In a recent paper entitled "Notes on the herpetofauna of certain provinces of Afghanistan," (*Zoologiske Listy*, vol. 18, pp. 55–66, 1969) Dr. B. Král documents the occurrence of *Psammophis leithi* in Afghanistan. His specimen came from 8 km. from Jalalabad, toward Sarsahi. He also adds two hitherto unrecorded species to the faunal list of the country: *Oligodon arnensis* (Family Colubridae), and *Bungarus caeruleus* (Family Elapidae).

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EXPLOSIVE SPREAD OF THE ORIENTAL GOBY *ACANTHOGOBIUS FLAVIMANUS* IN THE SAN FRANCISCO BAY-DELTA REGION OF CALIFORNIA

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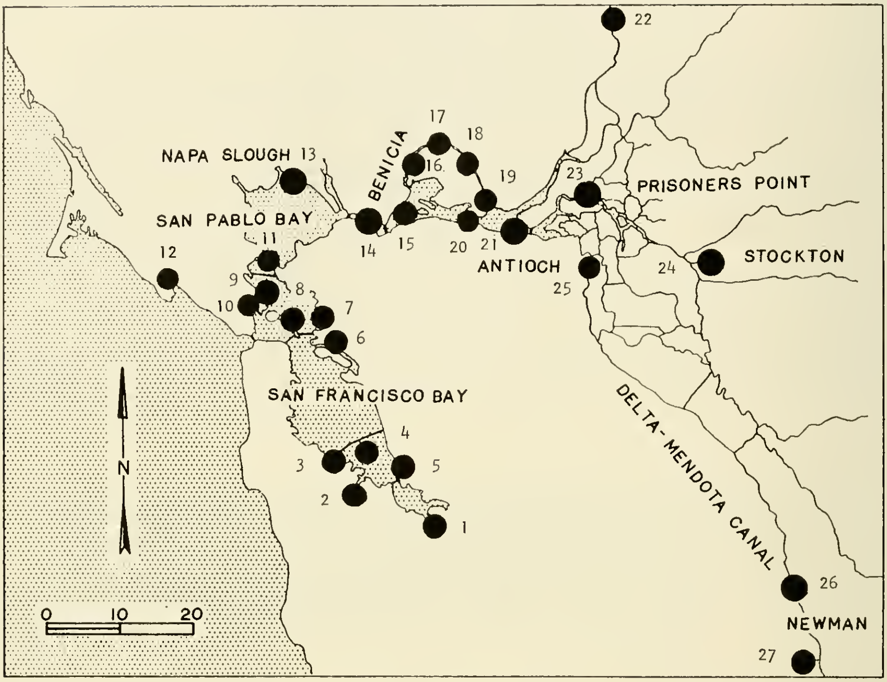
One of the features of animal distribution in recent years is the unexpected appearance of a species from far-off lands which rapidly, sometimes explosively, expands its range in its new homeland, often in direct competition with established elements of the native fauna.



Map 1. Collection localities for *Acanthogobius flavimanus* in the San Francisco Bay and Sacramento-San Joaquin Delta regions, 1963–1968 (the many verbal reports by fishermen in 1968 and later are not recorded). 1. Alviso, Santa Clara County. 2. Palo Alto Yacht Harbor, Santa Clara County. 3. Foster City Lagoon, San Mateo County. 4. San Mateo Bridge, San Mateo-Alameda counties. 5. Plummer Creek, near Newark, Alameda County. 6. Lake Merrit, Oakland, Alameda County. 7. Aquatic Park, Berkeley, Alameda County. 8. Treasure Island, San Francisco-Alameda counties; Angel Island, Marin County. 9. Tiburon, Paradise Cay, Belvedere, Marin County. 10. Richardson Bay, Belvedere, Marin County. 11. Marin Islands, San Rafael, Lower San Pablo Bay, Marin County. 12. Bolinas Lagoon, Solano County. 13. Napa Slough, Solano County. 14. Benicia, Carquinez Strait, Solano County. 15. Suisun Bay, Solano County. 16–19. Montezuma Slough, Solano County. 20. Suisun Bay, Solano County. 21. Antioch, San Joaquin River, Contra Costa County. 22. Snodgrass Slough off Sacramento River, opposite Walnut Grove, Sacramento County. 23. Prisoners Point, San Joaquin County. 24. Stockton (Deep Water Channel), San Joaquin County. 25. Tracy Pumping Plant, Alameda County. 26. Delta-Mendota Canal at Newman Wasteway, Stanislaus County. 27. San Luis Reservoir, Merced County.

In 1963 two specimens of *Acanthogobius flavimanus* Temminck and Schlegel, a euryhaline goby of Japan and adjacent mainland waters, were taken in the Sacramento-San Joaquin River Delta of California. The first specimen of the "mahaze" (its Japanese name; Okada, 1960) was taken on January 18 at Prisoners Point on Venice Island, and the second was taken on March 29 in the Stockton Deepwater Channel at the entrance of the Calaveras River, just below

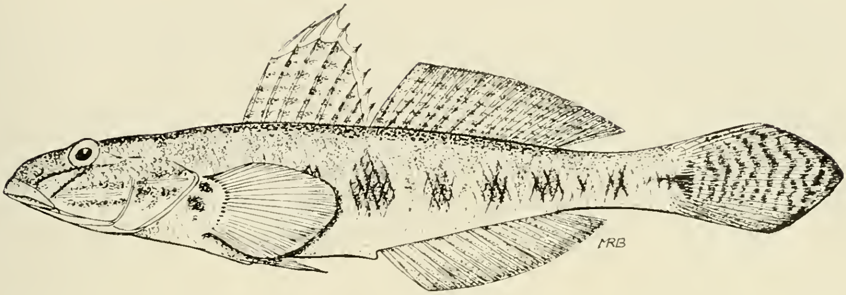


Figure 1. *Acanthogobius flavimanus* (Temminck and Schlegel). 123 mm. standard length, from the San Joaquin River at Prisoners Point, Venice Island, San Joaquin County (from Brittan, Albrecht, and Hopkirk, 1963). The higher outline of the dorsal fin added to the drawing is from a specimen of 176 mm. standard length from the Delta-Mendota Canal at Newman Wasteway, Stanislaus County, and illustrates the condition typical in larger individuals.

the Port (and city) of Stockton. The first 2 specimens were 123 and 69 mm. standard length, respectively.

No further examples were collected until late 1964 when several were taken from Palo Alto Yacht Harbor (Robert Hassur, verbal communication) and from a trap in Leslie Salt Company evaporation ponds at Alviso (4; 141–153 mm.). These localities are roughly 80–90 water miles from the initial collection points.

No further specimens were taken until August, 1965, when one was obtained off Marin Island near San Rafael, Marin County (male, 161 mm.) and, surprisingly enough at the time, an additional one at Newman wasteway on the Delta-Mendota Canal, which carries fresh water for irrigation from the Delta to the central San Joaquin Valley. The latter locality is approximately 80 water miles from the other farthest point from which the mahaze had been collected: Alviso, Santa Clara County.

In 1966, specimens of *A. flavimanus* were taken from widely spread localities and in increasing numbers, a trend which persisted during 1967. Starting in May, 1966, Jerrold Conners, using a small trawl mainly around Treasure Island, which lies adjacent to Yerba Buena Island between San Francisco and Oakland, took a total of 65 gobies on 12 different collecting trips; the largest number taken at any one time was 27. Specimens were also taken in San Francisco Bay in 1966 in the San Rafael Channel in May (1 male; 149 mm.), in the lower tidal reaches of Plummer Creek near Newark in May (3; 24–31 mm.), July (2; 44–64 mm.), and August (9; 80–108 mm.), and off Treasure Island in September (4 males and 2 females; 102–125 mm.), October (7 males and 1 female; 132–176 mm.), and November (1 male and 2 females; 124–129 mm., and 1 unsexed specimen of 115 mm.). A specimen was also taken in Richardson Bay in October (119 mm.). The small size of the first Plummer Creek specimens indicates breeding at that locality. J. A. Aplin of the California Department of Fish and Game (personal communication) notes that the Department's research vessel *Nautilus,* taking monthly samples at 6 stations in San Francisco Bay from the San Rafael Bridge southward 20 nautical miles to Dunbarton Bridge collected no Japanese gobies during the first 3 years of a biological survey of the Bay beginning in 1963, but during the fourth year (1966) took 10 specimens near Angel Island in September, 3 just south of the San Mateo Bridge (1 each in August, October, and November), and 1 just south of Dunbarton Bridge in November. Other material was collected in San Pablo Bay in May at McNear Beach (3 males; 139–168 mm.) and in November at Napa Slough (2 females and 1 male; 92–123 mm.), in Carquinez Strait between San Pablo and Suisun Bay at Benicia (4 males and 1 female; 107–177 mm.), and in the Delta at Antioch (1 male; 114 mm.). In March, a single adult was taken from the screen of the Tracy Pumping Plant; young fish would easily pass through the screen as water is pumped into the Delta-Mendota Canal.

During 1967 more records poured in. Fifty-five fish were taken in January between Angel Island and Treasure Island, and exhibited alive for several months in pure seawater at 50°F. at Steinhart Aquarium in San Francisco; these specimens were fully adult. In February, 7 females (117–155 mm.) were taken off Treasure Island and 20 females and 1 male (113–157 mm.) were collected east of San Rafael. In September, 5 were taken at Foster City Lagoon near the west end of San Mateo Bridge, and in December, 14 were taken at several locations in Suisun Bay and adjacent Montezuma Slough by the California Department of Fish and Game. During 1967, specimens also were taken in Lake Merritt, a tidal lake in Oakland, in Belvedere Lagoon near Belvedere-Tiburon, at Aquatic Park in Berkeley, at Paradise Cay on the Tiburon Peninsula, and at other localities on San Francisco Bay.

Two surprises came to light in 1967. In July, checking operations by the California Department of Fish and Game noted approximately 10,000 dead "trash" fishes in the San Luis Reservoir in Merced County, as a result of total depletion of oxygen because of an algal bloom and following die-off. This is a large, recently filled, man-made reservoir behind a gigantic earth-fill dam, and is located in the arid foothills of the inner Coast Range about 100 air miles southeast of San Francisco. It receives fresh water from the Delta (and eventually from the Feather River, a tributary of the Sacramento) via the California Aqueduct of the California Water Project and the Delta-Mendota Canal of the Central Valley Project. About half of the kill consisted of *A. flavimanus*! The balance were bluegills (*Lepomis macrochirus*), crappie (*Pomoxis*), and sticklebacks (*Gasterosteus aculeatus*). In December, a single goby (215 mm. total length) was taken from lower (tidal) Pine Gulch Creek in Bolinas Lagoon. This lagoon has no connection with San Francisco Bay except by approximately 15 miles of open rocky seacoast.

During 1968 the mahaze continued to be taken by biologists and fishermen in San Francisco Bay, in San Pablo and Suisun bays, and the Delta. Two collections indicate the species is spreading northward from the Delta in fresh water. In August, 1968, a specimen 95 mm. long was taken from Snodgrass Slough, a tributary of the Sacramento River near Walnut Grove (the mahaze is said by fishermen to be "common" here; Robert McKechnie, California Department of Fish and Game, personal communication). In October, an example 100 mm. in length was collected in the Sacramento Ship Channel just south of the Port and City of Sacramento.

Most of the collections made during 1963–67, which delineated the buildup of *Acanthogobius flavimanus* from 1 specimen or a few specimens taken at widely scattered localities to specimens taken nearly everywhere in the bays and the Delta, frequently in considerable numbers, were made by Conners while trolling for English sole in San Francisco Bay, by Al Aplin during the California Department of Fish and Game's biological survey of San Francisco Bay, and by the Department's Delta Study team. These collections and others, between 1963 and 1967, indicate a slow buildup period in which the goby was steadily increasing its numbers while wandering greatly (specimens taken from widely separated areas with many young of the year and of the previous year caught), followed by a great increase after widespread establishment. During 1966 the species apparently reached nearly the full extent of its distribution in San Francisco Bay and the Delta. When the species first gained access to the area it is impossible to say, but the first specimen collected in January 1963, was, from its size, probably entering its second year of life; the second specimen was a large subadult. It is probable they were spawned in the Delta. However, the fact that the species was not previously collected in spite of the considerable sport fishery in the region (as well as scientific collecting) indicates that the date of introduction was probably not more than 3 or 4 years previous to 1963.

In the central portion of San Francisco Bay the principal goby species taken with the mahaze is the bay goby, *Lepidogobius lepidus* (Girard), while in the collections made in the tidal portion of Plummer Creek, near its exit into south San Francisco Bay, it occurred with the mudsucker goby, *Gillichthys mirabilis* Cooper; the arrow goby, *Clevelandia ios* (Jordan and Gilbert); and the cheekspot goby, *Ilypnus gilberti* (Eigenmann and Eigenmann), the last being the most common. Salinities in Plummer Creek ranged from 16.9 percent on May 26 to 30.8 percent on August 17. At Palo Alto Yacht Harbor specimens belonging to *Acanthogobius flavimanus* have been taken since 1964; this species now heavily outnumbers the staghorn sculpin, *Leptocottus armatus,* formerly the commonest bottom fish (Robert Hassur, verbal communication).

The specimen taken one mile west of Antioch Bridge in the San Joaquin River was found with the cyprinids *Lavinia exilicauda* (Baird and Girard), *Orthodon microlepidotus* (Ayres), and *Pogonichthys macrolepidotus* (Ayres), the catostomid *Catostomus occidentalis* Ayres, the embiotocid *Hysterocarpus traski* Gibbons, and small striped bass, *Roccus saxatilis* (Walbaum) (Serranidae); all except the last are California lowland freshwater endemics. They were collected over a fine sand bottom; the water was fresh, but muddy, with an incoming tide. The 16 specimens taken from the Newman wasteway of the Delta-Mendota Canal were associated with white catfish, *Ictalurus catus* (Linnaeus) (1309 specimens), and with American and threadfin shad, *Alosa sapidissima* (Wilson) and *Dorosoma petenensis* (Günther) (1317 specimens, about 4:1 in favor of former); striped bass, *Roccus* (350); channel catfish, *Ictalurus punctatus* (Rafinesque) (7); splittail, *Pogonichthys* (2); and tule perch, *Hysterocarpus* (1). The specimens from the Delta-Mendota Canal were taken in freshwater in November, 1966, and December, 1965, and were examined by Michael Martin. On the basis of scale annulae and standard lengths, they were assigned to age classes: class 0 ranged up to 132 mm. for males and 130 mm. for females, class I from 107–171 mm. for males and 121–162 mm. for females, while 1 male of 177 mm. was assigned to class II. The ovaries of 7 class I females were measured by water displacement, the ovarian volume increasing from an average of 0.0061 cc. per millimeter (of the standard length) in early November (Napa Slough) to 0.015 cc./mm. in December (Delta-Mendota Canal), though average water temperature decreased 5 degrees F. in the interim. This rapid gonadal development indicates a spawning season from January to March, similar to that reported for Japan (Dotu and Mito, 1955). Sexual maturity in the California population may not arrive until the end of the second or third year of life. Ripe adults were generally scarce in the San Francisco Bay areas sampled by Conners from spring 1966 to winter of 1966–67. In addition, females predominate in the mahaze catch in February, 1967, the males apparently being in shallow water involved in the construction of territories and breeding burrows (Dotu and Mito, 1955). Males have darker and longer median fins, but do not differ noticeably in size from females. The largest specimen taken so far outside the Orient was taken in Aquatic Park, Berkeley, in March, 1970, measuring 185 mm. standard length and 234 mm. total length.

The species is unusually tough and resilient. Five adult specimens were taken from brackish water (sodium chloride concentration unknown) off Napa Slough in San Pablo Bay in September, 1968, and unceremoniously dumped into fresh water. They survived, and 10 days later were transferred to pure sea water at 24 hour intervals and in 20 percent increments. After 48 hours in salt water, they were transferred back to pure fresh water in the same manner. While not subject to any systematic temperature manipulation, the specimens were kept in water of various salinities that ranged between 52° and 83° F.

The dispersal of the mahaze up various freshwater river and canal systems appears less startling in view of the above facts. The goby obviously possesses the ability to penetrate up mud-bottomed lowland rivers; it commonly does this in the Orient and is doing it here. *Acanthogobius flavimanus* has apparently been carried out of the Delta in the strong southward flowing current of the Delta-Mendota Canal, which has a distinct problem with silting and with the establishment of a Japanese freshwater mussel, which will favor the establishment of such mud-associated bottom fish; its phenomenal increase in the San Luis Reservoir may be explained in terms of a habitat unoccupied by other bottom fishes (no catfishes were observed among the fish killed by the algal bloom and following die-off). The spreading of the species from San Francisco Bay to Bolinas Lagoon would be more difficult. While the mahaze can tolerate pure salt water, the shore between San Francisco Bay and Bolinas Lagoon is open rocky coast with a large assemblage of predaceous fishes. Either a migration occurred in the face of severe ecological opposition, or transfer through human agency took place. Ocean-going ships do not enter Bolinas Lagoon, so direct transfer from the Orient is contra-indicated, though fishing boats and pleasure craft sometimes make the trip from San Francisco Bay. Further, *A. flavimanus* is being used as a bait fish to some extent in the Bay and Delta regions. Consequently, it is likely introduction into Bolinas Lagoon came about through discarding of bait fish or by tiny young fish carried out in discharged coolant water. It is not known whether the species is firmly established in Bolinas Lagoon, as only 1 specimen (an adult) has been taken to date.

Aquarium specimens remain on the bottom, burrowing in mud or sand but not in gravel. Swimming is accomplished by short jerks. Buccal respiration, or air gulping, was observed on 1 occasion, apparently initiated by an oxygen deficiency in the water.

Virtually nothing is known of the ecology of the mahaze in California, although Okada (1960) gives some data for Japan. J. A. Aplin (personal communication) observed that regurgitant intended to be fed by 3 great blue herons to their young in a rookery on Bair Island, one mile north of the port of Redwood City, in early August, 1969, consisted totally of several mahaze, the larger ones being about 8 inches total length.

Besides *Acanthogobius flavimanus,* 2 other exotic fish species have appeared in San Francisco Bay in the last 10 years or so through unknown means of introduction (Ruth, 1964, on information supplied by W. I. Follett). The rainwater fish, *Lucania parva* (Baird), a cyprinodont from brackish waters along the U.S. Atlantic Coast, appeared first (Hubbs and Miller, 1965). Within a few years *A. flavimanus* and another Oriental goby, *Tridentiger trigonocephalus* (Gill), made their appearance. The latter, called "shimahaze" in Japan, is known from only 2 localities around the Bay (1966), but is assumed to be firmly established; it is also recorded from Los Angeles Harbor (Hubbs and Miller, 1965). Brittan, Albrecht, and Hopkirk (1963) give distinguishing characters for *A. flavimanus.*

In addition to the paper by Newman (1963) on the introduction into San Francisco Bay of an oriental commerical shrimp, *Palaemon macrodactylus*

(Rathbun), discussed by Brittan *et al.,* (1963), a recent paper by Nijssen and Stock (1966) concerning the explosive spread of an eastern North American euryhaline amphipod, *Gammarus tigrinus* Sexton, in the Yssellake (or Ijsselmeer, the present name for the old, now smaller, Zuydersee), Netherlands should be of considerable value to those interested in such phenomena. Certainly more foreign euryhaline fishes and invertebrates will show such sudden appearances, followed by rapid expansion of ranges, in estuarine systems the world over.

The authors wish to thank the following persons for information and assistance: J. A. (Al) Aplin, Dr. Harold Chadwick, John M. Huddleson, and Robert McKechnie, California Department of Fish and Game; Dr. Earl Herald and Walter Schneebeli, Steinhart Aquarium, California Academy of Sciences; and Robert Hassur, Stanford University.

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SOME NERVE PATTERNS AND THEIR SYSTEMATIC SIGNIFICANCE IN PARACANTHOPTERYGIAN, SALMONIFORM, GOBIOID, AND APOGONID FISHES[1,2,3]

By
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Some time ago while examining the salmopercoid genera *Percopsis* and *Aphredoderus* for the ramus lateralis accessorius, I noticed from superficial dissections on the head that these fishes had some strikingly interesting nerves emanating from one main point in the upper cheek region next to the preopercle (Freihofer, 1960). The nerves came up to the skin from their source below on the truncus hyomandibularis. There were four main nerves, one to each of the roofing membranes of the supraorbital, infraorbital, preopercular, and mandibular canals. In 1950 Ray had reported similar nerves for the lantern fish *Lampanyctus leucopsarus* and recognized them to constitute a group of nerves which she called the ramus canalis lateralis facialis system. The statement by Frost (1926) that the otoliths of *Apogon* and of the salmopercoid fishes strongly resembled each other led me to examine apogonids for these ramus canalis nerves. They were found to have these nerves in similar pattern. These facts suggested that there might be a relationship between lantern fishes, salmopercoid (or percopsiform fishes, as they are now called), and the supposedly percoid apogonids.

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[1] Research for this paper was supported by National Science Foundation Grant GB-198.
[2] A summary of results was kindly read for me by Dr. G. S. Myers at the New York City meetings of the American Society of Ichthyologists and Herpetologists in June, 1969.
[3] Submitted for publication February 2, 1969.

The salmopercoid fishes are especially intriguing since they obviously appear to combine features of both salmonids and percoids. Detailed studies of the nervous and skeletal systems of salmopercoids were begun as well as a survey of many fish groups for the ramus canalis lateralis system and the ramus lateralis accessorius. Two events influenced the survey. One was the publication in 1966 by Greenwood, Rosen, Weitzman, and Myers of a classification in which a new superorder of fishes, the Paracanthopterygii, was proposed which brought together six orders or parts of orders, some for the first time. The survey was directed to include all these groups. Its success was furthered by a second event, my fortuitously being present on cruise 16 of the R/V *Anton Bruun*. Bottom hauls frequently brought up large numbers of most major groups of paracanthopterygian fishes, thus affording material that could be processed in the Sihler technique. Preliminary observations of the nerves of all these paracanthopterygian fishes might, I thought, reveal nerve features that would test the validity of this new superorder as well as help in the question of codfish and brotulid relationships, fishes which looked much alike as they lay together on the ship's deck. A simple soul, but not perhaps an "educated" one, would think these latter two groups must be related. To suppose that the percopsids, batrachoidids, ogcocephalids, gobiosocids, lophiids, and their related families, had a relationship to each other let alone to the codfishes, hakes, ophidioids, and zoarcids would have and apparently still does strain beyond the bounds of belief the minds of most ichthyologists. The results of the nerve survey should lessen doubts now generally held about the Paracanthopterygii.

There is enough detail in the descriptive section of patterns of the ramus lateralis accessorius (RLA) to show how similar these are in brotulid, ophidiid, and gadiform fishes. Preliminary information is given on a special enlarged lateral-line branch (or several branches) which supply the pectoral-pelvic area in percopsiform, brotulid, batrachoid, and gobioid fishes and which is part of a segmental series of lateral-line nerves. This nerve and the segmental series of which it is a part may be a primitive paracanthopterygian feature inherited from lower fishes. A preliminary account is given of the manner in which the fin-ray nerves course in paracanthopterygian fishes in contrast to the way they do in acanthopterygian and numerous other fishes. It is a feature that appears characteristic but not unique to the Paracanthopterygii.

Brief, preliminary, comparative studies of the ramus canalis lateralis system of nerves are given for a number of families. A much fuller treatment is planned for a future paper.

One of the purposes of the present paper is to report some features of nerves which bear on the systematic validity of the Paracanthopterygii. Other main systematic questions to which the results presented are relevant are: (1) relationships of the salmopercoid fishes to other paracanthopterygian fishes; (2) the relationships of salmopercoid fishes to acanthopterygian fishes; (3) the origin of the salmopercoid fishes and of gadoid, ophidioid and batrachoid fishes; (4) the interrelationships of the gadoid and ophidioid fishes; (5) the relationships and reclassification of the gobioid fishes; (6) the relationships of the Apogonidae.

A note of explanation on the ramus lateralis accessorius. It supplies taste buds on the body and or fins. It is not a lateral-line nerve. The name ramus recurrens facialis is more descriptive and can be shortened to "recurrent facial," but the abbreviation "RLA" for the former term is used here.

MATERIALS AND METHODS

Specimens of *Merluccius gayi, Brotula clarkae, Physiculus talarae, Lepophidium prorates, Porichthys margaritatus, Bathygobius lineatus, Hoplostethus pacificus, Melamphaes* species, *Apogon astradorsatus, Scopelengys tristis,* and *Zalieutes elater* were collected on cruise 16 of the R/V *Anton Bruun* and specimens of *Brotuloides emmalas* by Margaret Bradbury on cruise 19 of the R/V *Te Vega.* All were kept in formalin until processed for the nerves by the Sihler technique (Freihofer, 1966), in which the stained nerves stand out in transparent whole specimens. Alizarin specimens were also prepared for examination of the skeleton. Both Sihler and alizarin preparations were also made of *Percopsis omiscomaycus, Percopsis transmontana, Aphredoderus sayanus, Hypomesus pretiosus, H. olidus, Dicrolene intronigra.* The following specimens were also examined by dissection under the microscope: *Chologaster papilliferus* and *Dicrolene kanazawi,* uncatalogued; *Lamprogrammis niger,* LACM (Los Angeles County Museum) 9708-5, *Watasea sivicola,* 26797; *Monomerepus* species, 57024; *Dinematichthys iluocoeteoides,* uncatalogued; *Eutyx diagrammus* uncatalogued; *Merluccius productus,* LACM 9815-8; *Eleginus gracilus,* 49233; *Microgadus proximus,* 49237; *Boreogadus saida,* 48810; *Urophycis floridanus,* 50878; *Laemonema barbatulum,* 63261; *Coelorhynchus scaphopsis,* 179; *Eleotris fuscus,* uncatalogued. Numerous other species of various families and orders were examined but are not listed. All catalogue numbers are from the Stanford University fish collections unless otherwise noted.

Many of the families and genera mentioned in the text were also examined from specimens in the Starks skeletal collection at Stanford University.

ACKNOWLEDGMENTS

I would like to express my appreciation for the generous and essential help the following people gave in sending specimens kept specially in formalin or who helped in the field: Carl Bond, Oregon State University; Margaret Bradbury, San Francisco State College; Daniel M. Cohen, Systematics Laboratory, U. S. Fish and Wildlife Service; E. J. Crossman, Royal Ontario Museum; William Eschmeyer, California Academy of Sciences; Carter Gilbert, Florida State Museum; Shelly Johnson, University of Southern California; Robert Lea, California Division of Fish and Game; the late Fr. Romeo O. Legault, University of Ottawa; Donald McPhail, University of British Columbia, John Massie, California Aqueduct Facility; William Weaver, Florida State Museum; James Davis, North Carolina, State Fish and Game.

Observations on osmerids are from Sihler preparations and serial sections made by Craig Findly as part of a special problems study he was doing at Stanford University.

Dr. Daniel Cohen identified the gadoid and ophidioid fishes collected on the R/V *Anton Bruun* except for *Lepophidium prorates* identified by Dr. C. Richard Robins; Dr. Ernest Lachner identified the apogonid and Doug Hoese the goby.

My special thanks are due Adair Fehlmann, Smithsonian Oceanographic Sorting Center, for arranging my participation on cruise 16 of the R/V *Anton Bruun* and for much additional help in procuring specimens. Leonard Compagno was a patient listener and excellent discussant while the work was in progress. Max Millsap, Stanford Anatomy Department, took all photographs except that in figure 17 which was taken by the author.

RAMUS LATERALIS ACCESSORIUS

DESCRIPTION OF RAMUS LATERALIS ACCESSORIUS IN THE OPHIDIIDAE

In *Lepophidium prorates* an enormous ramus lateralis accessorius (RLA) arises from the geniculate ganglion (fig. 1), passes dorsolaterally and posteriorly up to the cranial roof where it bifurcates into a large branch (RLA-PP) going to the pectoral and pelvic fins and a small branch (RLA-PDA), about ⅕ the size of the other, which goes to the dorsal and anal fins. The pectoral-pelvic branch turns posterolaterally beneath the cranial roof, enters an intraosseous passageway in the parietal, leaving it at its posterolateral corner by a large foramen.

The dorsal-anal branch, RLA-PDA, after leaving the parietal, passes posteriorly near the middorsal line, beneath skin back to the dorsal fin where it dips ventrally and passes posteriorly alongside the pterygiophores about ⅓ of their length below their outer distal ends. It forms a longitudinal plexus with crossing branches of the dorsal rami of the spinal nerves supplying the fin rays and membrane. At the seventh and eighth dorsal crossing segmental rami, 2 large branches are given off, one at each of these segments, which pass beneath the skin posteroventrally towards the origin of the anal fin. These 2 branches of RLA-PDA join at the second segment from the anal origin and pass inwardly and run posteriorly alongside the pterygiophores forming a longitudinal plexus with branches of the crossing ventral spinal rami supplying the fin rays and membrane. On their course from the dorsal to the anal fins the 2 branches of RLA-A cross numerous branches of the lateral line and segmental rami going to the skin and also exchange a few branches between each other. The nerves from the longitudinal plexi of

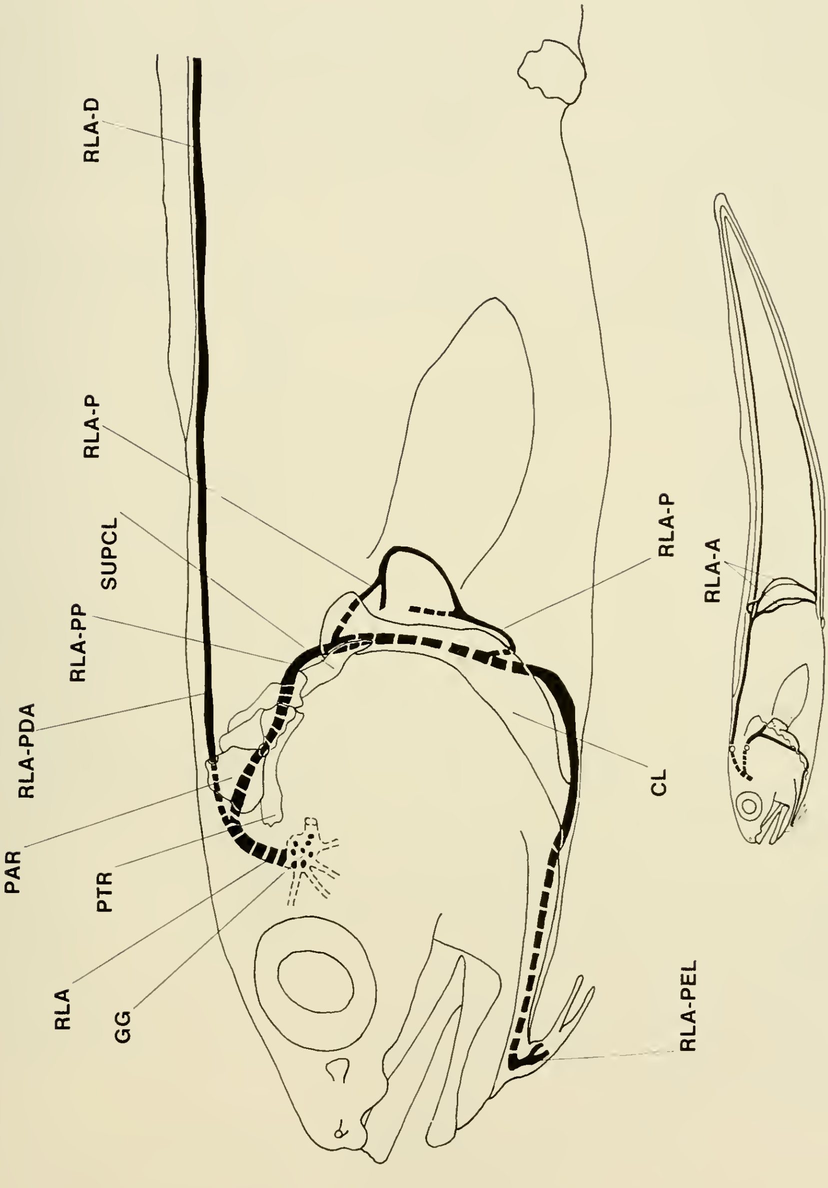

Figure 1. Pattern of ramus lateralis accessorius (recurrent facial nerve) in *Lepophidium prorates* (Ophiidae). See list of abbreviations.

the dorsal and anal fins enter the fin rays and membrane in a characteristic way. For each segment, a branch of RLA serves the half fin ray of its side and its half membrane lying posterior to the half ray. In doing so, the fin-ray nerve passes inward towards the opening in the base of the ray and gives off a branch which runs distally in the fin membrane of its side of the body. The rest of the fin-ray nerve passes forward into and through the split base of the fin ray and then onto the outer, external surface of the half of the ray of its side and along the half fin ray to its distal end. The longitudinal plexus of each side of the dorsal fin continues posteriorly and meets its counterpart from the anal fin at the mid point of the tip of the hypural fan.

Emerging from the posterolateral corner of the parietal, the pectoral-pelvic branch, RLA-PP, passes across the medial surfaces of the supratemporal canal bone and the epiotic arm of the posttemporal and ventrally beneath skin along the posterior edge of the supracleithrum and cleithrum en route to the pectoral and pelvic fins. A short distance above the pectoral fin a branch is detached which passes along the dorsal edge of the muscular base of the pectoral fin. A branch from the branchial plexus joins the pectoral branch of RLA and the compound nerve enters the bases of the fin rays ventrally, giving off branches to the half rays and membrane. As for the fin rays of the other fins, the nerves to each half ray course on the outside surface of the rays, not internally between each of the halves of each fin ray as is characteristic of percoid and most other fishes. As RLA-PP passes the ventral edge of the pectoral fin a branch is detached which joins a nerve from the brachial plexus which enters the ventral base of the pectoral fin and passes dorsally up through the pectoral fin giving off branches to each fin ray as described for the dorsal base of the pectoral fin.

The enormous remainder of RLA-PP passes anteroventrally beyond the pectoral fin to enter the pelvic fin. At the posterior end of the fleshy isthmus between the two gill openings, the large trunk of RLA-PP of each side of the body join in the midventral line and continue anteriorly as one trunk. Next, the common trunk is joined by a large spinal ramus of each side that comes to the surface at the midventral line after having passed down the medial side of the body wall. The resulting huge common spinal and recurrent facial trunk divides at the base of the pelvic fin. A branch is given to each of the two pelvic fin-ray bases. Each pelvic fin ray has the fin-ray nerve coursing on its external surface as in the other fins, a pattern which, as has been mentioned, is significantly different from that for percoid and many other fishes.

Description of the Ramus Lateralis Accessorius in the Brotulidae

In *Ogilbia ventralis,* studied from a dissected alcoholic specimen only, a very large RLA arises from the geniculate ganglion (fig. 2) and passes a rather long

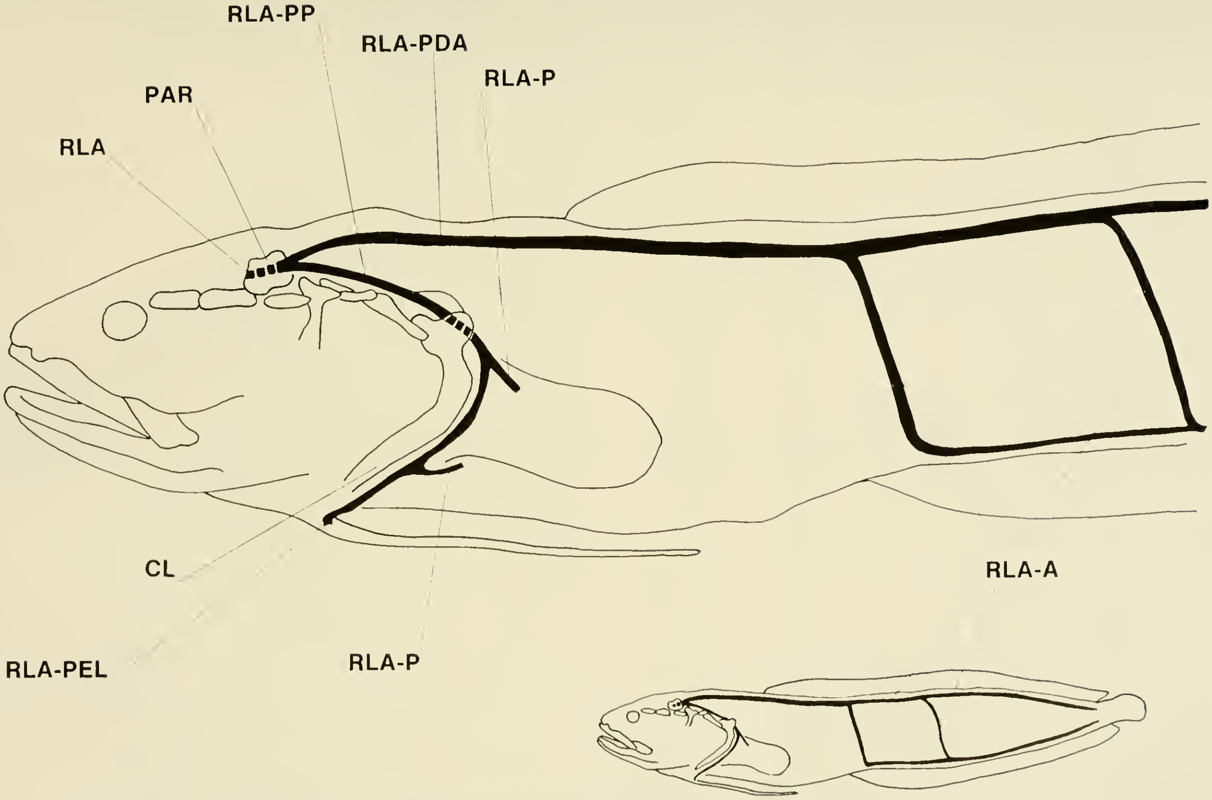

Figure 2. Pattern of ramus lateralis accessorius in *Ogilbia ventralis* (Brotulidae). See list of abbreviations.

distance posterodorsally up to the cranial roof where it is met by an extremely thin vagal ramus just before cranial exit through the parietal near its posteromedial corner. Immediately outside the cranium on the nape it divides into almost equal sized branches, RLA-PDA to the dorsal and anal fins, and RLA-PP to the pectoral and pelvic fins. Branch RLA-PP to the pectoral and pelvic fins passes posteroventrally following the posterior edges of the posttemporal, supracleithrum and cleithrum directly beneath skin. It passes medially behind the dorsoposterior end of the cleithrum and, upon emerging from its posterior edge, it detaches a large branch along the dorsal edge of the muscular base of the pectoral fin. This branch is joined by a large spinal nerve branch of the brachial plexus just before entering the upper end of the base of the pectoral fin. The remainder continues ventrally posterior to the cleithrum and beneath skin on its way to the pelvic fin where it is met at the midventral line by a large branch of a spinal nerve. In passing the ventral end of the pectoral fin, a small branch of RLA passes dorsoposteriorly to the ventral end of the pectoral fin base where it joins a branch of the brachial plexus that enters the ventral end of pectoral fin base.

Branch RLA-PDA runs along the base of the dorsal fin as in other brotulids. A large branch detaches from the dorsal fin branch at about the eleventh segment back from the anterior end of the dorsal fin. A second fair-sized branch arises at about segment 22.

With its 2 main branches arising from the main trunk of RLA outside of the parietal, the pattern in *Ogilbia* is basically like that in the gadiform fishes.

The same pattern was found in *Dinematichthys iluocoeteoides*.

In *Brotula clarkae* (fig. 3), the pattern of RLA is the same as that described for *Brotula multibarbata* from a dissection of an alcoholic specimen (Freihofer, 1963). An anal branch was not noted at that time. A Sihler preparation of *Brotula clarkae* shows that there is an anal branch similar to that in the ophidiid *Lepophidium* and the morid, *Physiculus*.

The branch to the dorsal and anal fins, RLA-PDA, passes into the trigeminal foramen with the supra- and infraorbital trunks, but inside the foraminal passageway of the prootic bone RLA-PDA departs and passes dorsoposteriorly through the body of the sphenotic and re-enters the cranium where it continues dorsoposteriorly over the cranial ceiling up to its exit via an osseous passageway in the parietal at its posteromedial corner next to the base of the supraoccipital spine. On one Sihler preparation 5 anal branches are detached from RLA-PDA. The first two, which join and separate again on their way to the anal fin, come off at segments 9 and 10 counting from the origin of the dorsal fin. The next three come off at segments 13, 14, and 19. These branches enter the anal fin respectively at 2, 7, 9, 10, and 19 segments from its origin. Four similar branches occur on the other side. Two other specimens had 4 anal branches similarly spaced. Fi-

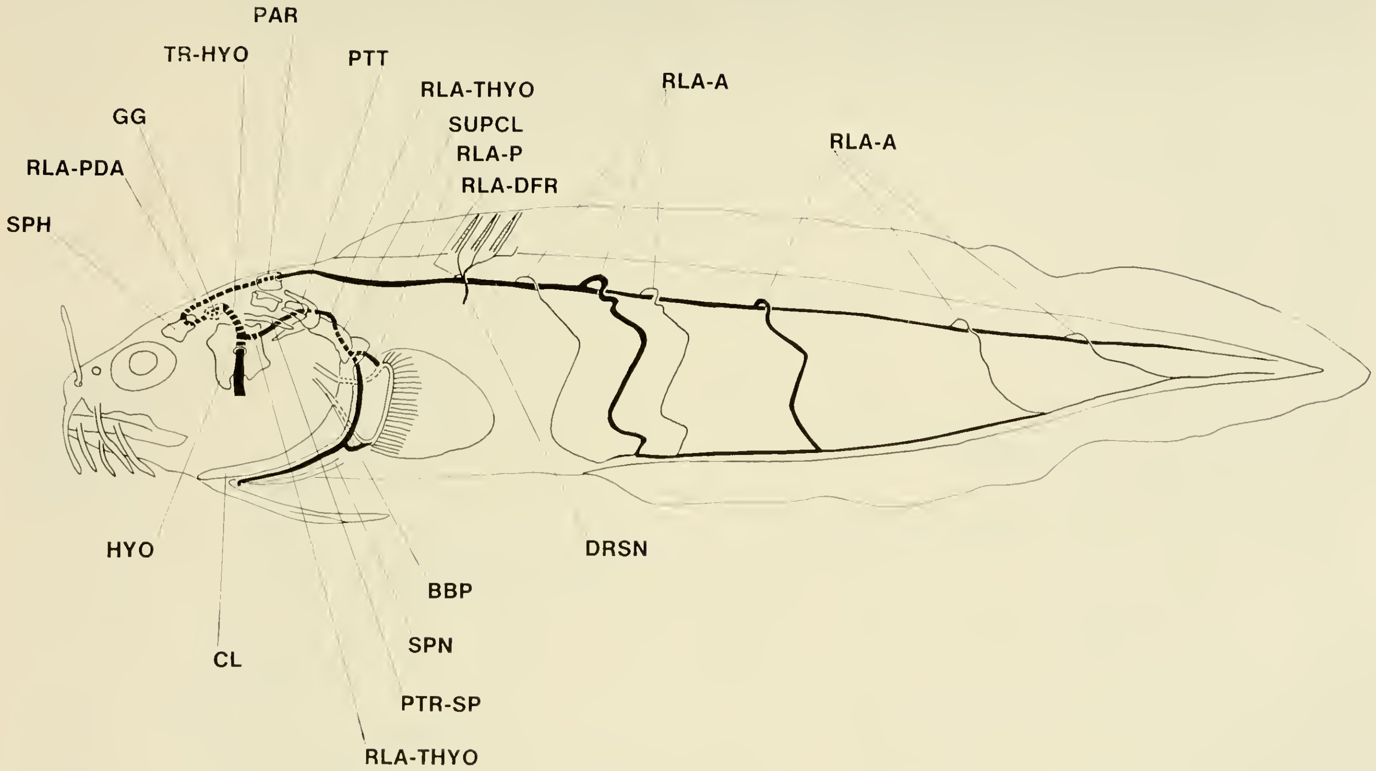

Figure 3. Pattern of ramus lateralis accessorius in *Brotula clarkae* (Brotulidae). See list of abbreviations.

nally, a fourth specimen had 1 large anterior anal branch entering the anal fin at the twentieth ray with no RLA innervation going to these first 20 rays, apparently, and with a second anal branch in the position of the last branch on the other specimens.

The pectoral-pelvic branch, RLA-THYO, leaves the cranium on the posteromedial surface of the truncus hyomandibularis, turns abruptly posteriorly, and runs along the medial side of the hyomandibular bone (fig. 3). Emerging from behind the posterior end of the hyomandibular, it passes dorsal to a large opercular muscle, then under the long pterotic spine, and onto the medial surface of the posttemporal. It runs for a short distance beneath skin between the posttemporal-supracleithral articulation then medially again behind the cleithrum, coming from behind this bone above the dorsal end of the muscular base of the pectoral fin where a fair-sized branch is detached which runs out the dorsal edge of the muscular pectoral base, being joined en route by a larger branch from the brachial plexus. The dorsal pectoral branch of RLA-THYO detaches 2 small nerves before joining the brachial branch. One of these goes to skin near the base of the fin rays on the medial side of the fin. The other goes to skin on the lateral side. Another branch to the lateral surface of the fin base is detached halfway down the fin. As RLA-THYO passes beneath skin near the ventral end, a large branch is detached which, together with a large branch from the brachial plexus, enters the ventral base of the fin rays. The dorsal and ventral fin-ray nerves become smaller as they approach each other as they pass through the bases of the fin rays giving off a branch between each 2 succeeding rays, the fin-ray branch of each side of the fin coursing distally in the membrane between each succeeding whole ray. The main trunk of RLA-THYO passes anteriorly beneath the skin paralleling the cleithrum. Near the base of the pelvic fin it joins with a large branch of a ventral spinal nerve, which, before joining RLA-THYO, gives off a branch to the pelvic muscles. Before joining with the branch from the brachial plexus, RLA-THYO detaches a branch which goes to the anterior surface of the first ray. It is joined by a branch from the ventral spinal ramus. The posterior external surface of the first ray plus the anterior and posterior surfaces of the second pelvic ray are innervated by 2 compound branches from RLA-THYO and spinal nerve trunk. In reaching the pelvic fin the ventral spinal nerve has passed down the wall of the body cavity medial to the pectoral girdle and comes to the surface at the midventral line near the base of the pelvic fins.

Description of RLA in Gadiform Fishes

In the morid *Physiculus talarae* a large RLA leaves the geniculate ganglion, courses dorsally in an open groove on the inner surface of the parietal, exits through a large foramen in this bone near its center and passes posterolaterally beneath the large muscle mass on top of the head and then dorsally between the

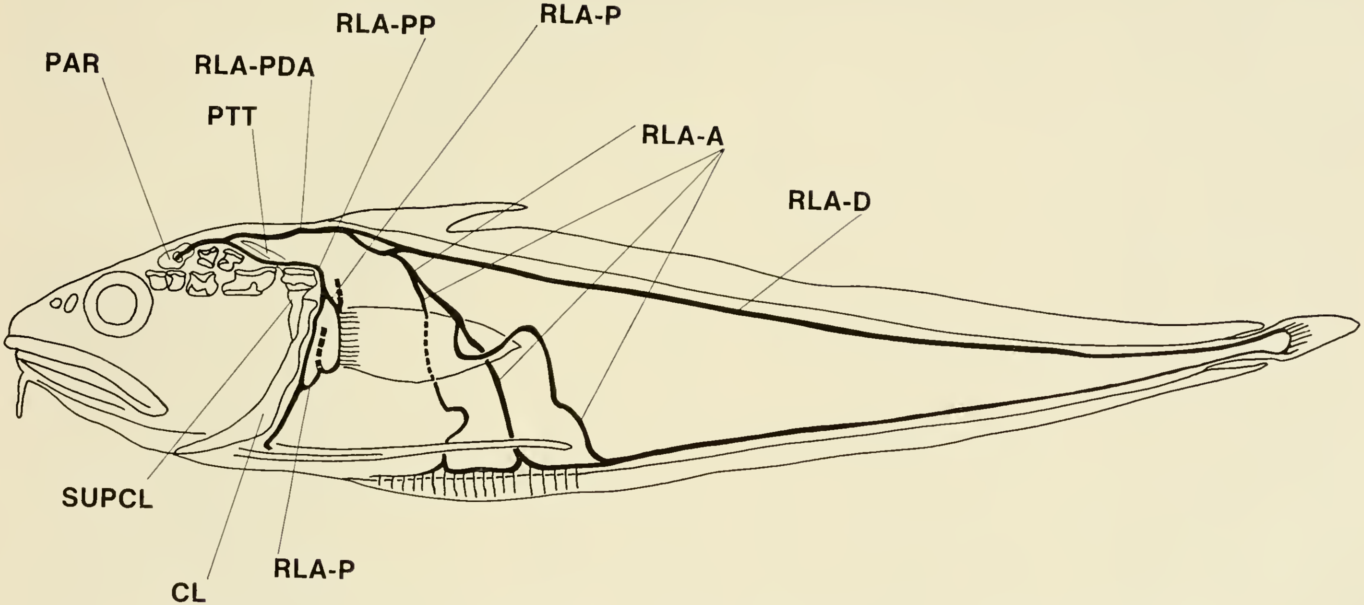

Figure 4. Pattern of ramus lateralis accessorius in *Physiculus talarae* (Moridae). See list for abbreviations.

side of the muscle mass and the medial surface of the supratemporal canal bone. A thin vagal ramus joins RLA at its exit through the parietal. Medial to the supratemporal canal RLA bifurcates into RLA-PDA, the dorsal-anal branch, and RLA-PP, the pectoral-pelvic branch. RLA-PDA curves medially beneath the skin on its course to the dorsal fin at the anterior end of which it detaches an anal fin branch, RLA-A, which on one specimen parallels the course of RLA-D for 3 segments and then curves ventroposteriorly under the skin. On another specimen the dorsal branch did not detach the first anal branch, a small one to the anterior part of the anal fin, until the ninth segment from the origin of the dorsal fin. The main large anal branch detaches on this specimen at the twelfth segment. On the specimen illustrated, the anal branch passes beneath the skin and divides en route into 3 parts (fig. 4), a smaller anterior branch which reaches the anal fin at the sixth segment from its origin and forms an anteriorly coursing longitudinal plexus with crossing ramuli of the segmental ventral spinal nerves. The second or main part of the three reaches the base of the anal fin at its fifteenth ray and forms a posteriorly coursing longitudinal plexus. The third branch joins the longitudinal plexus at the twenty-first ray. The plexus continues all the way to the caudal fin. On the other side of the specimen 2 anal branches course beneath the skin paralleling each other and joining at the base of the anal at about its fifteenth ray.

The branches of the longitudinal plexus that enter the fin rays do so in nearly the same way that they do in the ophidiid, *Lepophidium.* In *Physiculus* a fin-ray nerve passes to the posterior side of the base of each half fin ray of its side of the body. Before passing anteriorly through the opening between the two diverging bases of the half fin rays each fin-ray nerve of each side detaches a branch that runs distally out the posterior external surface of the fin ray. The remainder of the fin-ray nerve of each side passes through the opening between the base of the half fin rays and passes distally on the external anterior surface of the half fin ray. As was mentioned for the ophidiid *Lepophidium,* this is drastically different from the pattern shown in most other fishes, for which *Aphredoderus* (fig. 13) is an example, where the fin-ray nerves course in the hollow internal tube formed by the two concave half rays of each side meeting.

From its origin from the main trunk of RLA, the pectoral-pelvic branch, RLA-PP, passes posterolaterally on the medial surface of the supratemporal canal, crosses laterally over the epiotic arm of the posttemporal and ventrally beneath the skin slightly posterior to the supracleithrum and cleithrum but anterior to the pectoral fin and lateral to the base of the fin. Dorsal to the pectoral fin base a branch is detached from RLA-PP which joins with a large branch from the brachial plexus which together enter as one nerve the dorsal base of the pectoral fin and pass down through the basal opening between the fin-ray halves giving off a branch to each half fin ray as already described for the dorsal and anal fins. Further on its course ventrally over the lateral surface of the muscular base of the pectoral fin, a smaller branch detaches from RLA-PP and passes over towards the ventral end of the pectoral fin base where it is met by a large nerve from the brachial plexus. The compound nerve enters the ventral end of the base of the pectoral fin and passes dorsally through successive rays until it meets with the branch coming from the dorsal end of the pectoral base.

The very large remainder of RLA-PP passes ventrally beneath the skin to the slightly jugular pelvic fin where it is met by a large branch from the first ventral spinal nerve posterior to the occipito-spinal complex. The fin-ray nerves run distally on the external surface of the fin rays as already described for the other fins.

In the Merlucciidae, no RLA was found in a Sihler nerve preparation of *Merluccius productus.*

The pattern in the Gadidae as represented by *Microgadus* (fig. 5) differs significantly from that in the Moridae in that the anal-fin branch in the Gadidae detaches from the pectoral-pelvic branch not far above the base of the pectoral fin, whereas in the Moridae the anal branch detaches from the dorsal fin branch about a dozen segments back from the origin of the dorsal fin or by one or two additional branches more posteriorly.

Other gadid genera examined showing the same pattern as *Microgadus* are *Gadus, Boreogadus,* and *Eleginus.*

In the Macruridae the dorsal-anal branch detaches after the main trunk of RLA passes the epiotic arm of the posttemporal. This pattern bears a small resemblance to the gadid pattern but a larger one to the morid pattern. In *Macrurus* RLA crosses laterally the posttemporal bone and divides, one branch passing down the posterior edge of the supracleithrum and cleithrum to supply the pectoral and pelvic fins, and the other arching dorsally then straightening out, crossing several septa and then sending one branch up to the overlying dorsal fin and one ventroposteriorly to the anal fin.

A branch of a dorsal ramus to the first elongated spine of the dorsal fin was found which is of unusual interest for the speculation that it arouses as to its use in the life of macrurids. All the numerous species examined had it well developed but not as conspicuously developed as in *Lionurus gibber.* In this species a relatively enormous nerve extends out in the posterior groove of the elongated anterior dorsal spine and out beyond the spine in the protective sheath that is more than once again as long as the spine. This projection appears to be largely nerve. No enlarged nerve was observed in any of the other fins. For a supposedly deep-sea bottom swimming fish, this great dorsally directed tactile and taste feeler is surprising. As was mentioned, this development is much greater than anything seen on the ventral or lateral fins. Some important stimuli from above the fish must be perceived. It suggests that the elongated nerve-filled spine is a contact organ for use in touching other individuals swimming directly above in schooling.

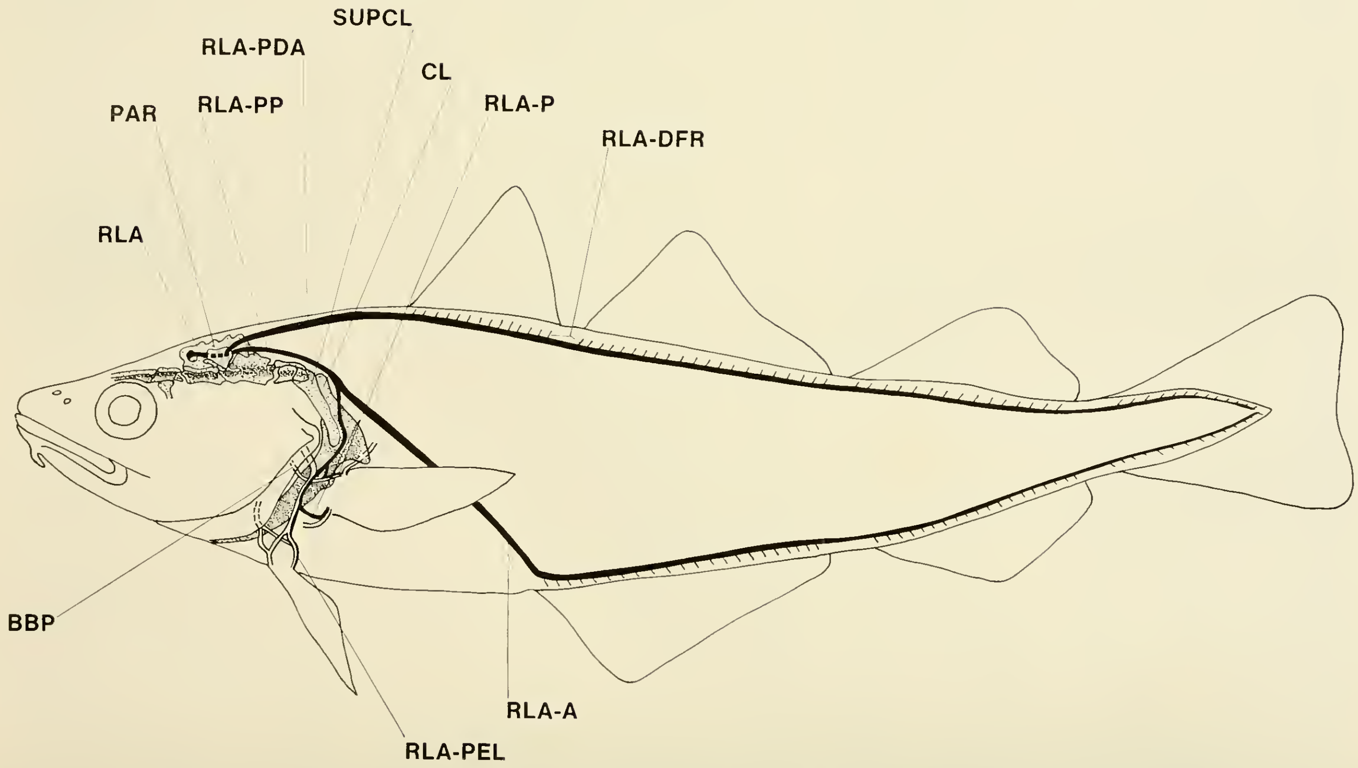

FIGURE 5. Pattern of ramus lateralis accessorius in *Microgadus proximus* (Gadidae). See list for abbreviations.

Pattern of RLA in Percopsiformes

In *Percopsis* (fig. 6) the sympathetic chain and RLA course bound together, the two forming a common trunk. All the branches that are given off from this common trunk may contain fibers from both these nerve trunks. The RLA-sympathetic common trunk is very large, 4 times the size of the ninth cranial nerve. The sympathetic chain alone in most fishes is usually less than ½ the size of the ninth cranial nerve.

The RLA part of the common trunk arises from the geniculate ganglion. What evidently is a sympathetic trunk, and which is about 1⁄20 the size of the RLA-sympathetic common trunk, curves anteromedially around the root of the truncus hyomandibularis. It was not followed further on the surface of the truncus hyomandibularis as this truncus and the truncus infraorbitalis come together as they pass medially towards the fifth-seventh complex. The common trunk of RLA + sympathetic chain leaves the truncus hyomandibularis shortly outside the cranium and passes posteromedially across the wall of the otic bulla, crossing the ninth cranial nerve en route to which it is connected by a thin branch which evidently is sympathetic. The common trunk passes onto the ventral side of the vertebral column and then along it to the caudal fin. As the common trunk passes the pharyngo-branchial roots of the vagus, 2 sympathetic branches leave from 2 ganglia located on the surface of the common trunk. One of the branches is about 1⁄10 the size of the common trunk; the other is about 1⁄20 its size. At the same point a large branch, about ¼ the size of the common trunk leaves from a bundle of fibers already formed anterior to the 2 sympathetic ganglia. This large branch must be mostly RLA fibers. It does not come from these 2 ganglia. This large branch passes to the base of the first and second ventral spinal rami of the occipito-spinal nerves. Opposite Baudelot's ligament a small branch detaches from the common trunk, runs parallel to the ligament, and then joins the third ventral occipito-spinal ramus. The next branch is a large one, about ¼ the size of the first large trunk branch. It goes to the fourth ventral spinal ramus. The next branch is about ½ as large as this one and each succeeding branch going to each ventral spinal ramus is small. The specimen illustrated in figure 6 is different from the specimen described in the text.

The Amblyopsidae have the same pattern as *Percopsis,* not as in *Aphredoderus.* In *Chologaster papilliferus* RLA appears even larger.

In *Aphredoderus sayanus* (fig. 7) the pattern is quite different from that in *Percopsis,* but one basic similarity remains, that of having the fibers of RLA destined for the pectoral fins, and perhaps for the pelvics also, distributed via the occipito-spinal complex.

In *Aphredoderus* a sizable RLA leaves the cranium through the parietal and courses beneath the skin towards the dorsal fin. Directly outside the cranium RLA detaches a branch down the posterior surface of the cranium that joins the

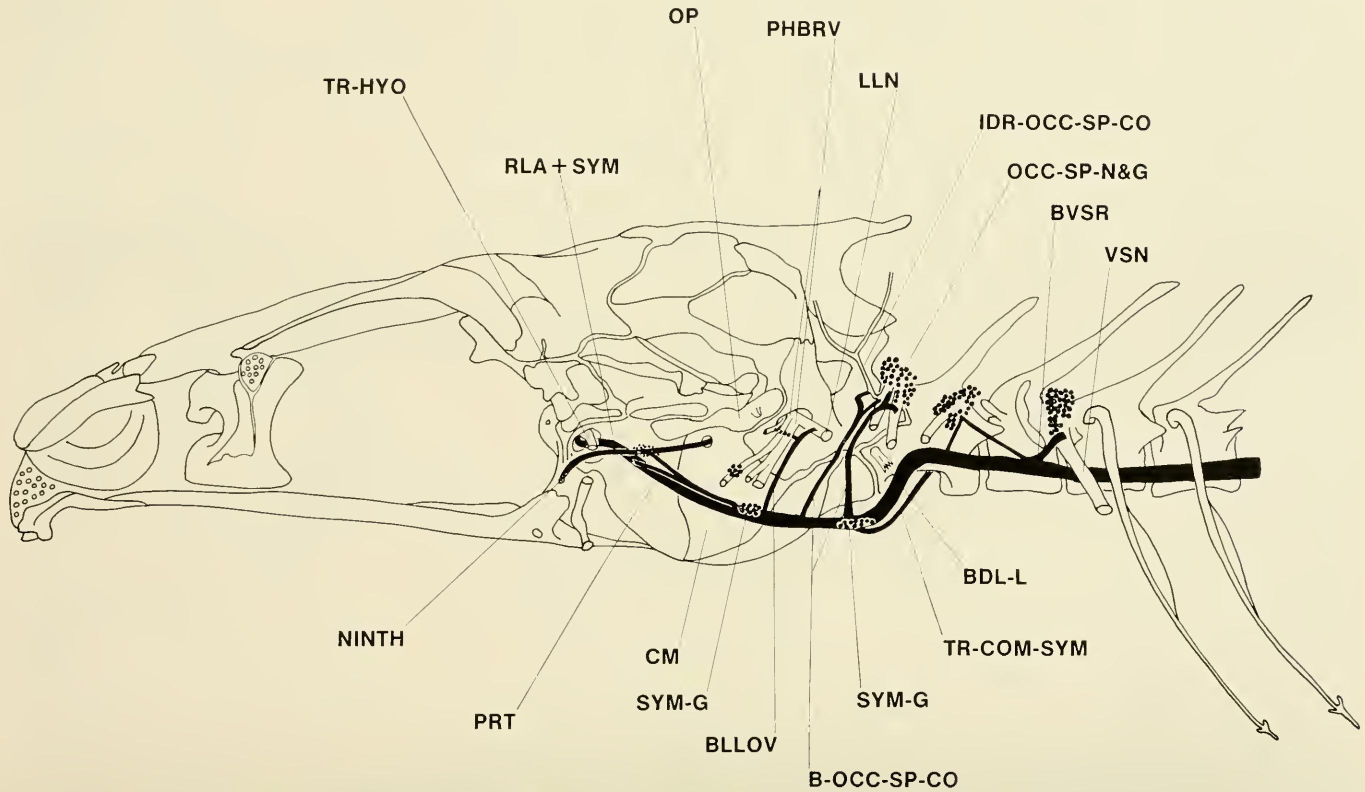

Figure 6. Pattern of ramus lateralis accessorius coursing with sympathetic system in *Percopsis omiscomaycus* (Percopsidae). See list for abbreviations.

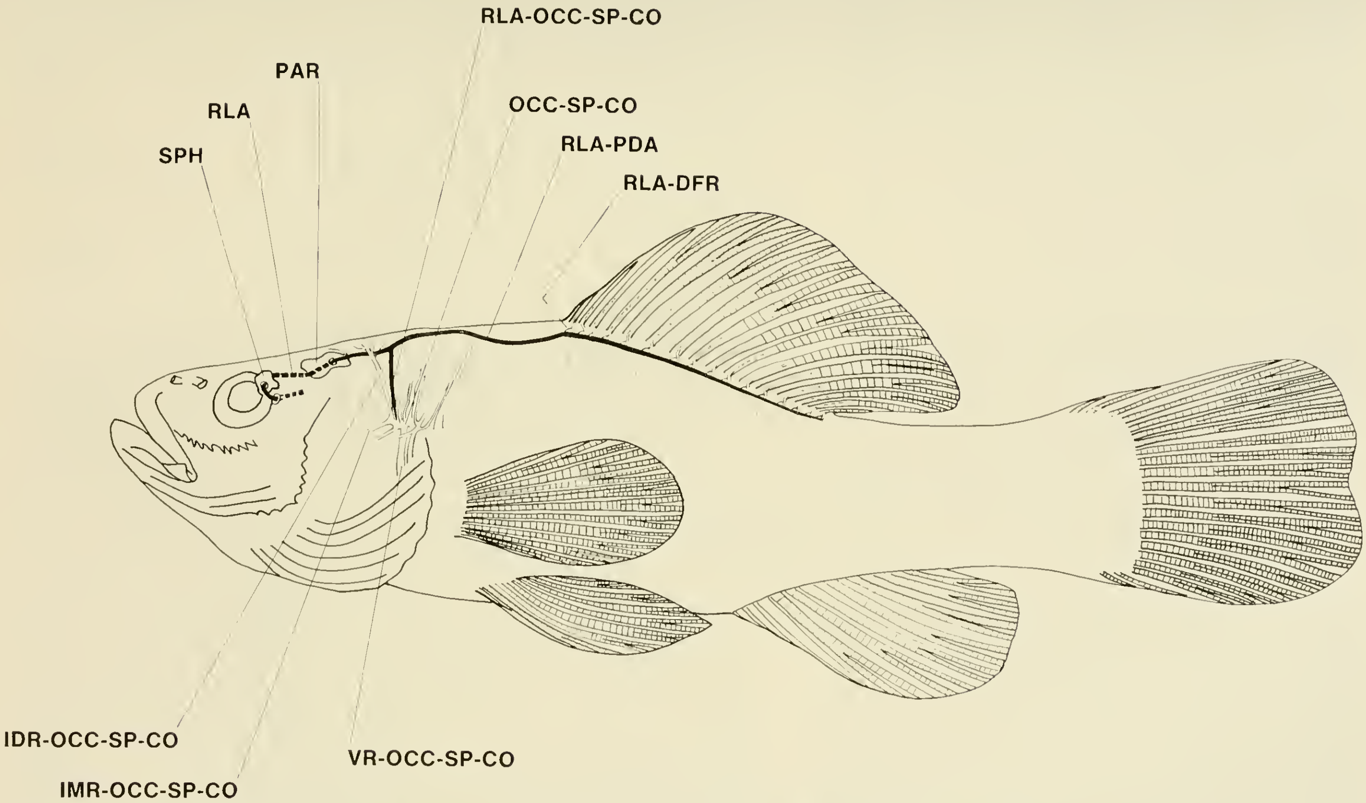

Figure 7. Pattern of ramus lateralis accessorius in *Aphredoderus sayanus* (Aphredoderidae). See list for abbreviations.

occipito-spinal complex where the first dorsal ramus leaves its vertebra. Varying with the specimen, this first branch of RLA either courses to the first occipito-spinal nerve independently of the first dorsal ramus which passes up the posterior surface of the cranium and innervates skin overlying the posterolateral area of the cranium; or the two run in common, or part of the way in common, but in opposite directions. As RLA continues towards the dorsal fin other dorsal spinal rami cross it. It appears that a second branch from RLA courses down the posterior edge of the first neural spine to join another part of the occipito-spinal complex. The crossing dorsal rami and RLA form a longitudinal plexus alongside the dorsal pterygiophores. The plexus continues beyond the dorsal fin but in diminished size until it reaches the caudal fin. It could not be determined if any RLA fibers remained in it that far. No branch of RLA to the anal fin was discernible nor was there a pronounced longitudinal plexus along the anal as there is along the dorsal fin.

The common trunk of RLA + sympathetic chain in *Percopsis* is about 20 times the size of the sympathetic trunk in *Aphredoderus* where this trunk crosses the wall of the otic bulla.

Pattern of RLA in Batrachoididae

In *Porichthys margaritatus* (fig. 8) RLA must be looked for in the same place as in *Percopsis,* that is, issuing from the facial foramen together with the truncus hyomandibularis combined with the sympathetic chain. Shortly outside of the facial foramen the common trunk of RLA + sympathetic chain leaves the truncus hyomandibularis, turns posteriorly and separates, the sympathetic trunk passing posteromedially across the wall of the otic bulla and onto the ventral side of the vertebral column and along it to the caudal fin. The trunk of RLA passes posterolaterally across the wall of the otic bulla, gradually diverging from the sympathetic trunk. RLA crosses the ninth cranial nerve, drops ventrally, is pierced by a branch of the vagal trunk with no exchange of fibers. This vagal branch passes directly laterally, then ventrally across the base of the opercular spine and innervates skin down as far as the branchiostegal rays. As the main trunk of RLA passes posteriorly medial to the cleithrum, the pectoral-dorsal and pelvic-anal branches arise (fig. 8). The pectoral-dorsal branch courses laterally, reaching the skin directly posterior to the cleithrum from which point it arches dorsoposteriorly towards the dorsal fin. A branch is given off which passes to the dorsal end of the pectoral fin base. The pelvic-anal branch crosses the medial side of the cleithrum and passes down the body wall medial to the base of the pectoral fin, dividing shortly beyond the cleithrum into the pelvic and anal branches. The anal branch slants towards the anal fin. The pelvic branch turns anteroventrally at the tip of the postcleithrum and courses beneath skin towards the base of the pelvic fin which it enters. A more complete description will be published elsewhere.

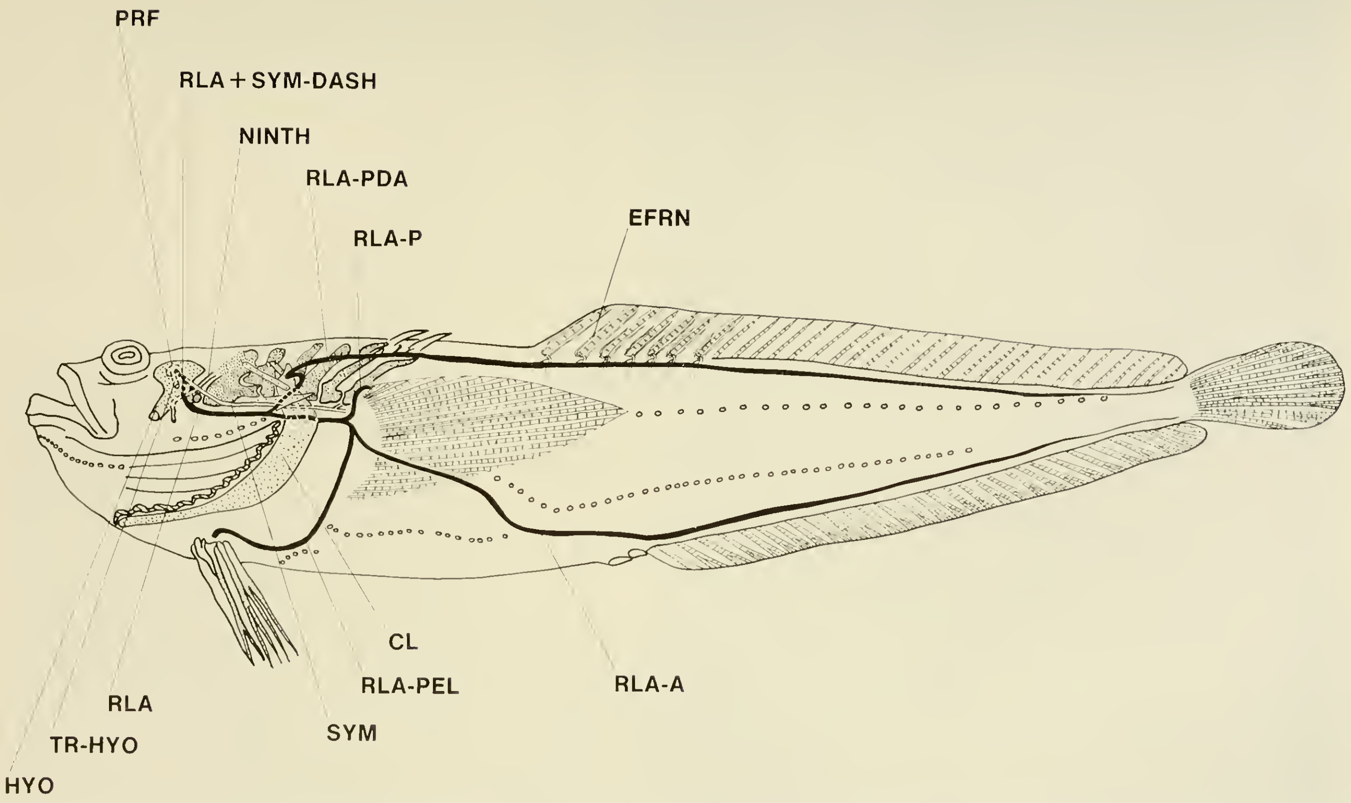

Figure 8. Pattern of ramus lateralis accessorius in *Porichthys margaritatus* (Batrachoididae). Prootic foramen shown as dashed circle medial to hyomandibular, the prootic itself being omitted. RLA + sympathetic trunk shown as dashed black line medial to hyomandibular.

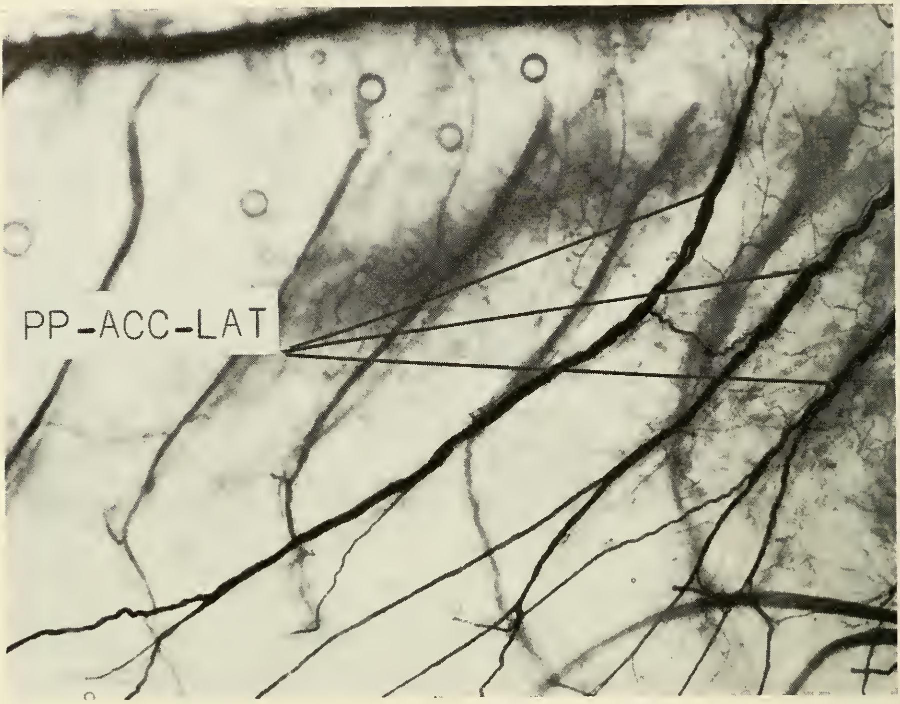

Figure 9. *Dicrolene intronigra* (Brotulidae) showing pectoral accessory lateral-line nerve (PP-ACC-LAT) and several succeeding ventral segmental accessory lateral-line branches. Nerve endings for scattered free lateralis organs visible as relatively short horizontal lines extending towards left (posteriorly) on six secondary branches of the ventral lateral-line nerves. Sihler preparation.

Pectoral-Pelvic Accessory Lateral-Line Nerves in Percopsiform, Gadoid, Ophidioid, Batrachoidid and Gobioid Fishes

Accessory, ventrally directed, segmental lateral-line nerves are poorly known in other fishes. They were known previously apparently only for the hatchetfish, *Argyropelecus* (Handrick, 1901). The account given here is brief; an extended treatment is to be published later. In *Percopsis* as in *Aphredoderus* (fig. 10, Pec-Pel ACC) a large branch is detached from the base of the ramus dorsalis of the main lateral-line nerve directly past the supracleithrum, the branch passing in the skin paralleling the cleithrum, curving anteriorly around the ventral end of the base of the pectoral fin, and sending out branches from where it begins to curve and on all the way around below the base of the fin onto the skin of the anterior surface of the muscular base of the pectoral fin. The branches radiate out towards the midventral line and the base of the pelvic fin. Two segments further posteriorly, there is another sizable but much smaller branch from

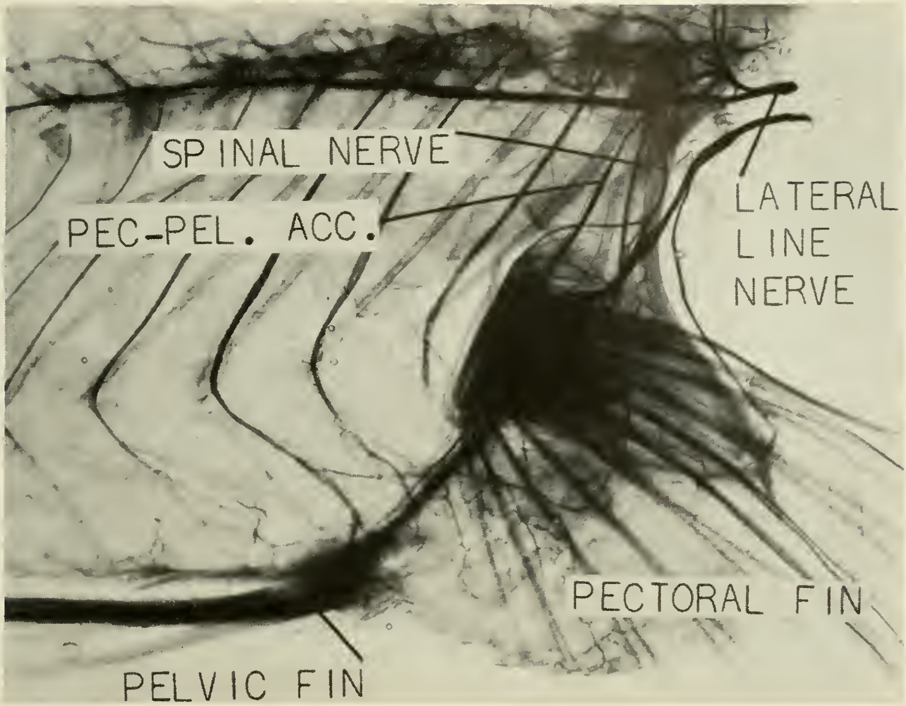

Figure 10. Pectoral-pelvic area of *Aphredoderus sayanus* showing pectoral-pelvic accessory ventral lateral-line nerve (PEC-PEL. ACC.). Another nerve appears connected to the main lateral-line nerve close to PEC-PEL. ACC. but it is a cut spinal nerve. Sihler preparation.

the ramus dorsalis of the lateral-line nerve. It passes ventrally, parallel to the large pectoral-pelvic accessory lateralis nerve but this smaller one serves mostly only skin at the ventral end of its segment. In each succeeding segment there is a similar but much smaller branch running ventrally. These lateralis branches innervate free lateralis organs scattered in the skin which are especially abundant in the area below and in front of the pectoral base and back to the pelvic base (fig. 11). The organs are borne on the scales.

The same large accessory lateralis nerve is present in *Aphredoderus*.

In the gadoid *Merluccius gayi* the segmental lateral-line nerves are present and in the same pattern as for *Percopsis* except that the anterior nerves are not enlarged.

In the brotulid *Dicrolene intronigra* (fig. 9, PP-ACC-LAT), in addition to the large first pectoral-pelvic accessory lateralis nerve, there is a second large one in the following segment and then 3 more smaller ventral lateralis nerves at about trunk segments 5, 8, and 14 and at least 4 more on the remainder of the trunk. The first and largest has a very similar course and distribution to

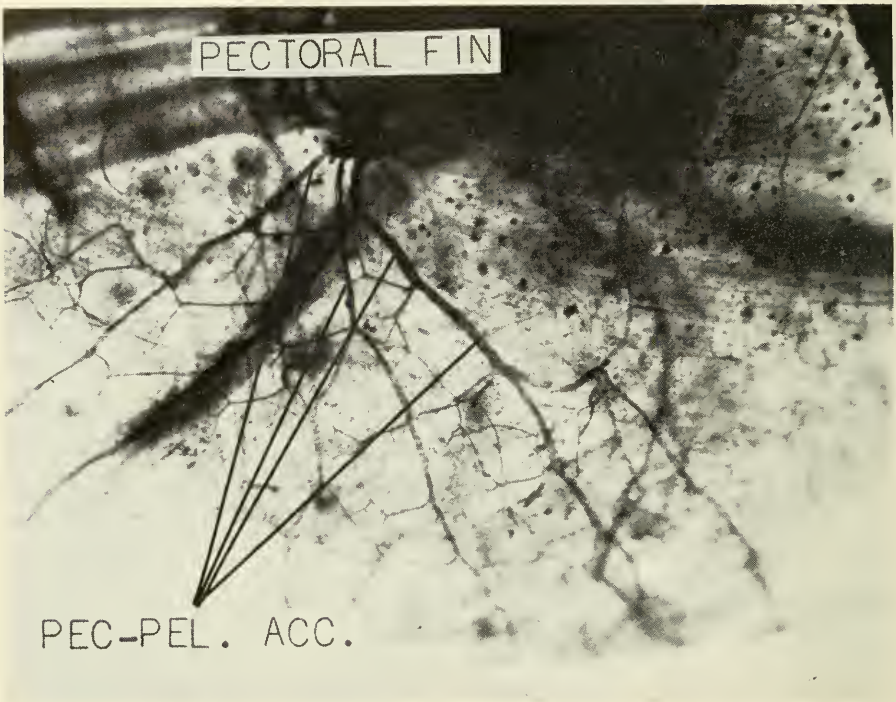

Figure 11. Detail of pectoral-pelvic accessory lateralis nerve breaking up into smaller branches below base of pectoral fin in *Aphredoderus sayanus*. Sihler preparation.

the first one in *Percopsis* except that it arises from the main trunk of the lateral-line nerve, not from the ramus dorsalis. It supplies large lateralis organs scattered in the skin ventral and anterior to the pectoral fin and up to the jugular pelvics. The second large branch passes ventroposteriorly and divides about halfway to the midventral line. The branches diverge supplying large lateralis organs in skin on the ventral body surface (fig. 9). The other branches start towards the anal fin and run horizontally at the ventral longitudinal septum supplying lateralis organs near this line.

Other brotulid genera examined showing similar pectoral-pelvic and ventral accessory lateralis nerves are *Bassozetus, Monomitopus, Monomerepus,* and *Porogadus.*

In the batracoidid *Porichthys margaritatus* a pectoral-pelvic accessory lateral-line nerve arises from the deep main trunk of the lateral-line nerve as this nerve approaches medial to the supracleithrum. Further ventrally the pectoral-pelvic accessory lateral-line nerve divides into a large branch which drops ventrally close to the posterior edge of the postcleithrum, curves anteriorly at the ventral end of the pectoral base, and supplies the ventral lateral line from a little posterior of the pectoral fin all the way to the most anterior extent of the ventral lateral line. The other smaller branch from the main pectoral-pelvic accessory lateral-line nerve passes ventroposteriorly and shortly divides into a branch that drops down to supply a segment of the ventral lateral line posterior to the pectoral fin and a branch which continues posteroventrally, joining consecutively with 2 small and 1 large branch all separated from each other by some distance where they come off the main deep lateral-line nerve. These fused longitudinal branches supply the ventral lateral line to the end of the abdominal area where additional branches from the main lateral-line nerve continue supplying the post-abdominal part of the ventral lateral line, these branches passing laterally out the horizontal septum independently of spinal rami. They leave from the deep lateral-line nerve located at the side of the vertebral column.

The ventral lateralis organs and nerves of *Dicrolene* and *Porichthys* are a very noteworthy similarity between these fishes.

In the gobies *Bathygobius lineatus* and *Acanthogobius flavimanus,* there is an accessory pectoral lateral-line nerve. In *Bathygobius* it detaches from the main lateral line midway between the location of the second and third ribs and courses ventrally close to the anterior edge of the third rib. The accessory pectoral branch innervates a row of about a dozen free neuromasts which ends at the ventral edge of the pectoral fin but 2 segments posterior to it. No other ventral segmental accessory lateral line branches were observed.

For the Gonostomatidae (*Gonostoma elongatum*) and Chauliodontidae (*Chauliodus macouni*) segmental ventral accessory lateral-line nerves extend to near the midventral line. The second such nerve is the largest and passes around the base of the pectoral fin. A single large accessory pectoral lateral-line nerve was reported for *Argyropelecus* (Sternoptychidae) by Handrick (1901). In the Osmeridae (*Hypomesus pretiosus*) a ventral segmental lateral-line nerve occurs in each body segment. The fourth and fifth are the largest and come close together as they pass anteriorly around the base of the pectoral fin. The rest form an interlocking network on the ventrolateral side where they innervate free neuromasts.

Pattern of RLA in Osmeridae

In *Hypomesus pretiosus* there is the same type of nerve as in *Percopsis* that leaves the truncus hyomandibularis and courses over the wall of the otic bulla, that is crossed by the ninth cranial nerve, that forms ganglia along its trunk, and that courses alongside the ventrolateral side of the vertebral column as far as the caudal fin.

In osmerids, however, this nerve is the sympathetic trunk and ganglia. The presence of RLA in it cannot yet be demonstrated. From leaving the truncus hyomandibularis up to halfway across the otic bulla, the sympathetic consists of 3 separated parts. Proximally, two of these parts pass anteriorly inside the

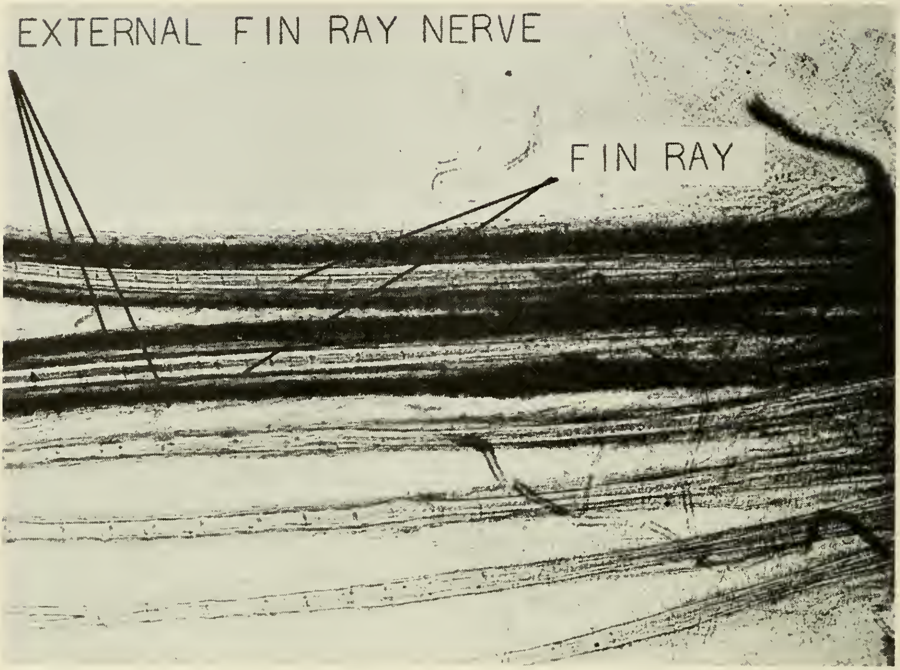

Figure 12. Pelvic fin of *Physiculus talarae* (Moridae) showing fin-ray nerves coursing external to fin rays. Sihler preparation.

cranium. They do not end in the geniculate ganglion. The third could not be followed. It is hypothesized that in some osmerid it may be found to contain RLA fibers. This prediction is based on the fact that osmerids and percopsids have both the ramus canalis lateralis system of cranial nerves as well as the pectoral accessory ventral lateralis nerves and the similar successive segmental ventral lateralis nerves for all body segments. Osmerids may be basically much like *Percopsis* and may have given rise to them.

THE RAMUS CANALIS LATERALIS SYSTEM

The ramus canalis lateralis nerves first named by Ray (1950) for the lantern fish, *Lampanyctus leucopsarus,* are here recognized as evidently a secondary system of lateralis innervation and perception that is found in numerous lower groups of fishes, the primary system being the neuromasts located in the cephalic lateral-line canals.

The ramus canalis lateralis system consists of several facialis and occasionally of one or more vagal lateral-line branches that usually course lengthwise anteriorly in the membranous roof of the cephalic lateral-line canals. Several of these canal branches radiate from a short trunk coming off the truncus hyo-

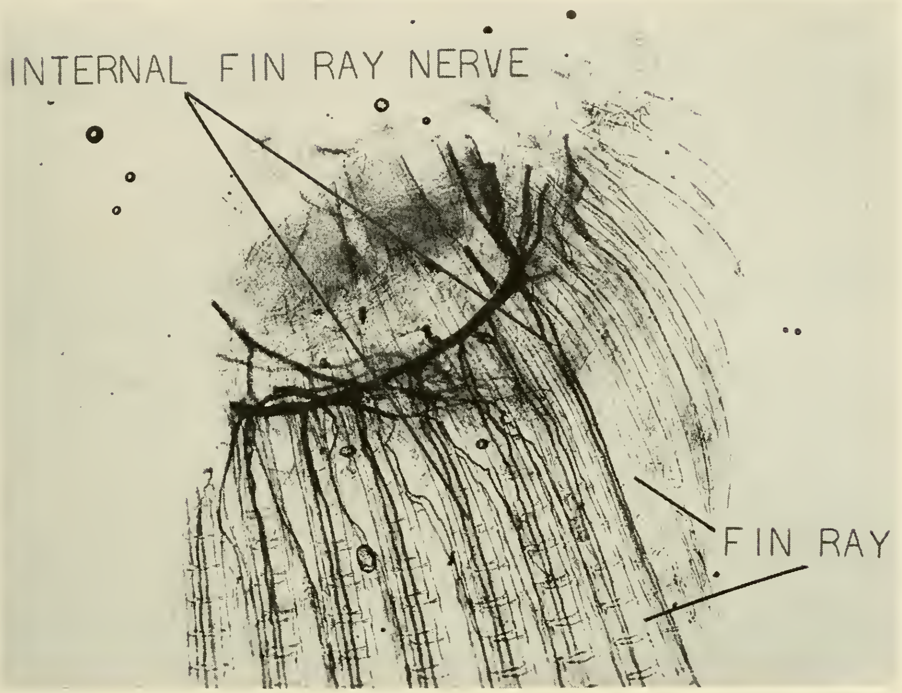

Figure 13. Caudal fin rays of *Aphredoderus sayanus* showing fin-ray nerves coursing internally down the centers of the hollow fin rays. Sihler preparation.

mandibularis close to the articulation between the opercle and hyomandibular bones. Although the system of branches looks complex (fig. 16), the presence of the system is simple to detect. If the skin is removed in the upper cheek region posterior to the eye, the most conspicuous branch will be seen. It comes up through cheek muscle close to the preopercle and runs forward beneath skin and into the cavity of the middle infraorbital bones and out along the overlying membrane of the anterior infraorbitals. This branch has been called the ramus buccalis accessorius. Branches of the canalis lateralis nerves innervate naked lateral-line organs (neuromasts) lying in the membrane roofing the canals and also innervate the same kind of organs lying in skin adjacent to the canals if such organs are present. The ramus canalis nerves do not supply the neuromasts (seismosensorial organs) lying in the floor of the head canals. The branches of the ramus canalis system appear to have great taxonomic importance. Patterns vary with different groups of fishes or are the same or similar for other groups. As far as presently known, these nerves are found only in certain fish groups of lower taxonomic placement; that is, not in the Perciformes or higher orders, or if they are, then the classification of such fishes should be questioned.

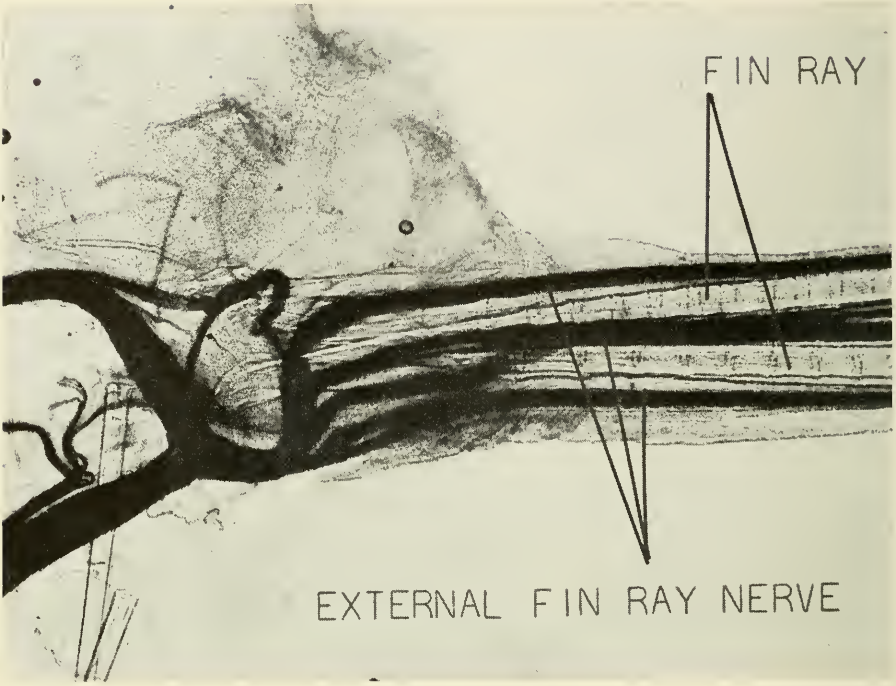

Figure 14. Pelvic fin of *Brotula clarkae* showing fin-ray nerves coursing external to fin rays. Sihler preparation.

The descriptions which follow are brief and preliminary. The ramus canalis lateralis nerves will be given extensive treatment in a later publication. *Percopsis omiscomaycus* is used as the basic reference form to which other forms are compared. Descriptions are reduced to cover 7 rami. The basic branches and their abbreviations are as follows:

r.c. 1a = supraorbital branch.
r.c. 1b = temporal branch of r.c. 1a.
r.c. 2 = anterior infraorbital branch plus dorsoanterior dentary and rictus branches.
r.c. 3 = posteroventral dentary branch plus rictus branches.
r.c. 4a = preopercular branch.
r.c. 4b = medial preopercular-mandibular ridge prolongation of r.c. 4a.
r.c. 5 = supratemporal branch.
r.c. 6 = posterior infraorbital branch.
r.c. 7 = branch from r.c. 4 arching dorsoposteriorly from operculum to anterior end of dorsal fin.

Some patches of naked lateralis organs are supplied by nerve fibers that course indistinguishably with the supraorbital and infraorbital trunks. These fibers are not considered further in the present report although they probably are part of the same system of nerve fibers as are the ramus canalis lateralis nerves.

Ramus Canalis Lateralis System in Percopsidae

The branches of the ramus canalis lateralis system for *Percopsis omiscomaycus* are shown in figure 15. Branches r.c. 1 through r.c. 5 are present and well-developed. No group other than the percopsiform fishes yet examined has branch r.c. 4b, the extension of r.c. 4a into the medial preopercular-mandibular ridge. The approximate distribution of the naked lateralis organs supplied by the ramus canalis lateralis system of the head is also depicted in figure 15. The branches are closely similar for the Aphredoderidae.

Ramus Canalis Lateralis System in Myctophidae

The ramus canalis lateralis nerves have been reported only in *Lampanyctus* (see Ray, 1950). A more complete description of them is given in figure 16 of the present work. The skin in lantern fishes is often damaged in capture. Complete descriptions of the nerves and the distribution of the organs they innervate therefore await specimens with nearly intact skin and organs.

Branch r.c. 1a is basically the same in both *Percopsis* and *Lampanyctus* except that the temporal branch, r.c. 1b, is absent in the latter. Branch r.c. 2 is essentially the same also if allowance is made for the very large mouth in *Lampanyctus*. Branch r.c. 3 is basically like that in *Percopsis,* but comes off the truncus hyomandibularis further down in *Lampanyctus*. Likewise for r.c. 4, except r.c. 4 is not prolonged into the medial preopercular-mandibular ridge, as is branch r.c. 4b. Branch r.c. 5 innervates the temporal and posttemporal canal membrane in *Lampanyctus,* a difference from what r.c. 5 innervates in *Percopsis,* where it supplies a patch of organs medial to the small supratemporal canal bone.

Ramus Canalis Lateralis System in Apogonidae

Free or naked neuromasts, all over the head in *Apogon,* are randomly but densely distributed on the snout, becoming progressively arranged in definite rows posteriorly.

Branch r.c. 1 seems to be basically the same as in *Percopsis* with both similar "a" and "b" branches (fig. 17). Branches r.c. 2 and r.c. 3 arise together as a main unit from the truncus hyomandibularis, whereas in *Percopsis* these branches arise separately. This origin of r.c. 2 and 3 as a common trunk would seem to explain the fact that r.c. 2 has no visible branch to the lower jaw as in *Percopsis*. That is, since r.c. 2 and r.c. 3 have a common trunk going back to the truncus hyomandibularis, it would seem likely that the part of r.c. 2 that

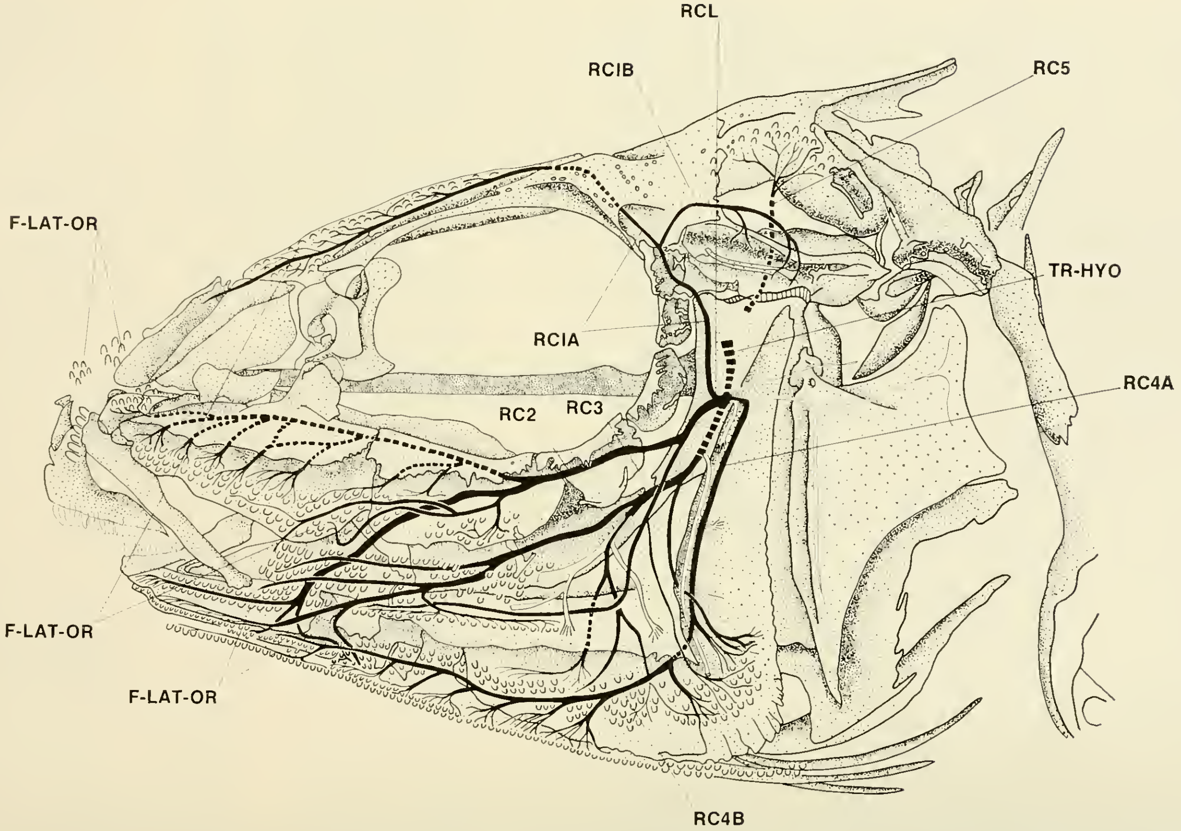

Figure 15. *Percopsis omiscomaycus* (Percopsidae) showing branches of ramus canalis lateralis system. Most of truncus hyomandibularis is omitted. See list for abbreviations.

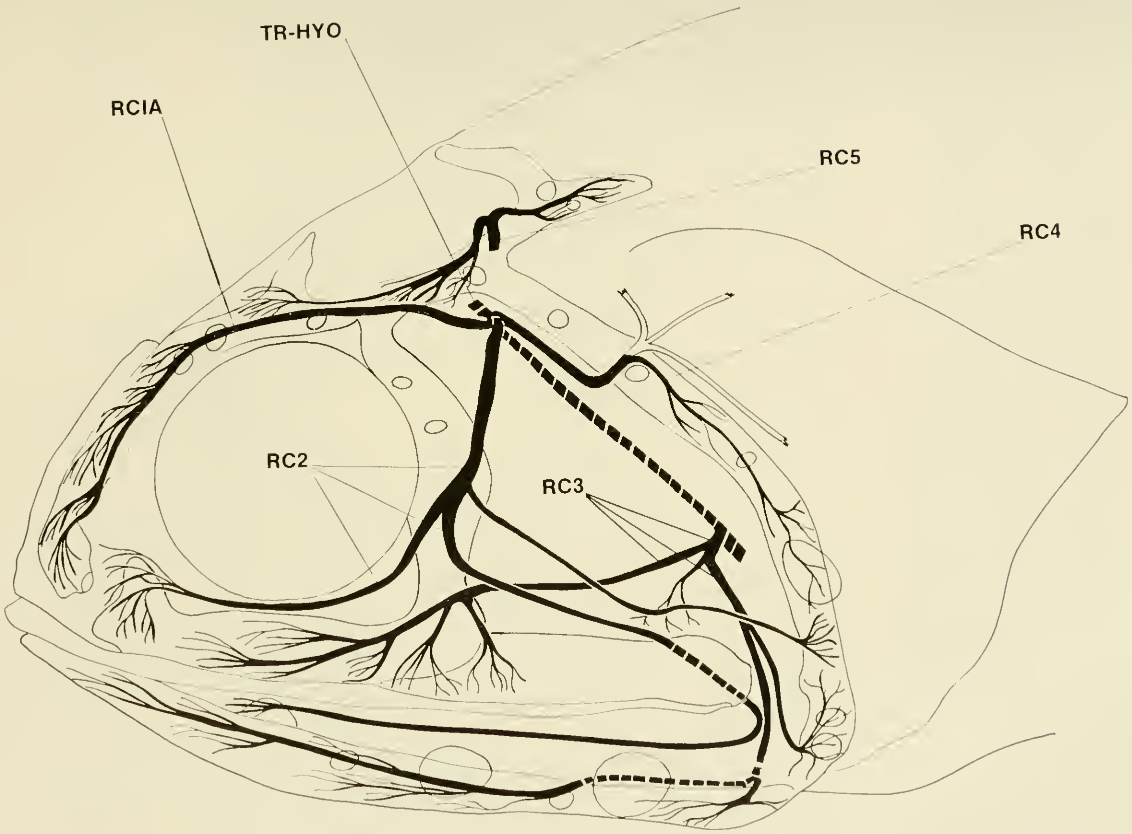

Figure 16. *Lampanyctus leucopsarus* (Myctophidae) showing branches of ramus canalis lateralis system. Most of truncus hyomandibularis is omitted. See list for abbreviations.

goes to the lower jaw as a separate branch in *Percopsis* would remain bound in *Apogon* with r.c. 3 which also goes to the lower jaw. Branches which go to the part of the preopercular canal that lies in the angle of this bone detach in *Percopsis* from the truncus hyomandibularis, but they detach from r.c. 3 in *Apogon.* Branch r.c. 4 is as it is in *Lampanyctus;* that is, without the extension of r.c. 4b. Branch r.c. 5 is similar to that of *Percopsis.* Branch r.c. 6 is apparently not represented in *Lampanyctus* or *Percopsis.* The branches in *Apogon* are in some ways more like those in *Lampanyctus* and in others more like those in *Percopsis. Synagrops bella* has a large branch r.c. 3 and branch r.c. 5 but apparently no r.c. 1 or r.c. 2 or r.c. 4. *Epigonus robustus* has a smaller r.c. 3 than has *Synagrops* but apparently none of the other independent rami.

Ramus Canalis Lateralis System in Neoscopelidae

On *Scopelengys tristis* (fig. 19) free neuromasts are variously arranged in short and long rows on all parts of the head. The pattern of the branches of the ramus canalis lateralis system in *Scopelengys* is closest to that of *Lampanyctus* but with differences. Closely similar are branches r.c. 1a and r.c. 2 in *Percopsis, Lampanyctus* and *Scopelengys.* Branch r.c. 3 has a distinctive branch, r.c. 3a, that goes to the membrane of the infraorbital canal lying above the posterior end of the maxillary ramus. The same branch is present in *Lampanyctus.* Branch r.c. 3b detaches from the truncus hyomandibularis further distally. *Scopelengys, Lampanyctus,* and *Apogon* all agree in having all of branch r.c. 3 come off the truncus hyomandibularis as one branch, whereas in *Percopsis* several smaller branches supplying the angle of the preopercular canal detach from different points of the truncus hyomandibularis. In *Scopelengys* branch r.c. 1b detaches independently from r.c. 1a, and branch r.c. 3c, not found in the others, detaches from the common trunk of the ramus opercularis superficialis facialis. No branches associated with the ramus supratemporalis vagi were observed. *Neoscopelus* differs interestingly from *Scopelengys* in having r.c. 7 which extends in an arch from near the opercular articulation dorsoposteriorly back to the anterior end of the dorsal fin, decreasing in size and ending there.

Ramus Canalis Lateralis System in Melamphaidae

Only one specimen of *Melamphaes* species prepared by the Sihler technique was available. Free neuromasts are extremely abundant on the head, especially in the membranous roofs of the cephalic canals as in *Lampanyctus.*

The ramus canalis lateralis nerves are thin. Branches r.c. 1a, r.c. 1b, and r.c. 2 are present. No independent r.c. 3 was observed. Branch r.c. 3 runs with the ramus mandibularis facialis to the lower jaw as part of the latter. Branch r.c. 4 extends at least halfway down the preopercular canal. No branch r.c. 5 was observed.

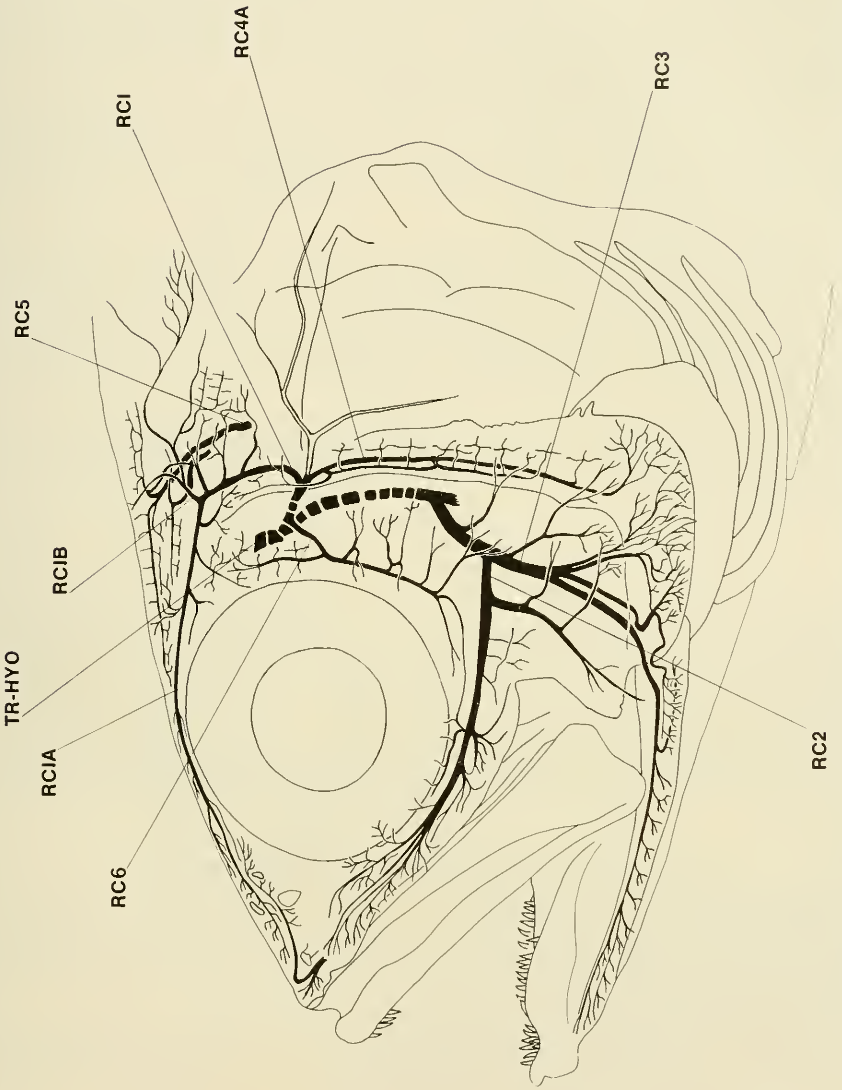

Figure 17. *Apogon astradorsatus* (Apogonidae) showing branches of ramus canalis lateralis system. See list for abbreviations.

Ramus Canalis Lateralis System in Merlucciidae

In *Merluccius gayi* branch r.c. 1 does not come off the truncus hyomandibularis as a separate branch at the same point that the ramus opercularis superficialis facialis does in *Percopsis*. Instead it detaches from the truncus supraorbitalis together with the branch that supplies the third neuromast from the posterior end of the supraorbital canal. From there on it runs separately in the membranous roof of the canal to its anterior end.

Branch r.c. 2 detaches from the truncus hyomandibularis high up on the cheek. It has two divisions: one to the membranous roof of the infraorbital canal all the way to its anterior end and one to the membranous roof of the mandibular canal up to its anterior end.

Branch r.c. 3 runs in common with, then separates from, r.c. 2, and goes to the lower jaw, giving off en route a branch to the angle of the preopercular canal roof and to a long horizontal row of organs located midway up the cheek. The rest of r.c. 3 innervates the posterior end of the mandibular-articular part of the canal membrane and extends along the membranous roof of the canal to its anterior end.

Branch r.c. 4 detaches from the ramus opercularis superficialis facialis and runs ventrally down the membranous roof of the preopercular canal to the angle of this canal.

Ramus Canalis Lateralis System in Brotulidae

In *Dicrolene intronigra* one large branch of the ramus canalis lateralis system is present. The first branch detached from it is small and passes to the infraorbital canal below the eye and ends there. The remainder passes to the lower jaw, giving off branches en route supplying large free neuromasts lying near the angle and horizontal arm of the preopercle, the rest supplying free neuromasts on the membranous roof of the mandibular canal extending almost to its anterior end.

Ramus Canalis Lateralis System in Osmeridae

The distribution of free neuromasts for *Hypomesus pretiosus* (fig. 18) is generally over all of the head even on the maxillary and supramaxillary and on exposed branchiostegal rays as well as on the membranes of all the fins and on the leading edges of the pectoral, pelvic, dorsal, and anal fins.

Branch r.c. 1a and r.c. 1b are both large and long. Branch r.c. 1b arches posteriorly all the way to the segment of the lateral-line canal attached to the supracleithrum. Branch r.c. 1a extends to the nasal canal.

Branch r.c. 2 runs along the infraorbital canal to its anterior end and detaches a branch which drops vertically down across the cheek to the canal of the horizontal arm of the preopercle. There is no independent branch of r.c. 3

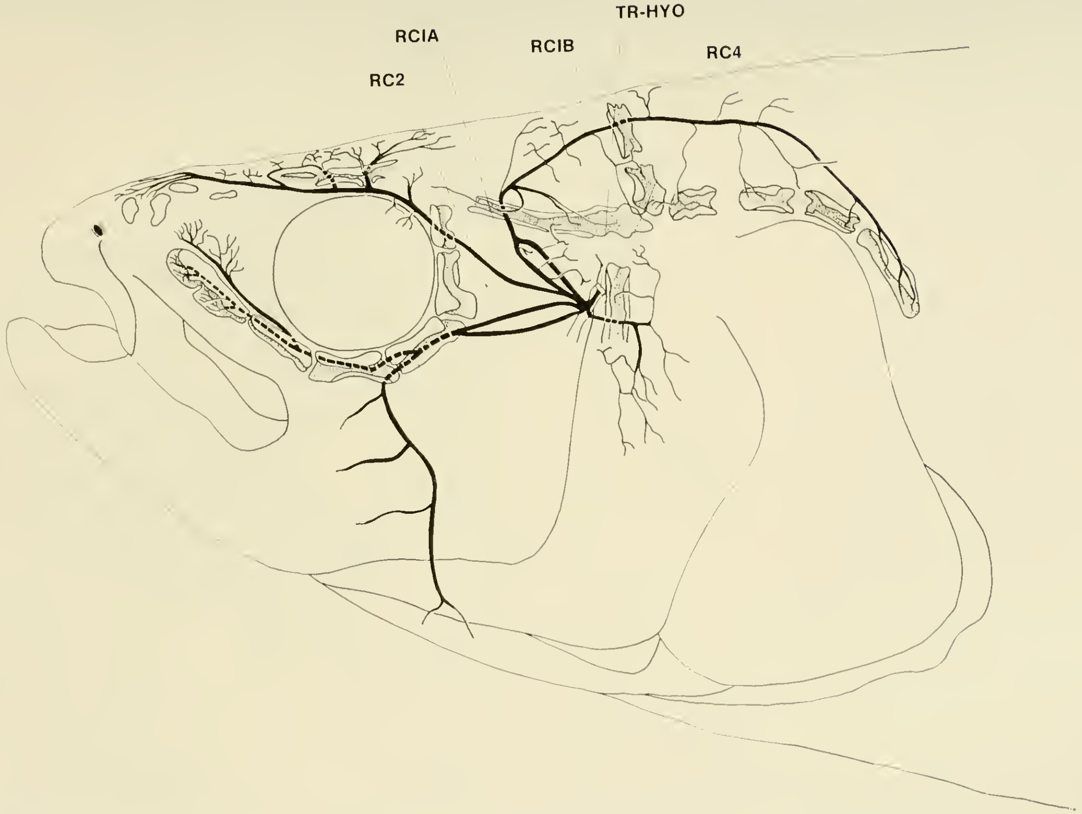

Figure 18. *Hypomesus pretiosus* (Osmeridae) showing pattern of ramus canalis lateralis nerve. Sihler preparation. See list for abbreviations.

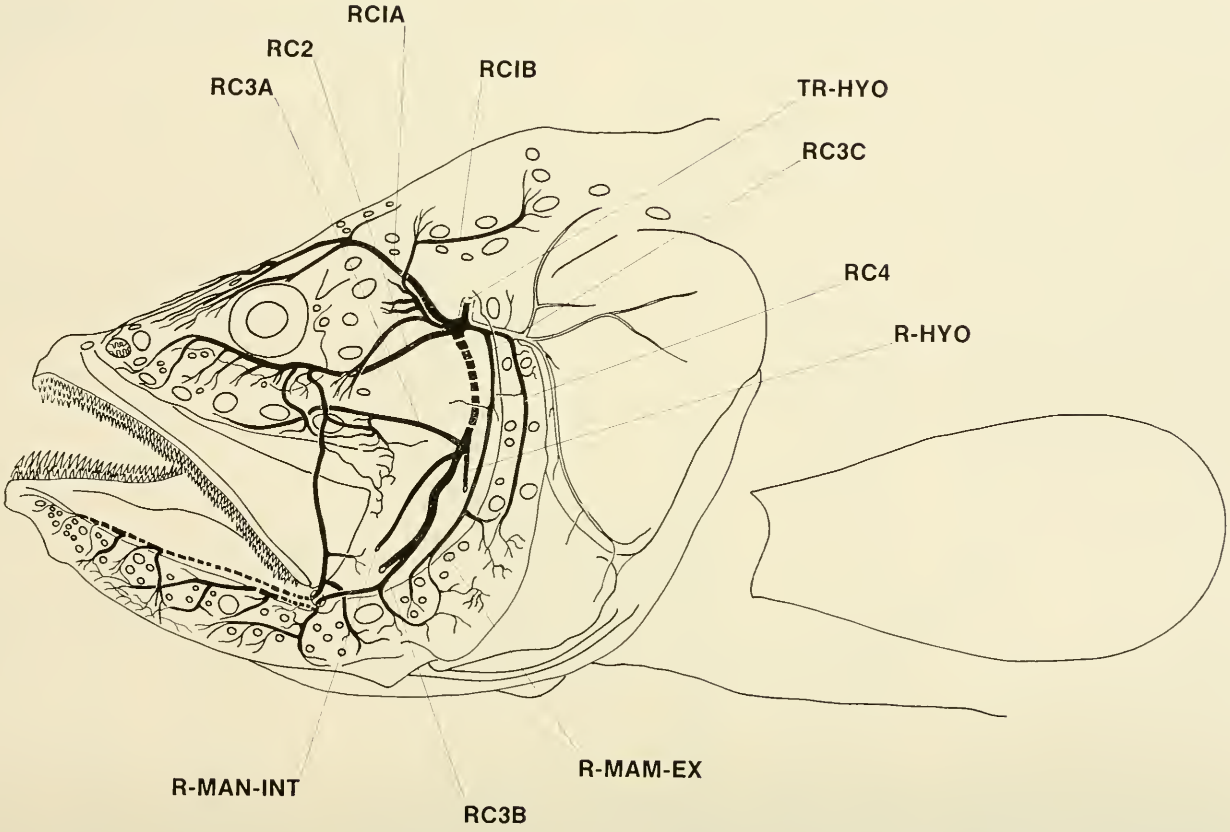

FIGURE 19. *Scopelengys tristis* (Neoscopelidae) showing pattern of ramus canalis lateralis system. See list for abbreviations.

to the lower jaw. Branches innervating free neuromasts of the preopercular-mandibular canal detach from the ramus mandibularis facialis to the lower jaw.

Practically the same pattern is present in *Spirinchus thaleichthys* and *Thaleichthys pacificus* as seen from dissections on alcoholic specimens; the same holds for *Bathylagus alascanus.*

Ramus Canalis Lateralis System in Gobiidae

In *Bathygobius lineatus* as in all gobioids there are various rows of free neuromasts associated with most of the cephalic head canals. These are innervated by several branches of what evidently is the ramus canalis lateralis system. Branch r.c. 1 is short, extending only from where the superficial opercular facial ramus passes onto the operculum and on up the dorsal end of the preopercle, ending at the posterior end of the temporal canal. The shortness of r.c. 1 reflects the fact that there are no free neuromasts for the supraorbital canal except at its anterior end.

Branch r.c. 2 is the main independent branch of the ramus canalis system that is present. At the point where the superficial opercular facial ramus detaches from the truncus hyomandibularis, the first branch of r.c. 2 also detaches and innervates a long line of naked neuromasts extending from just posterior of the eye to a little below the middle of the eye. A row lies some distance dorsal to this row and another somewhat below this dorsal row that together form a somewhat continuous row innervated by several branches from the truncus infraorbitalis. The main part of r.c. 2 continues forward beneath the skin innervating the ventralmost row of free neuromasts lying below the eye and in the area of the infraorbital canal. The row ends some distance anterior and dorsal to the rictus of the jaw. The main branch of r.c. 2 next detaches 2 branches that supply a row of free neuromasts that lie along the lateral (or dorsal) edge of the preopercular-mandibular canal, beginning with the angle of the preopercle and continuing forward as far as the angular bone. A row of free neuromasts lying along the medial edge of the same length of canal is supplied by branches from the ramus mandibularis facialis. Shortly before the rictus of the mouth, branch r.c. 2 divides. The smaller part innervates the remainder of the row of free neuromasts already mentioned that ends shortly beyond and above the rictus. The larger part of r.c. 2 passes ventrally around the rictus of the mouth and onto the lower jaw where it extends anteriorly to near the symphysis innervating a long row of free neuromasts lying on the lateral or dorsal edge of the mandibular canal. The row of larger organs extending along the medial edge of the mandibular canal is supplied by branches from the ramus mandibularis facialis.

Branch r.c. 4, or what appears comparable to it, has two main parts. One continues posteriorly about on the level of the horizontal rib of thickened reinforcement bone of the opercle and supplies a row of 24 organs on the posterior third of the opercle. The larger part of branch r.c. 4 passes down the posterior edge of the preopercular canal or close to it, out onto the ventral end of the preopercle and supplies a long vertical row of free neuromasts.

Branch r.c. 5 of the ramus supratemporalis vagi innervates free organs along the posttemporal and supratemporal canals and another branch passes forward supplying the temporal canal.

Ramus Canalis Lateralis System in Cyprinidae

Manigk (1934, fig. 1) reports for *Phoxinus laevis* a nerve which he calls the ramus buccalis accessorius that apparently belongs to the ramus canalis lateralis system but which has important differences from the patterns seen in the Percopsidae, Myctophidae, Osmeridae, Apogonidae, and Gobiidae. The pattern in the Cyprinidae differs in that (1) the rami do not course in the membranous roof of the cephalic lateral-line canals; (2) there is only one distinct branch, r.c. 2; and that (3) branch r.c. 2 does not have a ramus going to the lower jaw as occurs in all other families except the most generalized, the Osmeridae.

Ramus Canalis Lateralis System in Other Families

Other families among those examined having the ramus canalis lateralis system are, in the Salmoniformes, the Esocidae, Umbridae, Gonostomatidae, Sternoptychidae, Chauliodontidae, Alepocephalidae, and Chloropththalmidae; in the Beryciformes, the Trachichthyidae, Berycidae, Polymyxiidae, and Holocentridae. The Umbridae have r.c. 1, r.c. 2, r.c. 4, and r.c. 5. The pattern in *Gonostoma elongatum* is most like that in the Neoscopelidae and Myctophidae.

The beryciform families apparently have the ramus canalis lateralis pattern of *Melamphaes* or it is reduced.

Found not to have the system of nerves were the Amiidae; Elopidae; Clupeidae (*Clupea pallasii*); Salmonidae (*Salmo, Oncorhynchus, Coregonus*); Galaxiidae (*Galaxias*); Synodontidae; Atherinidae (*Menidia*); Plecoglossidae; Argentinidae.

EXTERNAL-INTERNAL FIN-RAY INNERVATION

So far as is known, most of the paracanthopterygian fishes have the fin-ray nerves coursing external to the fin rays, not internal in the space between the two halves of each fin ray as is true for percoid fishes and apparently for most other teleosts.

In the survey made thus far, the external position of the fin-ray nerves has been found for the codfishes, brotulids, ophidiids, zoarcids, gobiesocids, batrachoids, and ogcocephalids that have been examined. When external, the nerves course in contact with the surface of the fin ray or almost in contact. The fin-ray nerves are internal for the percopsiform fishes.

In *Gadopsis marmoratus,* a fresh-water percoid fish of Australia, in which the pelvic fins are long, narrow, and of 2 rays, similar to pelvic rays in brotulids, the huge combined spinal and RLA nerves to them course down the centers of the rays with some fibers, apparently out of physical limitation of space, coursing outside the fin rays beside the longitudinal split that exists down the two halves of each ray. The nerves of ophidiid and brotulid pelvic rays are huge also, but the nerves course entirely external to the pelvic rays. The fin ray innervation in *Gadopsis* is not ophidioid.

The fin-ray nerves are external also in the Liparidae and Cottidae (*Scorpaenichthys*). They are external also in the stichaeids (*Epigeichthys*). Thus the condition of the fin-ray nerves being external to fin rays is not unique to the Paracanthopterygii, but it is apparently a specialization within the fishes of this group. A survey for this interesting condition is being conducted with the preparation of specimens of many families by the Sihler technique in addition to some serially sectioned.

DISCUSSION

New facts presented in preceding sections have bearings on the taxonomic position and phylogenetic considerations of numerous kinds of fishes. Only some of the problems can be discussed here.

The new facts concern 4 nerve patterns: (1) the ramus lateralis accessorius (RLA); (2) the pectoral accessory ventral lateralis branch and succeeding segmental branches; (3) the ramus canalis lateralis system of nerves; (4) the external or internal innervation of fin rays.

ORIGIN OF BATRACHOIDID FISHES

The presence of greatly similar patterns in the first two of these nerve complexes in batrachoidid and percopsid fishes indicates that the batrachoidid fishes have most probably been derived from percopsid ancestors.

The patterns of RLA in *Percopsis* and *Porichthys* are similar in three important ways in that in each genus (1) RLA leaves the cranium together with the truncus hyomandibularis; (2) RLA leaves the truncus hyomandibularis bound up with the sympathetic trunk; (3) RLA courses over the wall of the otic bulla. *Porichthys* differs from *Percopsis* in that RLA departs from the sympathetic trunk shortly after the two leave the truncus hyomandibularis bound together. RLA courses across the otic bulla slightly diverging from the sympathetic. *Porichthys* differs also in its course beyond the cleithrum. In *Porichthys* RLA breaks up into the dorsal, anal, and pectoral-pelvic branches near the cleithrum, these branches going independently to their fins, whereas in *Percopsis* RLA continues along the vertebral column to the caudal fin bound to the sympathetic trunk. The pattern of RLA in *Porichthys* appears to be an intermediate stage or an offshoot development between the *Percopsis* pattern and a gadoid or ophidioid pattern.

Porichthys has a pectoral-pelvic accessory ventral lateralis nerve as has

Percopsis and also has several of the succeeding segmental ventral lateralis branches enlarged which supply sections of the ventral lateral lines. *Percopsis* lacks ventral lateral lines, having instead only scattered, free, lateralis organs mostly in the pectoral-pelvic area. *Porichthys* does not have independent branches of the ramus canalis lateralis system. It has the external rather than internal fin-ray innervation which *Percopsis* has, but, so far as is known, all paracanthopterygian fishes have the external fin-ray innervation pattern except percopsiforms.

The pattern of RLA is the most distinctive feature of similarity between batrachoidid and percopsiform fishes. It more than any other character points to a percopsiform origin for batrachoidids. Possession of accessory pectoral-pelvic and ventral segmental lateralis branches is almost as significant and also helps tie batrachoidids in turn to other lower taxonomically placed fishes having this same nerve development.

ORIGIN AND RELATIONSHIPS OF GADOID AND OPHIDIOID FISHES

There are several patterns of RLA in ophidioids indicating evolutionary divergence within the group. The pattern in the brotulid *Ogilbia* (fig. 2) is most similar to that in a gadoid such as *Physiculus* (fig. 4) being alike in all important points, especially in having two or more anal fin branches detaching from the dorsal fin branch posterior to the origin of the dorsal fin. The pattern of *Lepophidium* and of numerous other ophidioids is like that of *Ogilbia* and *Physiculus* except that the branch for the dorsal fin and that for the anal fin exit from the cranium through separate foramina some distance apart in the parietal bone. The pattern in *Brotula* is distinctive for an ophidioid or gadoid in that the pectoral-pelvic branch leaves the cranium together with the truncus hyomandibularis and then courses posteriorly, passing medial to the supracleithrum. Such a cranial exit is an important similarity to the pattern in *Percopsis* and *Porichthys*.

The presence in the brotulids *Dicrolene*, *Monomitopus*, *Monomerepus*, and *Porogadus*, of the accessory pectoral-pelvic ventral segmental lateralis nerve and several succeeding similar branches greatly similar to such nerves in *Percopsis* and *Porichthys*, is evidence also for a taxonomic and phylogenetic connection between these fishes. So is the presence in both the gadoid *Merluccius* and the brotulid *Dicrolene* of significant branches of the ramus canalis lateralis nerves, although these nerves are somewhat different in parts of their patterns from that in percopsiform fishes. The pattern of the fin-ray nerves coursing external to the fin rays in gadoids and ophidioids (as well as in all paracanthopterygian fishes except percopsiforms) is a further interesting and significant similarity when it is contrasted with the internal fin-ray innervation of percoid fishes (20 families examined) and numerous other large groups of fishes such as atherinids, cyprinodonts, salmonids and beryciforms. Other important similarities between gadoid and ophidioid fishes are (1) the large opisthotic, occupying part of the otic bulla wall, separating the prootic and exoccipital bones, and having the ninth cranial nerve exiting through it (McAllister, 1968); (2) presence of levator maxillae superioris muscle (Greenwood *et al.*, 1966); (3) a "percopsiform projection" often present on middle branchiostegal rays (McAllister, 1968).

RELATIONSHIPS OF ZOARCID FISHES

The Zoarcidae is still best placed together with the gadoids and ophidioids (Rosen, 1962; Freihofer, 1963; Greenwood *et al.*, 1966). The zoarcids have a pattern of RLA that is most like that of these fishes, especially like that of the ophidioids. Some zoarcids appear to have a remainder of the levator maxillae superioris muscle (Greenwood *et al.*, 1966). *Lycodapus* has what must be a good example of this muscle. Zoarcids have an external fin-ray innervation pattern.

Examination for RLA in *Lycodapus* has not yet been possible. Gosline (1968) has questioned the zoarcid affinities of *Lycodapus* and also tried to show that ophidioids and gadoids are not basically similar but that ophidioids are percoid derivatives. On the basis of patterns of RLA, the zoarcids most probably do not have a percoid ancestry as Gosline maintains, nor do they on the basis of ventral segmental lateral-line nerves present in zoarcids but not in percoids as far as is known.

RELATIONSHIPS AND CLASSIFICATION OF GOBIOID FISHES

Gobioid fishes show external similarities to percopsid and amblyopsid fishes. Gobioids and percopsids have weak spinous dorsal fins, rows of free lateralis organs on the head, and similar body form. McAllister (1968) lists many partial similarities between gobioids and percopsiforms and almost placed them in a relationship to the percopsiforms in his classification of teleostome fishes but could not quite do it. The problem has been that many of the similarities of gobioids to percopsiforms are halfway similarities, none being great enough to be convincing. Two important similarities of the nerves of gobioids and percopsiforms are now known. These are the presence of part of the ramus canalis lateralis system and of an accessory pectoral ventral lateralis branch. The only other spiny-rayed fishes so far known to have both of these nerve features are the Percopsiformes. This fact, plus all the other varying degrees of similarity listed by McAllister, suggests that the affinity of the gobies with the Percopsiformes is as he suspected. Examination of the opisthotic of *Eleotris fuscus* shows that it is large, separates the prootic and exoccipital, and has the ninth nerve coming out near its center. These opisthotic features in *Eleotris* are also those of gadoid and ophidioid fishes. The intermediateness of the condition of the opisthotic in *Eleotris* is suggested by the fact that the foramen for the ninth nerve on one side of *Eleotris fuscus* was connected by a long thin opening to the edge of this bone; on the other side the indentation did not reach the ninth nerve foramen.

Bathygobius lineatus shows a great reduction in lateralis organs located in the cephalic canals, only a few being present in the region of the upper preopercular and temporal canals. This may be a feature of all gobioids. The canals themselves are mostly open troughs. These features of the head canals of gobioids should have interesting ecological, behavioral, and physiological significance. Their usually small size, many lines of free lateralis organs on the head with associated near loss of canal organs, and relatively sedentary habits give credence to a depiction of gobies as microhabitat fishes.

With new nerve evidence and the many features of similarity of gobies to percopsiform fishes as given by McAllister, it seems justified to make the gobioids an order, the Gobiiformes, placed in the superorder Paracanthopterygii with closest relationships to the Percopsiformes and with other characters as given by Regan (1911) for his suborder Gobioidea.

RELATIONSHIPS AND CLASSIFICATION OF APOGONIDAE

Nerves identified as the ramus canalis lateralis system in *Apogon* (fig. 17) are strikingly similar to those of percopsiforms (fig. 15), myctophoids (figs. 16 and 19), stomiatoids, and osmerids (fig. 18). The ramus canalis lateralis system is recognized in an apparently reduced form in gadoids, ophidioids, beryciforms, and gobioids. If this system of nerves in *Apogon* is homologous with that in the other groups listed, it would be an important preperciform feature found even in salmoniforms but unknown in any perciform group except the gobioid fishes. That it is homologous in all these groups needs to be rigorously shown but judging from the similarity of the patterns illustrated in this paper I think that it is broadly homologous in these groups. It is one of the most complex and distinct system of nerves on the head. Its absence as far as known in the perciforms is explained as loss through reduction in preperciform ancestors. The system is apparently considerably reduced in beryciforms or absent in some. The great development and similarity of the canalis lateralis system in apogonids to that in *Percopsis, Scopelengys,* and melamphaeids is strong evidence for questioning the perciform character of apogonids.

There is also evidence of an apogonid-salmopercoid relationship from the otoliths. Frost's systematic statements, based as they were only on characters of the otoliths and made from study of otoliths of only certain species, have often been confusing. An example is in the salmopercoid fishes. Frost (1925) says that their otoliths "closely resemble (in some respects) those of *Ophichthys gomesii* (Apodes). —On the other hand there is a strong resemblance to those of the percoid genus *Apogon* which differs from the remainder of the percoids in the sulcus." We still do not have any other characters pointing to a systematic relationship between apodal and salmopercoid fishes but we do have an important similarity in nerves identified in both salmopercoid and apogonid fishes as belonging to the ramus canalis lateralis system. Frost (1927) also states that "the sagitta of *Apogon melanotaenia* resembles that of *Acerina* (Percidae) in the sulcus" and that the otolith of *Cepola rubescens* (Cepolidae) resembles closely that of *Apogon*. The systematic significance of these similarities remains doubtful. Without doubt, however, there is a great need for atlases of fish otoliths published family by family until all families are covered.

A reasonable alternative hypothesis suggested here to that of Regan (1913) and of Greenwood (1966) for the origin of the Perciformes is that the percopsiforms gave rise to lines leading to both the Paracanthopterygii and the Acanthopterygii. In this hypothesis apogonids could lie on one of the lines tending towards the percoid expression. It is suggested that the Apogonidae be tried in a preperciform position in an experimental classification as a suborder of beryciform fishes allied to percopsiform fishes as all beryciforms may be so allied.

ORIGIN OF PERCOPSIFORM FISHES

Several important facts point to an origin of the percopsiform fishes from the salmoniforms, in particular, from the Osmeridae. The hypothesis in Greenwood *et al.* (1966)[1] leaves room for other possibilities.

The fact most weakening to the Greenwood hypothesis is that the nerve evidence in the descriptive section of the present paper indicates a percopsiform origin for the batrachoidids, gadoids, and ophidioids. In the Greenwood hypothesis, these fishes, including the percopsiforms, are each independently derived from a neoscopelid-like ancestor (e.g., *Sardinioides*), which in turn is derived from myctophoids.

In the percopsiform hypothesis, the myctophid and neoscopelid-like fishes evolved from a common ancestry with percopsiform fishes. Weitzman (1968) has shown osteologically that the origin of stomiatoid fishes evidently is in the Osmeridae. With present knowledge of the nerves, an osmerid ancestry is also hypothesized for the percopsiform fishes. The osmerids have a more generalized pattern of the ramus canalis lateralis system and also of the pectoral accessory ventral lateralis nerves and succeeding ventral segmental lateralis branches. Neither of these systems of nerves is present in the Salmonidae or Plecoglossidae as far as known. The Osmeridae are completely generalized in their freshwater-saltwater tolerance, a fact that a basal ancestral group for such a radiation should be expected to have. An observation of osmerid otoliths by Frost (1925) is of greater interest now. Frost said "In *osmerus eperlanus* . . . . there is a distinct advance in this form (of the otolith) towards those observable in later groups, notably the berycoids."

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[1] The important paper of Rosen and Patterson, *The structure and relationships of the paracanthopterygian fishes*, Bulletin of the American Museum of Natural History, vol. 141, art. 3, pp. 357–474, came too late (July, 1969) to be used.

The ramifications of the percopsiform hypothesis are shown in figure 20.

No RLA is yet known for the osmerids nor for the suborder Myctophoidei nor is the pectoral accessory lateralis or succeeding segmental branches present in the myctophoids, *Lampancytus* and *Scopelengys*. The ramus canalis lateralis system apparently is not present in *Aulopus, Harpodon,* and *Synodus.*

In the words of its original describer, Louis Agassiz, no better candidate exists among known teleosts for being "a true intermediate type between Percoids and Salmonidae than my *Percopsis*" . . . . as it "shows peculiarities which occur simultaneously in the fossil fishes of the chalk epoch, which however soon diverge into distinct families in the tertiary period, never to be combined again" (Agassiz, 1850).

Aphredoderus also is important in this picture but must be taken up in a later paper.

SUMMARY OF SYSTEMATIC RESULTS

Various combinations of four general features of the nerves plus some specific nerve characters were used to arrive at the systematic interpretations discussed above and summarized below. The nerve complexes are (1) the ramus lateralis accessorius (RLA or recurrent facial nerve), (2) the ramus canalis lateralis facialis system, (3) the ventral segmental lateral-line nerves of the trunk, and (4) the external or internal pattern of fin-ray innervation. The systematic results are as follows:

(a) Ophidioid relationships lie with gadoid fishes as advocated by Rosen and his coworkers (1962, 1966, 1969) and Freihofer (1963), not with blenniid-like perciforms. More complete descriptions in the present paper of RLA in these fishes show patterns of RLA to be more important systematically and more alike in these groups than was first thought. Possession of the ramus canalis lateralis facialis system and of ventral segmental lateral-line nerves in gadoids and ophidioids add strong support to the gadoid placement of the ophidioids. Both groups have the external pattern of fin-ray innervation.

(b) Specific relationship of ophidioids with percopsids is shown by cranial exit of RLA through the facial foramen beside the truncus hyomandibularis in *Brotula* and *Percopsis*. Similar cranial exit is known for *Anguilla,* the cobitid *Nemacheilus,* and the goatfish *Parupeneus,* but it is considered convergent in these groups. Doubt about the percoid affinities of the peculiar goatfishes is raised. Presence also of both the ramus canalis lateralis facialis system and of ventral segmental lateral-line nerves in the brotulid *Dicrolene,* and of the latter system and probably the former system also in the brotulids *Monomitopus, Monomerepus,* and *Porogadus,* are important nerve features found also in stomiatoid, myctophoid (only the ramus canalis lateralis system), and osmerid fishes but of neither system in salmonid fishes as far as known.

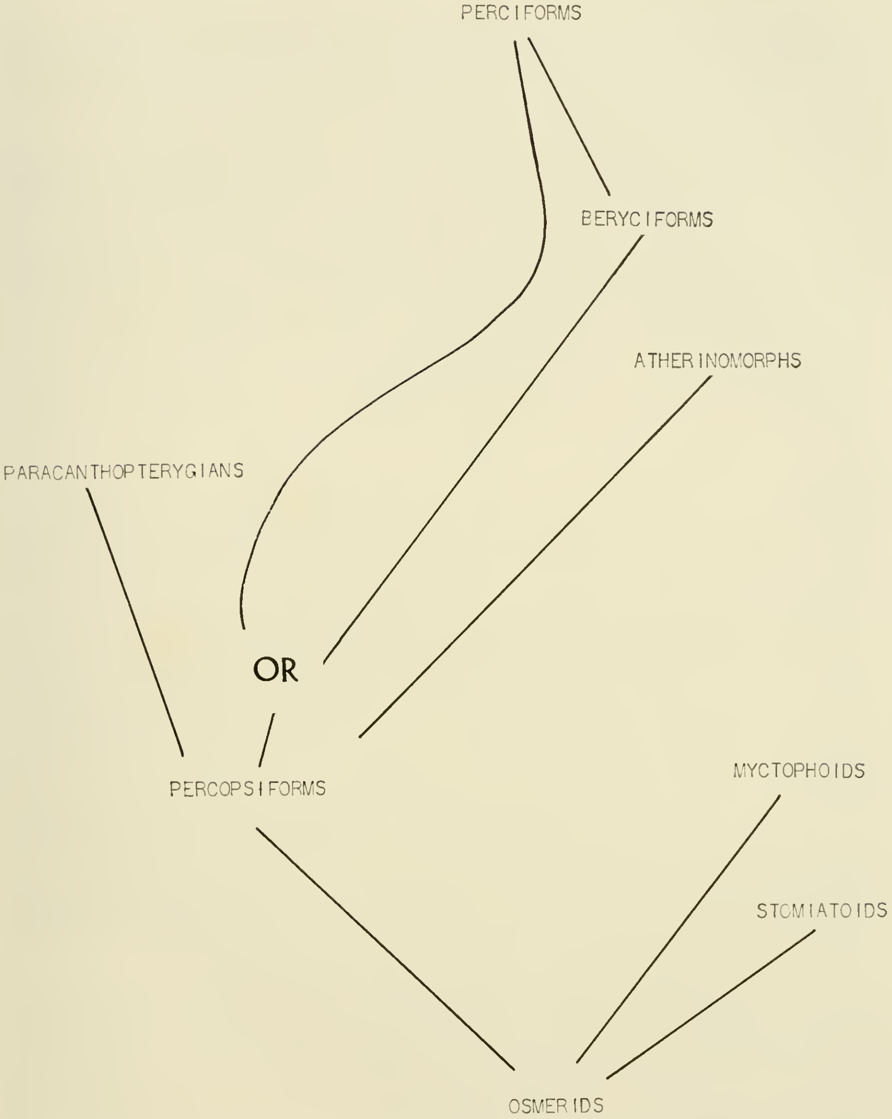

Figure 20. Scheme of possible relationships of percopsiform fishes. Two alternative hypotheses of relationship to perciforms are shown, one direct and one by way of the beryciforms.

(c) Gadoids have an affinity with percopsids as shown by the presence in *Merluccius* of both the ramus canalis lateralis facialis system and of ventral, segmental lateral-line nerves on the trunk, the latter more generalized in *Merluccius* than in *Percopsis*.

(d) Batrachoidids have an affinity with percopsids. *Porichthys, Percopsis,* and Amblyopsids are the only fishes known to have RLA leave the cranial cavity through facial foramen and bound with the trunk of the sympathetic nervous system. *Porichthys* possesses ventral segmental lateral-line nerves but in a more specialized condition than in *Percopsis.*

(e) Amblyopsids have a closer affinity with percopsids than with *Aphredoderus.* Pattern of RLA in *Percopsis* is found also in *Chologaster* and *Porichthys.* It is judged more primitive than the pattern in *Aphredoderus,* a pattern much different from that in *Percopsis* and more like that found in gadoids, ophidioids (except for the percopsid-like cranial exit in *Brotula*), and higher fishes.

(f) A percopsid-like ancestry is hypothesized for batrachoidid, gadoid, and ophidioid fishes based on evidence from the nerves.

(g) RLA in *Percopsis, Porichthys,* and *Physiculus* are described for the first time.

(h) Pattern of RLA in Macruridae is more like that in Moridae than in Gadidae.

(i) Pattern of RLA in *Ogilbia* and *Dinematichthys* resembles that in Moridae and Gadidae more than does RLA pattern in other brotulid and ophidiid fishes. *Ogilbia* and *Dinematichthys* and related genera merit familial rank.

(j) A well developed ramus canalis lateralis facialis system is present in osmerids, stomiatoids, myctophoids, percopsiforms, gadoids, ophidioids, and batrachoidids; reduced patterns are present in berycomorphs; the system is absent in advanced paracanthopterygians and in perciforms, except in gobioids and apogonids.

(k) Ventral segmental lateral-line nerves are present in osmerids, stomiatoids, percopsiforms, gadoids, batrachoidids, ophidiids, zoarcids, and gobioids.

(l) Presence of ventral segmental lateral-line nerves in zoarcids is strong evidence for continued placement of zoarcids close to gadoids and ophidioids. Zoarcids also have the external pattern of fin-ray innervation.

(m) External pattern of fin-ray innervation is found only in certain groups: all paracanthopterygian fishes, except percopsiforms and gobiiforms (placed in Paracanthopterygii in present paper); scorpaenids, cottids, liparids, stichaeoids. The survey is incomplete. Apparently most fishes have internal pattern of fin-ray innervation. Presence of the external pattern in nonparacanthopterygian fishes is considered convergent.

(n) Osmerids have the ramus canalis lateralis facialis system and ventral segmental lateral-line system in the most generalized state but have no RLA. Stomiatoids have the first two systems and lack RLA as far as known. Salmonids, aulopids, and synodontids lack all three systems so far as known. It is hypothesized that percopsids have an osmerid ancestry.

(o) Apogonids may be quasi-percoid. They possess a well developed non-perciform ramus canalis lateralis facialis system. It is proposed that they be placed with the beryciforms as a percopsid offshoot.

(p) Nerves identified as belonging to the ramus canalis lateralis system have been found in gobioid fishes. One anterior nerve identified as belonging to the ventral segmental lateral-line system known elsewhere only from preacanthopterygian fishes has also been identified in gobioids. These two systems are known to occur together in spiny-rayed fishes only in percopsiforms. These important similarities of the nerves, together with those summarized by McAllister (1968), add strongly to his suggestion that these fishes should stand in systematic relationship to the percopsiform fishes. It is proposed they be given ordinal status, the Gobiiformes, with characters as given in McAllister (1968), Regan (1911), and with the nerve and sensory canal features given in the present paper.

ADDENDUM

The excellent paper by Rosen and Patterson (1969) on the structure and relationships of paracanthopterygian fishes was received too late to be of use in the present study. The systematic results in both papers are mostly in agreement. Four differences are noted. One is the addition of gobioid fishes to the Paracanthopterygii. Rosen and Patterson state that they could not find any other group that should be included. Gobioids lack the caudal fin structure of percopsiforms but some (*Dormitator* and *Gunnellichthys*) have what may be a levator maxillae superioris muscle (W. Eschmeyer, unpublished information). So do the Sciaenidae, but here it is evidently convergent. The Gobiesocidae have neither of these features but are included by Rosen and Patterson on other evidence. The gobies qualify by the nerves and numerous other similarities to percopsids which together add weight to an argument for percopsid relationships. Another difference concerns the placement of the Amblyopsidae. Rosen and Patterson put them in the same suborder with the Aphredoderidae. The occurrence of the same unique pattern of RLA in both the Amblyopsidae and Percopsidae, and of a very different pattern in *Aphredoderus* resembling those of other paracanthopterygians and of acanthopterygians, would seem to outweigh the similarities Rosen and Patterson used for their placement of amblyopsids. The question needs further study. Maybe no suborders are needed here. Another difference concerns the origin of the Paracanthopterygii, needless to say a difficult question on which to have good information. In the present paper an osmerid ancestry is hypothesized for the percopsiforms. Rosen and Patterson thought (as of going to press in 1969) that important parallel developments of myctophoids to paracanthopterygians and acanthopterygians do not indicate that paracanthopterygians originated from myctophoid fishes. They give these three groups superordinal rank representing three "parallel radiations into a neoteleostean grade" (Rosen and Patterson, 1969). They state further that "polymixioids can tentatively be viewed as the closest relatives of the paracanthopterygians." Figure 20 of the present paper agrees in general with their superordinal relationships but it shows a percopsiform ancestry for the acanthopterygii and an osmerid ancestry for the percopsid fishes. Nerve evidence and an intuitive finger point in an osmerid direction. In the search for percopsiform ancestors the guidelines of levator maxillae superioris muscle and percopsiform caudal fin structure break down. New guidelines have to be looked for and followed. These at present are nerves. An exciting problem emerges as to what living fishes may be closest to the ancestors of the percopsids.

A final point of difference to be mentioned is that Rosen and Patterson suggest that primitive percopsiforms had sensory head canals enclosed in bone and spinous suborbitals and preopercle and that these features were reduced and lost in paracanthopterygian but not acanthopterygian derivatives. Their evidence for these assumptions is slim. An osmerid ancestry makes it unnecessary to build closed canals. None of the percopsiform fishes living or fossil, have enclosed canals except for a very small part at the posterior end of the supraorbital canal in *Percopsis*. Osmerids have open canals in all bones; smooth suborbitals, lacrymal, and preopercle; an antorbital; an adipose fin; the ramus canalis lateralis system less specialized; and ventral segmental lateralis nerves less specialized than in *Percopsis*. Closed and spinous canals would have come afterward in percopsiform lines leading to beryciform fishes.

Evidence in support of the Paracanthopterygii is now substantial and comes from bones, muscle, nerves, and fossils. It provides new understanding of fish evolution. We should thank Dr. Rosen and his coworkers for their achievements.

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LIST OF ABBREVIATIONS

BBP.—branch from brachial plexus.
BDL-L.—Baudelot's ligament.
BLLOV.—branch to lateral-line nerve and opercular nerve of vagus.
B-OCC.-SP-CO.—branches to occipito-spinal complex.
BVSR.—branch to ventral spinal ramus.
CL.—cleithrum.
CM.—cartilaginous membrane.
DRSN.—dorsal ramus of spinal nerve.
EFRN.—external fin-ray nerve.
F-LAT-OR.—free, naked lateralis organ.
FDR-OCC-SP.—first dorsal ramus of occipito-spinal complex.

FR.—fin ray.
GG.—geniculate ganglion.
HYO.—hyomandibular.
IDR-OCC-SP-CO.—first dorsal ramus of occipito-spinal complex.
LLN.—lateral-line nerve.
NINTH.—glossopharyngeal nerve.
OBRN.—opercular branch from vagus nerve.
OCC-SP-N&G—occipito-spinal nerves and ganglia.
OP.—opisthotic.
PAR.—parietal.
PEC-PEL. ACC.—ventral pectoral-pelvic accessory lateral-line nerve.
PHBRV.—pharyngo-branchial nerves of vagus.
PP-ACC-LAT.—ventral, segmental accessory lateral-line nerves.
PRF.—prootic facial foramen shown as dashed black line medial to hyomandibular.
PRO.—prootic.
PTR.—pterotic bone.
PTR-SP.—pterotic spine.
PTT.—posttemporal.
RC1A.—supraorbital branch of ramus canalis lateralis system.
RC1B.—temporal branch of ramus canalis lateralis system.
RC2.—anterior infraorbital branch plus dorsoanterior dentary and rictus branches of ramus canalis lateralis system.
RC3, RC3A, RC3B.—posteroventral dentary branches plus rictus branches of ramus canalis lateralis system.
RC3C.—branch of ramus canalis lateralis system detaching from ramus opercularis superficialis facialis and extending to anteroventral area of preopercular canal membrane.
RC4, RC4A.—preopercular branch of ramus canalis lateralis system.
RC4B.—medial preopercular-mandibular ridge prolongation of RC4A.
RC5.—supratemporal branch of ramus canalis lateralis system.
RCL.—ramus canalis lateralis nerve.
R-HYO.—ramus hyoideus.
RLA.—ramus lateralis accessorius or recurrent facial nerve.
RLA-A.—branch of RLA to anal fin.
RLA-D.—branch of RLA supplying dorsal fin.
RLA-DFR.—branch of RLA to dorsal fin ray.
RLA-OCC-SP-CO.—branches of RLA to occipito-spinal complex.
RLA-P.—branch of RLA to pectoral fin.
RLA-PDA.—a main branch of RLA extending from parietal to dorsal fin.
RLA-PEL.—branch of RLA to pelvic fin.
RLA-PP.—a main division of RLA extending from parietal bone to pectoral and pelvic fins.
RLA + SYM.—common trunk of RLA + sympathetic.
RLA + SYM-DASH.—ramus lateralis accessorius plus sympathetic common trunk shown as dashed black line medial to hyomandibular.
RLA-THYO—a main division of RLA extending from prootic foramen to pectoral and pelvic fins.
R-MAN-EX.—ramus mandibularis externus.
R-MAN-IN.—ramus mandibularis internus.
SPH.—splenotic.

SPN.—spinal nerve.
SUPCL.—supracleithrum.
SYM.—sympathetic trunk.
SYM-G.—sympathetic ganglion.
TR-COM-SYM.—transverse commissure of sympathetic.
TR-HYO.—truncus hyomandibularis.
VR-OCC-SP-CO.—ventral ramus of occipito-spinal complex
VSN.—branch of ventral spinal nerve.
VSR.—ventral spinal ramus.

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A NEW GYMNOTOID FISH FROM THE RIO TOCANTINS, BRAZIL

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INTRODUCTION

Amongst the gymnotoids in the fish collection of the Cailfornia Academy of Sciences in San Francisco, I found three unusual specimens which were collected in 1924 at Porto Nacional, Rio Tocantins, Brazil, by Dr. Carl Ternetz. According to the keys in Ellis (1913) and Schultz (1949), these specimens fall into the genus *Sternopygus,* but the unusual appearance of the new fish suggested that it might be different. Accordingly, the three specimens were radiographed, and, after morphometric data were taken, one was cleared and stained for osteological study. Although these fish superficially resemble *Sternopygus*, their affinities do not appear to lie with this genus. I believe that the species described below requires generic recognition. Osteological nomenclature follows Weitzman (1962).

ACKNOWLEDGMENTS

I am grateful to Dr. W. I. Follett and Mrs. Robert Dempster of the California Academy of Sciences in San Francisco for their kind assistance in obtaining study materials from the fish collection there. I am also indebted to Professor George S. Myers, Mr. Leonard Compagno, and Dr. Warren C. Freihofer for their encouragement and criticism of the work at various stages.

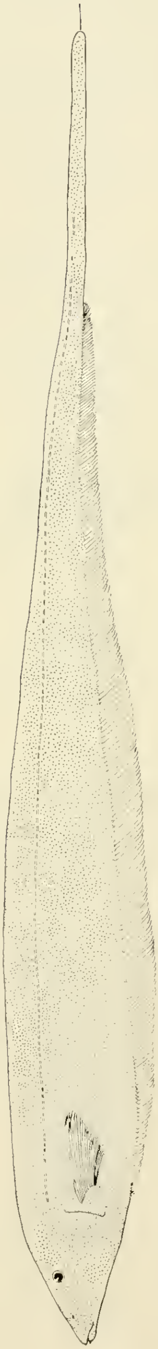

Figure 1. *Archolaemus blax*, holotype, CAS 24743. Total length 435 mm.

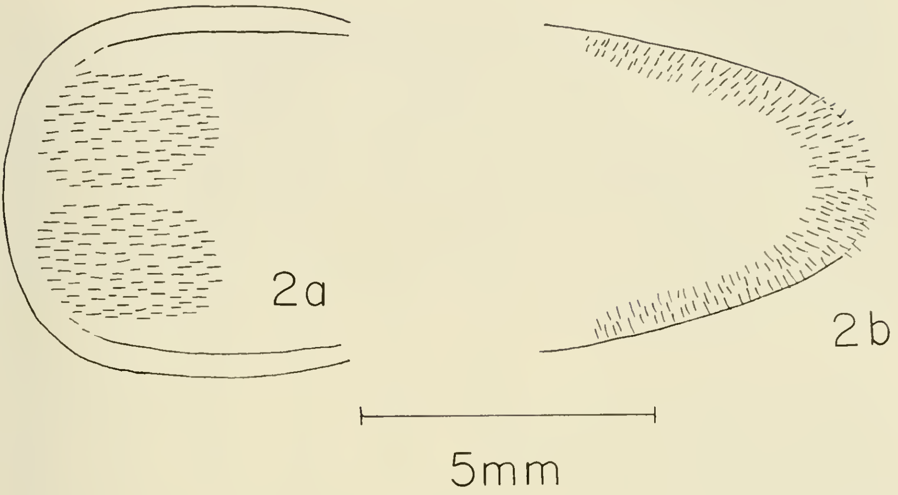

Figure 2. *Archolaemus blax,* holotype. View of jaws, indicating shape of tooth patches and showing mandibular teeth outside mouth. 2a. Upper jaw; 2b. lower jaw.

Archolaemus Korringa, new genus

Type species. *Archolaemus blax* Korringa, new species.

Elongate compressed gymnotoid fishes, lacking caudal fin and dorsal thong. Frontal and parietal fontanels large. Tail extending beyond end of anal fin. Body completely covered with scales, with several rows of large scales near and below lateral line; back and lower parts of sides covered with very small scales. Head naked. Orbital margin free. Mesopterygoid with approximately 10 small villiform teeth. Premaxillaries and dentaries each carrying numerous villiform teeth in a single patch on each bone (see fig. 2); a number of dentary teeth are outside the mouth and project forward in larger specimens. Premaxillaries small, about one and one-half times as long as wide, about one-fourth as long as the maxillaries. Maxillaries more or less straight, virtually parallel to the body length of the fish. Branchiostegal rays 5, 4 on ceratohyal, 1 on epihyal. Posterior process of the lower pharyngeal bones with a patch of approximately 12 teeth. The upper pharyngeals each with a patch of about 8 teeth. In both upper and lower pharyngeals these teeth are small and villiform. Mesocoracoid absent.

Certain lateral line canals of the head are much larger in diameter than others, and larger even than the canal of the body. Especially prominent are the nasal-supraorbital canal (anterior to the eyes), the infraorbital canal (excepting the posterior 2 bones, which are of small diameter), and the preopercular-mandibular canal. In conjunction with this increase in diameter, there is a progressive reduction of the superficial walls of the canals, so that they resemble troughs roofed over by arches.

Table 1. *Measurements in millimeters. Figures in parentheses are measurements expressed as percentage of the distance from tip of snout to end of anal fin base.*

	Holotype *CAS 24743*		*Paratype* *CAS 24744*		*Paratype* *CAS 24745*	
Total length	435	(127)	313	(124)	235	(137)
Snout tip to end of anal fin	344	(100)	253	(100)	172	(100)
Snout tip to origin of anal fin	46	(13.4)	45	(17.8)	26.5	(15.4)
Longest anal fin ray	16.5	(4.8)	14.5	(5.7)	8.5	(4.9)
Snout tip to vent	23	(6.7)	18	(7.1)	17	(9.9)
Snout tip to occiput	33.5	(9.7)	30	(11.9)	20	(11.6)
Snout tip to pectoral fin origin	47	(13.7)	45	(17.8)	25.5	(14.8)
Length of pectoral fin base	8	(2.3)	6.5	(2.6)	3.5	(2.0)
Snout tip to tip of pectoral fin	75.5	(21.9)	71	(28.1)	42	(24.4)
Snout tip to anterior margin of eye	19	(5.5)	18	(7.1)	11	(6.4)
Snout tip to rictus[1]	6	(1.7)	—	—	3.5	(2.0)
Snout tip to posterior edge of opercle	43.5	(12.7)	40	(15.8)	23	(13.4)
Snout tip to anterior nostril[1]	4.3	(1.3)	—	—	2.7	(1.6)
Posterior nostril to eye	13.5	(3.9)	11.5	(4.5)	6	(3.5)
Distance between orbital margins	4.5	(1.3)	3	(1.2)	2.6	(1.5)
Depth at eye	22.5	(6.5)	19	(7.5)	12.5	(7.3)
Depth at occiput	29	(8.5)	25	(9.9)	15.5	(9.0)
Maximum depth of body[2]	40.5	(11.8)	40	(15.8)	19.5	(11.3)
Width of mouth	6	(1.7)	5.5	(2.2)	2.7	(1.6)
Width of head at eye	13.5	(3.9)	11	(4.3)	6	(3.5)
Width of head at occiput	15.5	(4.5)	14	(5.5)	9	(5.2)
Anal fin rays	218		202		202	
Pectoral fin rays, right side	19		20		20	
Pectoral fin rays, left side	19		20		19	
Lateral line scales[3]	137		143		146	
Abdominal vertebrae	15		14		14	
Caudal vertebrae	59		51		75	

[1] Snout of this specimen too severely damaged to take accurate measurements.

[2] Maximum depth of body is approximately at tip of pectoral fins.

[3] Counted between dorsal margin of gill opening and end of anal fin base.

Abdominal vertebrae 14 or 15; caudal vertebrae 51 to 75 in the three specimens; actual range doubtless greater. Two pyloric caeca present. Vent and genital papilla lie directly below the eye. Snout moderately long, conical; distance from snout tip to eye approximately equal to distance from eye to posterior margin of opercle.

Archolaemus blax Korringa, new species.

(Figures 1, 2.)

Study material. Three specimens. Holotype: CAS 24743, male; 435 mm. in total length; Porto Nacional, Rio Tocantins, Estado de Goiás, Brazil; collected by Carl Ternetz, February 8, 1924. Paratypes: CAS 24744, female full of eggs, 313 mm.; and CAS 24745, 235 mm. (cleared and stained with alizarin, in glycerine), both collected with the holotype.

Description. See table 1 for counts and measurements. Dorsal profile of head straight; ventral profile slightly convex to slightly concave. Tail somewhat flattened and ribbonlike (this may be an artifact, as all the tails possess, instead of vertebrae, a slender flexible rod, indicating that regeneration has taken place). One paratype (CAS 24744) is a ripe female; the eggs are slightly ovoid, about 1.5 mm. in length. The first gill arch of the right side possesses 7 to 10 nubbins representing rakers (9 in holotype, 10 and 7 in paratypes). In *Sternopygus* each nubbin has imbedded in it a number of very small spines or teeth. I have not been able to determine if this is true for *Archolaemus,* as the spines or teeth are not present in the cleared and stained specimens.

Color in alcohol an even tan; area around orbital margin and tip of snout pale. There is no evidence of the dark brown banding found in many gymnotoids.

Origin of name. Greek, *archos,* anus; *laimos,* throat, from the location of the vent under the eye; Latin, *blax,* doltish, in reference to the fish's general appearance.

DISCUSSION

Regan (1911) places all short-snouted gymnotoids with frontal and parietal fontanels, but lacking caudal fins and dorsal thongs, in the subfamily Sternopyginae of his family Sternarchidae (properly Apteronotidae). I assigned *Archolaemus* to this subfamily on the basis of 1) absence of mesocoracoid, 2) presence of large fontanels, 3) absence of caudal fin and dorsal thongs, 4) presence of mesopterygoid teeth. *Sternopygus* and *Archolaemus* are the only members of the subfamily with a free orbital margin. However, *Archolaemus* is distinct from *Sternopygus* in several ways. Sternopygus has a pectoral girdle with a short suture between the coracoid and the scapula, the scapular foramen being open anteriorly. In *Archolaemus,* the suture between the two bones is considerably longer, and a distinct scapular foramen is present. The former type, as Regan points out, is found in *Steatogenys,* whereas the latter is characteristic of *Eigenmannia.* The pectoral girdle of *Hypopomus* resembles that of *Eigenmannia* and *Archolaemus* in possessing a long suture, but lacks a conspicuous scapular foramen. *Archolaemus* is further distinguished in having the anus and genital papilla directly below the eye; in all specimens of *Sternopygus* examined, these were well posterior to the eye. The eye of *Archolaemus* is considerably larger (about 4.5 to 5.5 times in the distance between the eye and the posterior margin of the opercle) than that of *Sternopygus* (6.5 to 11). Other distinguishing features are: premaxillaries small, about one-fourth the length of the maxillaries; as opposed to slightly over one-half in *S. macrurus*; few anal rays, generally less than 220, whereas *Sternopygus* has 234 to 320 (counts between 260 and 280 are typical). The maxillaries are fairly long and almost horizontal, whereas *Sternopygus* has oblique maxillaries. The body cavity of *Archolaemus* is short (6.3 to 8.3 times in length to end of anal fin base), and few (14 to 15) abdominal centra are present; *Sternopygus* has a longer body cavity (about 3.5 to 5 times in length to end of anal fin base) and more abdominal centra (generally 20 to 25). *Archolaemus* has a much longer snout than *Sternopygus,* the distance from snout tip to eye being about 1.2 times the distance from eye to occiput, as opposed to 0.7 for the latter genus.

Archolaemus blax is distinguished from all species of *Eigenmannia* by the presence of a free orbital margin. Except for *E. virescens,* no species of *Eigenmannia* that I have examined has the vent as far forward as the eye. *Archolaemus* has a significantly longer snout than does *Eigenmannia*; snout tip to center of eye is contained 13 to 16 times in the length to the end of anal fin base in the former, 20 to 28 times in members of the latter genus. *Archolaemus* has a long maxillary disposed almost parallel to the body length, whereas the maxillaries of *Eigenmannia* are much shorter and vary from 45° to perpendicular to the body length. *Archolaemus* appears to have a proportionately longer gape than *Eigenmannia.* No specimen of *Eigenmannia* that I have examined has teeth outside the mouth.

Rhabdolichops (Eigenmann and Allen, 1942) is distinguished from *Archolaemus* principally by its squamation, gill rakers, and general body shape. The back of *Rhabdolichops* is naked to a point about two-thirds of the distance to the end of the anal; anteriorly, the entire region above the lateral line is naked; posteriorly, only the top of the back. The body of *Archolaemus* is entirely covered with scales. *Rhabdolichops* has long, well developed gill rakers, a short snout, and a concave upper head profile. I do not yet have osteological material of this genus and therefore am not certain of its affinities.

The edentulous Steropyginae (*Hypopomus, Steatogenys,* and *Parupygus*) appear to be highly distinct from the foregoing genera. Most notably, *Archolaemus, Sternopygus, Eigenmannia,* and *Rhabdolichops* have similar lateral line canals while in *Steatogenys, Hypopomus,* and *Parupygus* (Hoedeman, 1962) all the canals are tubelike and of small diameter. The circumorbital tubes lack platelike stays. Many of the canals seem to be isolated from the bones with which they are normally associated in other groups of fishes; e.g., there is no apparent bony connection between the dentary and the chain of tubules lying ventral to it. Furthermore, these 3 genera lack teeth on the premaxillaries, dentaries, and mesopterygoids and not one has a long snout. *Archolaemus* further differs from *Steatogenys* in the absence of "mental filaments" and lacks the banded color pattern found in this genus and in some species of *Hypopomus.*

COMPARATIVE MATERIAL EXAMINED

Sternopygus macrurus (Bloch and Schneider): SU 21997, 2 specimens, Botanic Garden, British Guiana. *Eigenmannia virescens* (Valenciennes): SU

54508, 2 specimens, Lagoa Grande, Brazil. *Eigenmannia macrops* (Boulenger): SU 54473, 2 specimens, São Gabriel Rapids, Rio Negro, Brazil. *Eigenmannia conirostris* Eigenmann and Allen: SU 54461, 1 specimen, Lagoa Grande, Lower Amazon, Brazil, in alcohol. *Rhabdolichops longicaudatus* Eigenmann and Allen: SU 54377, 1 specimen, Santerém, Amazon, Brazil; SU 64076, 1 specimen, Cucuhy, Rio Negro, Brazil; both in alcohol. *Hypopomus brevirostris* (Steindachner): SU 24769, 1 specimen, Lago Gatún, Three Rivers Plantation, Panamá. *Steatogenys elegans* (Steindachner): SU 22445, 2 specimens, Belém do Pará, Brazil. *Parupygus savanensis* Hoedeman: Zoological Museum of Amsterdam 106,074, 1 specimen, Botopasi, Surinam River, Surinam. Except as noted, all are alizarin preparations in glycerine.

SUMMARY

Archolaemus blax Korringa, a new genus and species of gymnotoid fish is described. It is one of the toothed Sternopyginae, a group consisting of *Sternopygus, Eigenmannia,* and *Rhabdolichops.* These are united by the possession of hypertrophied lateral line canal bones in the head. *Archolaemus* shares many characters with *Sternopygus* and *Eigenmannia,* though its affinites lie more with the latter.

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ON THE TRAIL OF THE GOLDEN FROG: WITH WARSZEWICZ AND GABB IN CENTRAL AMERICA

By

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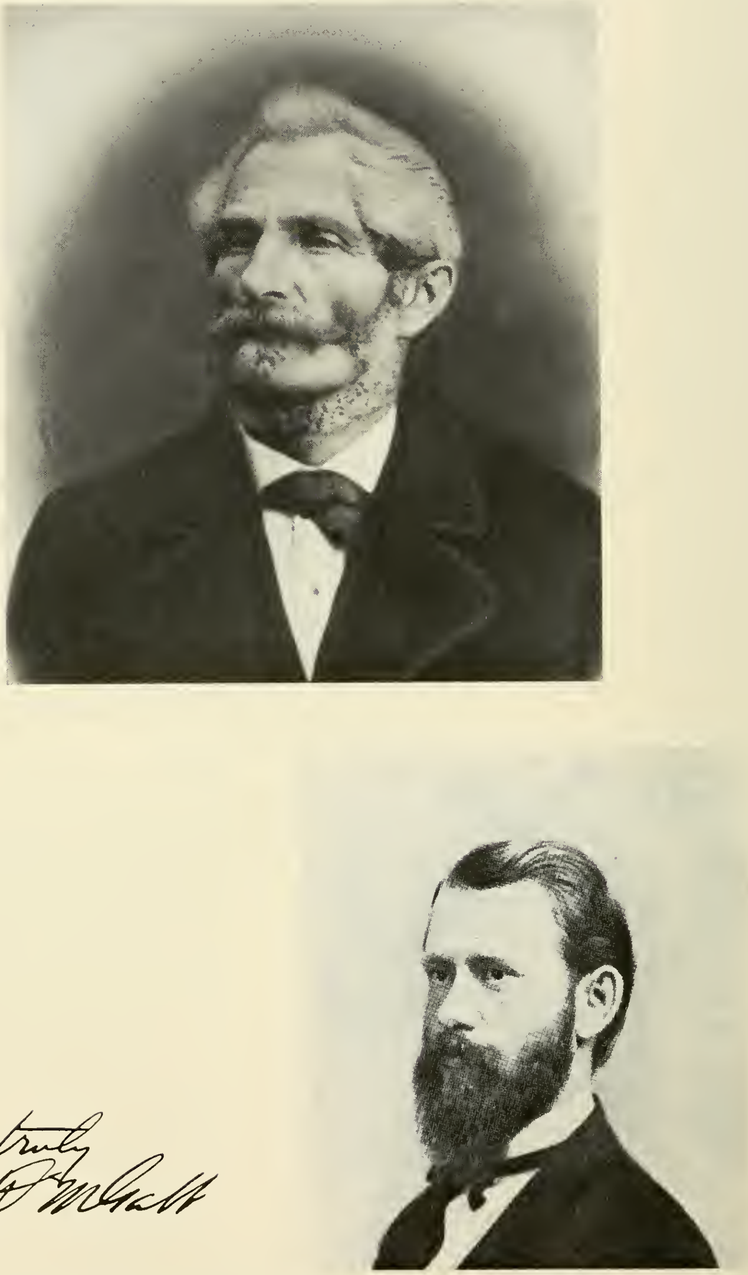
Those who have viewed at first hand the steep, dark-green, forest-covered slopes of the Cordillera de Talamanca-Chiriquí of Costa Rica and Panamá, with their ever changing aspect of sun and cloud, moon and mist, bright blue sky and bright green mantle, driving rain and boiling fog, come away with a feeling of overpowering awe and mystery at the variety of nature and the magic of the human soul. It is not surprising that the primitive peoples in this region also regarded the mountains and their forests with mystical reverence, so near and yet towering abruptly upwards to 4,000 meters from their lowland valley habitations.

Among the Bribri, Cabécar, Boruca, Changina, and Chiriquí, when the chicha has been drunk, the night grows late and dark, and the fires die down to burning embers, the wisest old man of the tribe tells his engrossed listeners of a beautiful miraculous golden frog that dwells in the forests of these mystical mountains. According to the legends, this frog is ever so shy and retiring and can only be found after arduous trials and patient search in the dark woods on fog shrouded slopes and frigid peaks. However, the reward for the finder of this marvelous creature is sublime. Anyone who spies the glittering brilliance of the frog is at first astounded by its beauty and overwhelmed with the excitement and joy of discovery; almost simultaneously he may experience great fear. The story contin-



Yours truly
W M Gabb

FIGURE 1. Upper, Josef Warszewicz, original by Artura Grottgera, now the property of the Department of Plant Geography, Jagellonian University, Krakow; lower, William M. Gabb, original, the property of the Academy of Natural Sciences of Philadelphia.

ues that any man who finds the legendary frog finds happiness, and as long as he holds the frog happiness will follow him everywhere. The story tellers record many men who have scaled the highest peaks and searched the darkest forests for even a glimpse of the golden frog, but only a few ever see it. Fewer still capture the cherished creature and hold him for a few moments, and a very few are able to carry him with them for a longer period of time. One story tells of the man who found the frog, captured it, but then let it go because he did not recognize happiness when he had it; another released the frog because he found happiness too painful.

Like the Indians of Talamanca and Chiriquí, each human being is also on a mission searching for the golden frog. Field biologists in particular seem always to be searching for mystical truth and beauty in nature, and frequently at some unperceived level, for that happiness promised by the Indian seers. The present paper is appropriately about two 19th Century scientists who joined this search in the very regions where the golden frog abounds, and we may assume that for a time, at least, they captured that joy guaranteed to beholders of the frog.

INTRODUCTION

Both Josef Warszewicz and William M. Gabb (fig. 1) were pioneer collectors of herpetological materials from lower Central America. Since they were among the first to sample the region, many of the animals they collected became types of previously undescribed species, most of which remain recognized as valid today. Neither of these men was a zoologist, and both collected in regions not visited again by herpetological collectors until the present century. Confusion and doubt as to the origin of their collections have clouded the issue of the validity of certain names and the synonymy of others subsequently described. In the present paper the routes followed by the two pioneers and the sources of their materials are delineated for the first time.

ACROSS THE GREAT DIVIDE: WARSZEWICZ IN WESTERN PANAMA

Josef Warszewicz was born in Litwie (Wilno), Poland in 1812. He apparently studied some botany at the University of Kraków. He took part in the Polish Revolution against Russia of 1830–31 and rose to the rank of officer. After the defeat of the Polish insurgents he left Poland. From 1840–1844 he worked as a gardener in the Botanical Gardens in Berlin. There he came to the attention of a Belgian, Van Houtte de Gandawy, who owned a large garden in Santo Tomás (St. Thomas), now Matías de Galvéz, Guatemala. Warszewicz was sent to inventory the garden and to collect materials for Belgian gardens. He sailed from Europe, December 5, 1844, and was active in Guatemala by March 1, 1845. He added many local species to his employer's gardens and in 1846 began work for himself, and forwarded living and dry plants, especially orchids, to Europe. In 1848

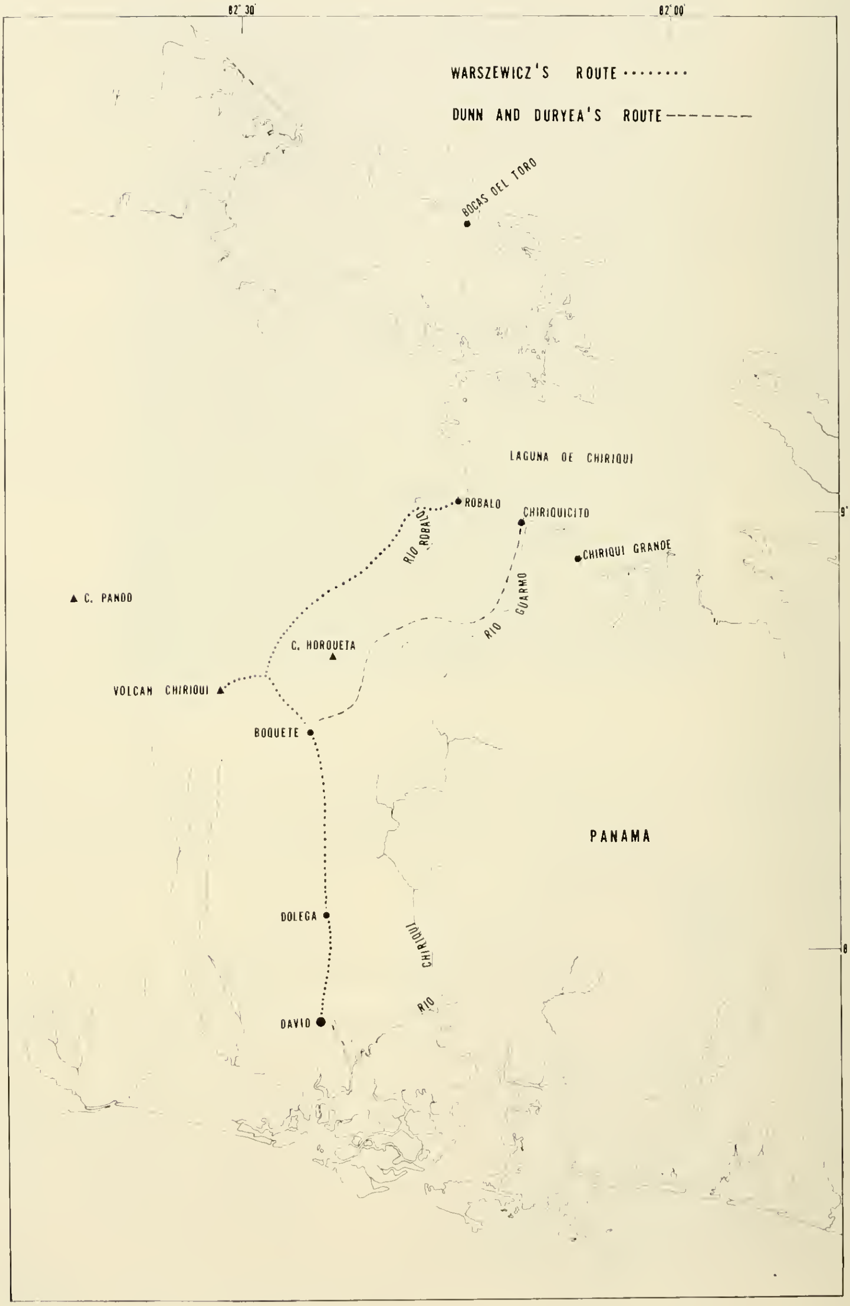


Figure 2. Map of western Panamá, showing Warszewicz' route across the Continental divide and principal localities discussed in text.

Warszewicz undertook a major trip through Central America. He traveled by land from Guatemala to San José, Costa Rica, where he was situated by February, 1848. On March 1, he climbed Volcán Irazú. Later he arrived in western Veragua (Chiriqui), Panamá, where he climbed Volcán Chiriquí and crossed over to the Caribbean coast. Most of the amphibians and reptiles collected by Warszewicz were taken in western Panamá. In 1851 he was again in the Chiriquí region and later that year he proceeded to South America, being in Guayaquil, Ecuador, at the end of the year. Warszewicz spent 1852 in South America, primarily in Perú and Bolivia. He is known to have visited Lima, Perú, and was at La Paz, Bolivia, on June 15, 1852. At the end of the year, December 28, he was at Huancabamba on the headwaters of the Río Marañón, upper Amazon drainage, Departamento Piura, Perú. He returned to Germany in October 1853 and became Inspector of the Botanic Gardens in Kraków. He died there December 29, 1866. (Regal, 1867; Rouppert, 1927). A bust of Warszewicz was erected in the University Botanical Garden in Kraków about 1880, where it still stands.

Herpetological materials collected by Warszewicz were deposited at Berlin, Vienna, and Kraków. The last city had been made the capital of a small free state after the Napoleonic wars in 1815. In November 1846, it was annexed to the Austrian-Hungarian Empire, following a revolt in Poland. Through exchange, some specimens came to the museum at Munich and to the British Museum. The Central American specimens are all from Panamá and were taken in 1848 and 1851. The former collection seems to have gone to Kraków and Vienna, the last to Berlin. The long residence of Warszewicz in Berlin prior to his American travels explains deposition of specimens there, probably as the result of long-time contacts. Apparently he loaned and gave some material to the Vienna Museum on his establishment in Kraków in 1843, since the latter city was then part of the Austrian-Hungarian state. Fortunately Warszewicz' route through the Chiriquí massif may now be traced with some accuracy (fig. 2). Information provided by Wagner (1863) and his map clearly define the route from David on the Pacific slope across the divide to the Laguna de Chiriquí. Wagner records that Warszewicz penetrated the interior of Chiriquí and traversed the great Cordillera to the Atlantic shore. Regel (1867) noted that Warszewicz climbed the 16,000 foot Volcán Chiriquí in 1848. Wagner (1863), using the same guides and carriers employed by Warszewicz, followed the same trails to the Chiriquí highlands. This route runs from David through Dolega and then up to Boquete (1158m.), from where there were two trails leading to the Caribbean shore. One trail skirted the east slope of Volcán Chiriquí and continued to Ranchos de Róbalo, the other passed around the east slope of Cerro Horqueta and continued to the mouth of Cabbage Creek (Río Guarmo) near present day Chiriquí Grande. Warszewicz certainly followed the Boquete-Róbalo trail, since a branch from it leads to the top of Volcán Chiriquí (3478m.). Nevertheless, he may have returned via the other route. Emmett R. Dunn and Chester B. Duryea seem to have followed the latter trail from Chiriquí Grande to Boquete, in 1923 when they became the first herpetologists to re-collect several of Warszewicz' species.

HERPETOLOGICAL SPECIMENS COLLECTED BY WARSZEWICZ

Most of the amphibians collected by Warszewicz were described by Oskar Schmidt (1857) and more extensively described and illustrated by him in 1858. The following are involved, with the Kraków Museum in the Department of Systematic Zoology, Jagellonian University (KM) numbers listed. These specimens were presented to the collection in 1870 and were examined by E. R. Dunn in 1928. Some of them are still extant. Location of other types and other Warszewicz material noted in preparation of this report is also indicated, but probably is not complete. Abbreviations for other collections are: Zoologisches Museum, Berlin (B); British Museum (Natural History), (BM); Zoologischen Museum, Hamburg (H); Zoologischen Staatssammlung in München (M); Naturhistorisches Museum Wien (W). An asterisk (*) indicates a new species.

Specimens Collected by Warszewicz

**Leiuperus sagittifer.* New Granada (Colombia).

**Ixalus warschewitschii.* KM 1006/1338; near Volcán Chiriquí, between 6000 and 7000 feet (4500–5250 feet = 1370–1600 m.).

**Hyla pugnax.* KM 1009/1339; Río Chiriquí near Bocas del Toro.

**Hyla splendens.* KM 1008/1340 ♀ :Río Chiriquí near Bocas del Toro.

**Hyla molitor.* KM 1010/1341, 2 ♂ ♂ ; W 16494, female designated as lectotype by Savage and Heyer (1969):Río Chiriquí near Bocas del Toro.

**Hyla molitor marmorata.* KM 1010/1342 ♀ :Río Chiriquí near Bocas del Toro.

**Hylodes fitzingeri.* KM 1012/1343; Mountains of New Granada (Panamá), 4000 feet (3000 feet = 915 m.); now lost.

**Dendrobates speciosus.* KM 1017/1345 nine specimens; W one specimen:trail between Bocas del Toro and Volcán Chiriquí, 5000–7000 feet (3777–5250 feet = 1150–1600 m.); now lost.

**Dendrobates pumilio.* KM 1018/1346:trail between Bocas del Toro and Volcán Chiriquí, 5000–7000 feet (3777–5250 feet = 1150–1600 m.); now lost.

**Dendrobates lugubris.* KM 1016/1347:trail between Bocas del Toro and Volcán Chiriquí, 5000–7000 feet (3777–5250 feet = 1150–1600 m.); now lost.

Bufo margaritifer. Between Bolivia and Perú, 3000 feet (2250 feet = 685 m.).

**Bufo pleuropterus.* KM 1030/1348:between Bolivia and Perú, 3000 feet (2250 feet = 685 m.).

**Bufo veraguensis.* KM 1032/1350; New Granada, Provincia de Veragua.

**Bufo simus.* BM 95–9–14.6; H 1527; KM 1029/1351, 5 specimens (now lost); M 543/20; W 16521:Río Chiriquí near Bocas del Toro.

**Hylaemorphus dumerilii.* KM 1014/1345:New Granada, Provincia de Chiriquí, 8000 feet (6000 feet = 1830 m.).

**Hylaemorphus bibronii.* KM 1015/1355; New Granada near Panamá, 2000–3000 feet (1500–2500 feet = 460–760 m.).

**Phirix pachydermus.* KM 1013/1356; Western New Granada near Buenaventura, 5000 feet (3777 feet =1150 m.); now lost.

Other specimens collected by Warszewicz.

At Kraków:

Basciliscus mitratus. KM 932/1317 America.
Stenostoma albifrons. KM 962/1296 America.
Cyclophis aestivus. KM 981/1270 America.
Pelamis bicolor. KM 989/1304 Pacific Sea.
Lacerta muralis viridis. KM 1019/1270 America.
Bufo vulgaris. KM 1020 America.
Phyllomedusa hypochondrica. KM 1024/1344 Guyana.
Bufo chilensis. KM 1031/1349 Bolivia.

At Berlin:

*_Rhinotyphlops albirostris._ B 9529, 2 specimens; Veragua (Peters, 1857).
*_Anolis humilis._ B 500; Veragua (Peters, 1863a).
*_Anolis intermedius._ B 503; Veragua (Peters, 1863a).
*_Hyla sordida._ B 3141; Veragua (Peters, 1863c).
*_Hyla punctariola._ B 4918; Veragua (Peters, 1863c).
*_Strabomantis biporcatus._ B 3222, 3330; Veragua (Peters, 1863b).
Bufo haematiticus. B 3404; Veragua.
Bufo typhonius. B 3442; Veragua.

Most of the animals collected by Warszewicz are from what is today western Panamá, but in his time constituted the Provincia de Veragua of the country of Nueva Granada (Colombia). Today the old Veragua comprises the Provincias de Veraguas, Chiriquí, and Bocas del Toro. In Warszewicz' day, western Veragua was called Chiriquí and the Atlantic lowlands were called Bocas del Toro. Several corrections seem necessary in dealing with the data associated with his specimens. First, all altitudes listed are extremely high and well above the known distributions for the species. As I have previously pointed out (Savage, 1968) 19th Century Polish feet contained the equivalent of only nine English inches. Therefore I have given the corrected elevations in parentheses above. Regel's (1867) report of Warszewicz' climbing 16,000 foot Volcán Chiriquí as previously cited shows the same point, since the mountain is 3478m. (11,311 feet) in height. Even these figures are out of the altitudinal range for several species, but since they were probably estimated, the differences are not extreme after the corrections have been made.

Several forms described from Warszewicz' materials by Oskar Schmidt have never been retaken in Central America but, because of the lack of details regarding his route and the inaccessibility of the area on the continental divide visited by him, herpetologists have assumed that these animals would ultimately be rediscovered in the field. Recently, I (Savage, 1969) demonstrated that one species, *Bufo veraguensis,* was based on a mislabeled Peruvian or Bolivian toad. At least three others, *Hyla splendens, Hyla molitor,* and *Hyla molitor marmorata* may similarly be removed from any list of Central American amphibians. Savage

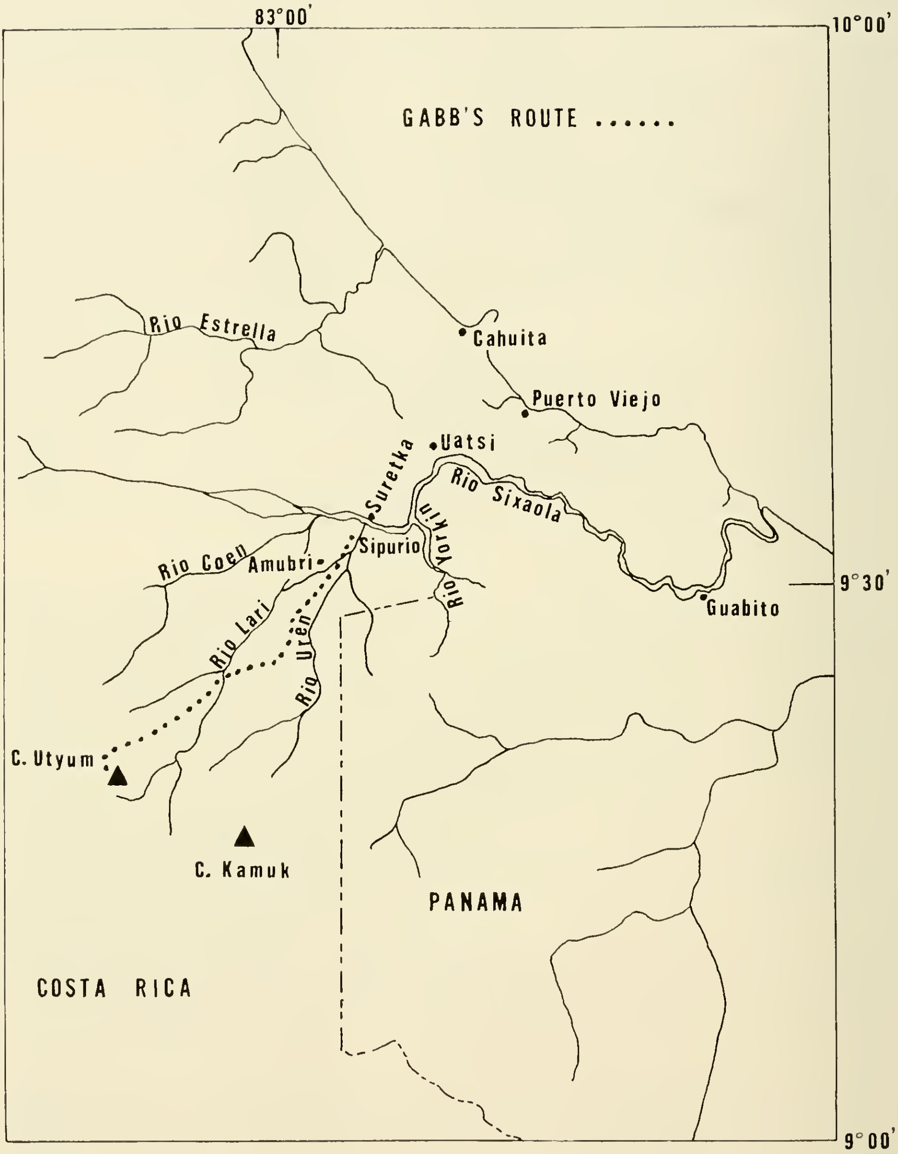


FIGURE 3. Map of southeastern Costa Rica, indicating area of Gabb's collections and the route followed in his ascent of Cerro Utyum.

and Heyer (1969) have shown that the latter two are totally unlike any Central American forms. Very likely they are also mislabeled South American frogs. The type of *Hyla splendens* appears to be a female of the genus *Gastrotheca*. Charles F. Walker, the leading student of this genus, informs me that the type is very similar to some Peruvian *Gastrotheca* species and unlike any Panamanian or Colombian form.

GABB AND THE EXPLORATION OF THE TALAMANCA

William More Gabb was born in Philadelphia on January 20, 1839. He is the subject of a biographical memoir of the National Academy of Science (Dall, 1909). Only details omitted from the memoir or matters directly related to his Central American experience are recounted here. Gabb was interested in geology and mineralogy and became associated with the California Geological Survey in 1862. As part of this work he spent the period 1862–1867 in California and was involved in the Survey's study of Baja California in the latter year. In 1869–1870 Gabb was active in geological work in Santa Domingo.

Gabb came to Costa Rica in February, 1873, to undertake a study of the geography, geology, resources, and climate of the southeastern section of the country, the Talamanca (fig. 3). During the 19 months of his contract, 17 were spent in the field (until August, 1874). He returned to the United States in 1876 whence he again visited Santa Domingo. Malaria apparently contacted in Costa Rica was inflamed in Santa Domingo and he ultimately succumbed to tuberculosis of the lungs after his final return to the United States in April, 1878. He died in Philadelphia May 30, 1878.

Gabb's fantastic activities during his Costa Rican stay are summarized in his reports (Gabb, 1875, 1877, 1913a, 1913b; Pittier, 1875, 1913). Most of his work was centered on the Valle de Talamanca, the region of the Río Sixaola drainage. The upper portion of this area: The Valle de Río Telire and the drainages of the Río Urén, Río Lari, Río Coen, Río Telire, and Río Taberi, forms Alta Talamanca. The lower part of the valley from a line between Uátsi and the mouth of the Río Yorkin to the coast is Baja Talamanca. The towering spires of the Cordillera de Talamanca border the Valle de Talamanca on the northwest. The Valle de Talamanca was the original Spanish settlement in Costa Rica, where La Ciudad de Santiago de Talamanca was founded, near the present site of Suretka (60m.) on October 10, 1605. In Gabb's day the central settlement of the area (it had the only church and was the home of Mr. John H. Lyon, an American, who had administrative responsibility for the district) was San Bernardo de Sipurio (70m.) between the Río Suedi and Río Urén about 3 miles above the mouth of the latter. This village and the Catholic church were destroyed by a flood of the Río Lari in 1909. A new mission was established at Amubri (75m.) in 1910 and serves as the central settlement in the area today. In 1873–74 about 1240 people lived in the region. Gabb was accompanied on most of his many trips through the area by two Costa Rican collectors, Jose Zeledón and Juan Cooper, both later famous naturalists in their own right, who collected most of the vertebrates.

Gabb married an Indian girl, Victoria, and one son Guillermo was born to this marriage in 1874 or 1875. At least three grandchildren, Alfonso, Melania, and Francisco Gabb were alive in 1964 when I visited the Talamanca. Several great-grandchildren were also living including a Victoria Gabb, an exceedingly beautiful girl, who may have recalled the Indian beauty who married Gabb.

Gabb visited almost every locality in the valley. As part of his fieldwork (Gabb, 1913b: 105–106, 114; 120–122, 127–128) he attempted to climb Pico Blanco (Cerro Kámuk) the highest peak (3554m.) in the southern Talamanca-Chiriqui range. Gabb tells it all—"We followed hunter's trails over a long, narrow, and very crooked ridge between the *Urén* and the *Lari* to a place called *Bitsung-wo-ki,* often scaling precipices, climbing around rocks, and in some parts scrambling over bad places by means of ladders and bridges made of sticks placed there for this purpose. Beyond *Bitsung-wo-ki,* but two men had ever gone, and with one of them for a guide, we were forced to climb down to the *Lari* River, and ascend the mountains on the other side, to avoid impassable rocks. At the end of seven (7) days, we found ourselves on the side of a peak, which we ascended, made our observations, and returned." His party consisted of 21 persons and subsisted mainly on *plátanos*. They were on the peak June 13, 1873, after starting the ascent June 6.

Gutiérrez (1960) has conclusively shown that Gabb, by detouring up the Río Lari, actually ascended Cerro Utyum (3084m.) (Cerro Cruz del Obispo) rather than Kámuk. The route followed by Gabb, his altitude record for the peak, 9562 feet (2915m.), as well as his observations (1913b: 106) as pointed out by Gutiérrez (1960) and confirmed by Carballo (1960) who scaled Kámuk, substantiate this conclusion. Gabb apparently returned to Alta Talamanca via the Río Lari. I ascended the latter river in 1964 to a point approximately where Gabb crossed over the ridge from the Río Urén. This place is 3 days hard hiking from Amubri and lies at 800m., near the juncture of the Río Dipári and Río Lari.

In view of these data, none of Gabb's animals should be listed from Pico Blanco (Cope 1875, 1876) but rather from Cerro Utyum.

One of the principal supporters of Gabb's explorations was the legendary Costa Rican entrepreneur Minor C. Keith, then manager of what became the Costa Rican Northern Railroad, that today connects Puerto Limón and San José. Keith began the planting of bananas along the rail lines, originally to keep the railroad hands busy and to provide food. Gradually bananas became the basis for the development of the United Fruit Company. The Compañía Bananera began to exploit the Valle de Talamanca in 1916. Poor and thin soils led to reduction of activity in 1922. The Valle was abandoned to local farmers in 1925. A railroad that connected with the United Fruit Company lines in the Bocas del

Toro region of Panamá, at Guabito, formerly extended up river past Suretka. The bridge across the Río Sixaola above Suretka was washed out in 1925 and the rails abandoned. In 1964 the railroad still ran from Sixaola to Volio (Uátsi). A truck road connects Puerto Viejo and Cahuita to Fields where another truck road runs to beyond Suretka. A jeep trail runs north from this road to Pandora in the Valle de Estrella.

HERPETOLOGICAL SPECIMENS IN THE GABB COLLECTIONS

The herpetological materials from Gabb's explorations were deposited at the United States National Museum (US) and reported on by E. D. Cope (1875, 1876) in a large monograph. Many examples served as types of new taxa as indicated below by an asterisk (*). Cope's paper was originally published as a separate, with a limited letterpress run of 50 copies on November 26, 1876. The journal run (Cope, 1876) appeared early the next year. This original report on Gabb's material has been reissued as a special number of the journal *O'Bios* and may be purchased from the Departamento de Biologia, Ciudad Universitaria, Costa Rica. Because the Gabb material is well known I have indicated catalog numbers only for type materials. Unless otherwise denoted all specimens are from Provincia de Limón, Canton de Limón in Costa Rica.

Specimens Collected by Gabb

Siphonops mexicanus. Holotype, US 29762; Paratype US 29763; Limón (described as new species *Siphonops proximus* Cope, 1878).

Opheobatrachus vermicularis. One specimen from Cerro Utyum, 6000 feet (1830 m.); 2 examples from lower country 20 miles (30 km.) from Coast.

Oedipus moro ?. Eastern slope Cerro Utyum.

**Cranopsis fastidiosus*. Lectotype, US 32585; paratypes US 32584, 32586–87; Cerro Utyum, 2500 feet (760 m.).

**Crepidius epioticus*. Cerro Utyum, 5000 feet (1520 m.) (type lost), Savage and Kluge, 1961.

**Ollotis coerulescens*. Cerro Utyum, 3000–5000 feet (915–1520 m.) (type lost).

**Bufo auritus*. US 30676; east coast region (substitute name *Bufo gabbi* Taylor, 1952).

Bufo valliceps. US 30592; eastern Costa Rica (described as new species, *Bufo melanochloris* Cope, 1878).

Bufo agua. Eastern coast.

Bufo haematiticus. Sipurio.

Atelopus varius. Cerro Utyum and lower country.

Dendrobates typographus. Low country about 10 miles (15 km.) inland.

Dendrobates tinctorius. Lower country.

**Dendrobates talamancae*. Near Old Harbour on east coast (type lost).

**Hyla gabbii*. US 30658–59; near Sipurio.

**Hyla uranochroa*. US 30651; near Sipurio.

**Hyla nigripes*. US 30685–86; Cerro Utyum, 5000–7000 feet (1525–2135 m.).

**Hyla elaeochroa*. Lectotype, US 30689, paratypes US 30688, 30690; east foot of mountains near Sipurio.

**Hyla punctariola pictipes*. US 30652; Cerro Utyum, 5000–7000 feet (1525–2135 m.).

**Hyla punctariola monticola.* US 30661, Cerro Utyum.
**Phyllobates hylaeformis.* US 30687; Cerro Utyum, 7000 feet (2135 m.).
**Lithodytes podiciferus.* US 30662, 30665–75 (US 30663 now at Harvard, US 30664 now at Michigan); Cerro Utyum, 5000–7000 feet (1525–2135 m.).
**Lithodytes muricinus.* Cerro Utyum (type lost).
**Lithodytes habenatus.* Cerro Utyum (type lost).
**Lithodytes melanostictus.* US 30608; Cerro Utyum, 7000 feet (2135 m.).
**Lithodytes megalocephalus.* US 32578; spur of Cerro Utyum, 6000 feet (1830 m.).
**Lithodytes gulosus.* US 32590; spur of Cerro Utyum, 6000 feet (1830 m.).
**Hylodes cerasinus.* US 32572; eastern slope of Cerro Utyum.
Gnathophysia ocellaba. East side of the Cordillera.
Ranula brevipalmata. Cerro Utyum.
Mocoa assata. Old Harbour.
**Mabuia alliacea.* US 30619–20; from the low country.
Mabuia cepedei. Below Sipurio.
**Chalcidolepis metallicus.* US 30568; Provincia de Alajuela, Fila de Aguacate.
**Amiva gabbiana.* US 32614–16; Old Harbour.
Gerrhonotus fulvus. Summit of Cerro Utyum.
Sphaerodactylus glaucus. Near Sipurio.
Thecadactylus rapicaudus. North of Río Estrella or North River.
Anolis copei. Old Harbour (Puerto Viejo).
Anolis trochilus. Talamanca.
**Anolis pachypus.* US 30683; slope of Cerro Utyum.
**Anolis oxylophus.* US 30556–57; Costa Rica.
Anolis intermedius.
Anolis capito. Old Harbour.
Corythophanes cristatus. Sipurio.
Iguana rhinophila. Low country.
Basiliscus vittatus. Sipurio.
**Basiliscus plumifrons.* US 32622–6; Sipurio.
**Xiphosoma annulatum.* US 32580.
Boa imperator. Foot of mountains.
**Leptognathus argus.* US 30656; Sipurio.
**Leptognathus pictiventris.* US 30657; eastern Costa Rica.
Leptognathus nebulata.
Sibon annulatum. Old Harbour.
Oxyrrhopus plumbeus. Low country
Oxyrrhopus petola. Sipurio.
**Leptophis aeruginosus.* US 30684; low country.
**Leptophis saturatus.* US 32563; Sipurio.
Leptophis praestans. Sipurio.
**Dendrophidium melanotropis.* US 32597.
Drymobius boddaertii. Talamanca.
Herpetodryas carinatus. Low country.
Spilotes corias. Talamanca.
**Spilotes chrysobronchus.* US 30623; coast region.
Coniophanes fissidens. Sipurio and Old Harbour.
Rhadinaea decorata. Sipurio.
Erythrolamprus venustissimus. Sipurio.
Xenodon angustirostris. Sipurio.

Stenorhina ventralis. Old Harbour.
**Contia pachyura.* US 30618; Sipurio.
**Catastoma psephotum.* US 62972; Cerro Utyum, 5000–7000 feet (1525–2135 m.).
Elaps circinalis. Talamanca.
Teleurapsis schlegelii. Eastern Costa Rica, Old Harbour to 5000–6000 feet (1525–1830 m.).
Bothriechis nigroviridis. Cerro Utyum.
**Bothriopsis proboscideus.* Sipurio (type lost).
Bothrops atrox. Coast region.
**Lachesis stenophrys.* US 32479; Sipurio.
Sphargis coriacea. Puerto Limón.
Cinosternum leucostomum. Old Harbour and Sipurio.
**Chelopus gabbii.* US 45905.
**Chelopus funerus.* US 45900–01; 56134–35; Puerto Limón.

Old Harbour, located on the coast between Punta Cahuita and the Boca de Sixaola, is now referred to as Puerto Viejo de Limón.

A FINAL WORD

At certain levels both Warszewicz and Gabb were successful in their quest. The modern observer who has been over some of the same ground can only marvel at the courageous determination, dedication, and curiosity of these scientific pioneers. In regions sparsely settled, without roads or other communication, dominated by primitive and rugged terrain, demanding climate and debilitating disease, they still prevailed against all odds to open a new and exciting world to those that followed. They could do no more.

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TELEOST HYBRIDIZATION STUDIES

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"Traditionally, studies such as ours have been based on morphology, especially the skeleton, which is the only complete organ system available for detailed comparisons with fossils. However, with the variety of both primitive and advanced teleosts living today, we are most emphatically of the opinion that approaches other than morphological ones would be exceedingly fruitful in the investigation of teleostean interrelationships."

The above quotation from Greenwood *et al.* (1966) clearly states George S. Myers' philosophy that systematic studies are central to biology. Any difference or similarity between two groups of organisms can be of value in estimating the amount of divergence; therefore, all biologic investigations can provide direct or indirect taxonomic information. Similar or identical organisms should be used in order to obtain repeatable experimental results; therefore, all biological investigations can be considered to be based on systematic research.

At the present time, the classification of most major taxa is based on their gross anatomy. Although this is due primarily to tradition, there is a valid scientific basis. Most experimental* analyses cover such small fractions of the taxonomic subdivisions that experiment-based classifications would have major gaps. Moreover, a typological concept has no place in modern systematics.

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* Hereafter the word experimental should be considered to equal all types of analyses that are not traditional studies of museum specimens.

When we contrast several related taxa we should compare the *spectra of attributes* in the diverse members of each taxon. Because of the difficulty of obtaining data and the short history of such studies, most experimental investigations contrast supposed typical representative members of the taxa to be compared (= typology).

In contrast, experimental studies are not burdened with traditional taxonomic relationships. The refreshing new viewpoint can challenge the validity of an unsupported traditional taxonomic conclusion. The resulting interaction between morphological taxonomists and experimentalists can provide a realistic arrangement of organisms approximating their phylogenetic relationships. The primary contribution of the taxonomist to this interaction may be to point out taxonomic problem groups so that the experimental biologist can concentrate his efforts efficiently.

Among the host of problems faced by the ichthyologist concerned with taxonomic problems has been the separation of environmental and genetic factors. Tåning (1952) and many others have shown that a single environmental variable can concurrently alter several morphologic entities regardless of genotype. Therefore, a morphologic comparison that emphasizes those attributes might produce a dichotomy between those fishes reared in warm water and those reared in cold water, despite their genetic affinities.

Environment-related problems can further plague taxonomy because survival in similar environments tends to select for similar morphologic attributes. For example, fishes that live in rock crevices tend to be elongate. Existence in this environment seems also to be enhanced by small eyes and scales. Some may be blind or naked. Many also have anteriorly located or reduced pelvic fins and small gill slits. Theoretically, distortions of true relationships by convergent or parallel evolution can be resolved by the use of diverse attributes. Practically, one must be careful not to use apparently divergent characters that happen to have selective value in similar habitats. Use of "non-adaptive" characters for taxonomy should help resolve problems of this type, but can one be certain that any character is not adaptive?

Johnson and Wicks (1964) have advocated the use of molecular biologic (= electrophoretic) studies because they may provide the "ultimate" information on relationships. Studies of DNA hybridization seem to offer even more promise of approximating the degree of phylogenetic divergence. Even this "ultimate" systematic tool may have potential weakness. Assume that we have two ancestral species of omnivorous fishes occupying estuaries. Both evolve into a freshwater herbivore and a saltwater carnivore. The DNA sequences in each species pair would diverge so that each saltwater type would have a sequence of codings favorable for survival in high salinity. Similarily each would have their DNA controlling their digestive enzymes designed to break down animal material. The freshwater representatives of each pair would have their nucleotide sequences designed to produce enzymes different from their sibling species, but the same as those of their more distantly related ecological counterpart. The above simplified model is undoubtedly extreme, but may indicate how dependence on a single analysis could be hazardous. It is also possible that this type of convergence would be missed despite the type of analysis used.

In effect, we have returned to the premise that taxonomic conclusions should be based on the sum (or product?) of the biological studies available. Nevertheless, each investigator should not attempt to carry out investigations in all areas, but should concentrate on those for which his aptitude, experience, and interest suit him. During recent years, I have used hybrid survival as an index of phylogenetic relationship. This approach has three major merits: 1) It necessitates minimal expenditures, 2) It measures genetic divergence, and 3) The results approximate those of classical morphological taxonomy.

The general agreement between hybrid survival experiments and classical fish taxonomy (Hubbs, 1967) and the potential hazards in such tests (Hubbs and Drewry, 1960) combine to make such tests valuable contributions to, but not the ultimate answer for, problems of phylogenetic relationships. The experiments reported below relate to two levels of relationships: 1) Arrangement of fishes within the family Cyprinodontidae and 2) Arrangement of various fish families.

MATERIALS AND METHODS

The techniques of Strawn and Hubbs (1956) were used for removal and mixing of the gametes. Two modifications were used that reduced some of the experimental difficulties. Most of our experiments have used gametes from "wild" fish, that is, the individuals were removed from natural populations when nearly ripe and taken to the laboratory for the experiments. This necessitated hurried field work to avoid having eggs shed or becoming overripe (= stale) during transport. We have found that the gametes can be stripped and mixed in the field and then taken to the laboratory as they develop. Large numbers of experiments can be done in this manner if the trip is properly planned. We have used petri dishes for transportation of individual experiments. The ripe eggs attach to the surface of the basal unit and the top is held in place with rubber bands. A piece of tape on the edge of the basal unit permits water circulation, another on the bottom is used as a lable. The sets of petri dishes are placed in styrofoam containers and the water changed when necessary. One still must be careful not to remain away from the laboratory for too long because careful examination of development is difficult in the field and newly hatched larvae can escape from the petri dishes. Keeping the transportation equipment cool prolongs the time that one can remain in the field.

We find that fertilization can be enhanced by use of mashed testes. Typically, semen is removed from males by coelomic pressure. Some species have such small quantities of semen that milt is seldom extruded by this technique, but eggs can be fertilized by extracting and mashing the testes. The same technique works with males whose sperm supply has been depleted in previous experiments.

When pertinent, the sources of the stocks will be presented with the listing of the experiments.

CROSSES OF CYPRINODONT FISHES

Moenkhaus (1910), Newman (1908), Hubbs and Drewry (1960 and 1962), Archer (1966), Drewry (1967), and others have reported on many successful crosses among species of *Fundulus* and with species of related genera such as *Adinia, Lucania, Rivulus, Jordanella, Crenichthys,* and *Cyprinodon.* Unfortunately, the last two listed papers are in thesis form and have limited circulation. In general, the level of success parallels the estimate of phylogenetic similarity as determined by morphological taxonomy. Most species of *Fundulus* can be crossed with the others and the hybrids reared to mature size. Two previously unlisted crosses, *F. seminolis* ♀ (Sumpter Lake, Florida) × *F. cingulatus* ♂ (Green Cove, Florida) and *F. seminolis* ♀ (Sumpter Lake, Florida) × *F. heteroclitus* ♂ (Matanzas Inlet, Florida) can be added to the extensive list of reared hybrids.

Many authors have reported that hybrids between *F. majalis* or its near relative (race?) *F. similis* and other species of *Fundulus* will hatch if *F. majalis* type sperm is used and not if *F. majalis* type eggs are used. Six tests with *F. zebrinus* (Iraan, Texas) sperm and *F. similis* (9 mile pond, Texas) eggs had over 100 fertilized eggs fail to hatch.

Drewry (1967) reported difficulties in crossing *F. notatus* or *F. olivaceus* with other species of *Fundulus,* but hybrids between them are easily reared (Thomerson, 1967). Drewry reported that only 1 of the 17 hybrids using *F. olivaceus* sperm (none available with *F. notatus*) hatched and it died shortly. The reciprocal experiments had 9 fertilized eggs of which 6 hatched but were not reared, indicating a difference between reciprocals that more recent results support. Archer (1966) also failed to rear hybrids between *Fundulus notatus* or *F. olivaceus* and 2 other *Fundulus* species. *Fundulus notatus* ♀ (Blanco R., Texas) has been crossed with *F. kansae* ♂ (Colbert, Oklahoma) and *F. grandis* ♂ (Port Aransas, Texas) and one fish from 8 and 5 fertilized eggs respectively reared, but both were deformed. *Fundulus olivaceus* ♀ (Scraper Park, Oklahoma) × *F. kansae* ♂ (Colbert, Oklahoma) had 13 of 18 eggs hatch but the deformed larvae shortly died. The difficulty of rearing the hybrids supports Drewry's observations, but they can be reared. The reciprocal hybrids are much more difficult to rear. *Fundulus kansae* ♀ (Colbert, Oklahoma) × *F. olivaceus* ♂ (Scraper Park, Oklahoma) (twice); *F. kansae* ♀ (Colbert, Oklahoma) × *F. notatus* ♂ (Blanco R., Texas) (12 times); *F. kansae* ♀ (Miller Cr., Texas) × *F. notatus* ♂ (Little Piney Cr., Texas), *F. zebrinus* ♀ (Iraan, Texas) × *F. notatus* ♂ (Onion Cr., Texas) (5 times); *F. cingulatus* ♀ (Dog Lake, Florida) × *F. olivaceus* ♂ (Baker, Florida), and *F. similis* ♀ (Port Aransas, Texas) × *F. notatus* ♂ (Blanco River, Texas) all failed to develop late embryos. The "greatest level of success" achieved in these 22 tests was 1 egg (*F. kansae* Colbert × *F. notatus* Blanco) that produced chromatophores but did not show indication of gastrulation. The low success and high frequency of abnormalities supports Drewry's hypothesis that *F. notatus* and *F. olivaceus* are phylogenetically similar to each other but dissimilar to other species of *Fundulus*. Six of 7 attempts to cross *F. notatus* and *F. olivaceus* were successful but only 4 of 6 control tests.

The previous intrageneric hybridization tests have not used the West Coast species, *F. parvipinnis* (Mission Bay, California, population). Failure of crosses with *F. kansae* (both reciprocals), *F. grandis* sperm, and eggs of *F. cingulatus* (3 tests, 2 populations), *F. heteroclitus* (2 tests), *F. majalis, F. similis* and *F. olivaceus,* indicates that this species is separate from other species now placed in *Fundulus*. Of course, only 10 failures may not be enough tests to insure valid results. The better results of hybridizing *F. parvipinnis* with *Crenichthys baileyi* (Hubbs, 1967) may indicate a common ancestry.

Only Archer (1966) has previously reported hybridization tests with *Jordanella floridae*. He reported that one set of *Jordanella* eggs crossed with *Cyprinodon variegatus* sperm died as late embryos. Three tests with *Cyprinodon* females from Iraan, Texas, resulted in no fertilization, but 1 of 2 and 3 of 4 tests with female *Fundulus zebrinus* and *Lucania parva* respectively from the same locality produced late embryos, but none hatched. This indicates that *Jordanella* is distinct from those 3 species. Drewry (1967) reported difficulty in rearing hybrids between *Lucania* and *Fundulus*; however, Archer (1966) reared several *F. pulvereus* × *L. parva* individuals to adult size. Apparently the hybrids did not exhibit sexual dimorphism.

INTRAFAMILIAL HYBRIDIZATION

The relationship of hybridization success to phylogenetic divergence of teleost families may be shown to have significant importance in the taxonomic arrangement of living fishes. In part this approach resurrects those of Moenkhaus (1910) and Hertwig (1936). The ability of producing late hybrid embryos in a series of cyprinodontid × atherinid crosses has been considered support of their close relationship (Rosen, 1964). One more combination can be added to the series already reported (Hubbs, 1967, and citations). Two of 15 eggs from *F. notatus* ♀ (Denison Dam, Texas) exposed to *Menidia audens* ♂ (U. Oklahoma

Biological Station) sperm gastrulated. Both produced heads, one was attached to the yolk mass and the other was free. Black pigments covered the yolk mass on both. The one with the head free also had extensive orange pigmentation and remained alive until almost all of the yolk was expended. These results resemble those of the reported series of cyprinodontid-atherinid hybrids. The failure at gastrulation of a parallel experiment with *Notemigonus crysoleucas* sperm shows that fundulines will not hybridize with all fishes.

Menidia audens has not previously been reported to have been tested in rearing experiments. The series (4) of controls done the same day all had 50 percent plus fertilization and hatching. Similar to most atherinids, the controls died a week later apparently due to starvation. Intrafamilial hybrids between *M. audens* ♀ and *Labidesthes sicculus* ♂ (Tishomingo, Oklahoma) (twice) had 25 percent–50 percent fertilization and all hatched and died with the maternal controls, showing that *Menidia* hybrids can be reared as far as the controls.

Menidia audens has also been tested for hybridization survival with members of several other families. The tests with *Notropis cornutus, Notemigonus crysoleucas* (3 times), *Gasterosteus aculeatus,* and *Aphredoderus sayanus* all terminated before gastrulation. Gastrulation and embryonic formation occurred in tests with a centrarchid and several percids. One egg gastrulated among 2 sets of *M. audens* eggs exposed to *Lepomis macrochirus* sperm. It died before pigmentation. Another set of *M. audens* eggs exposed to *Etheostoma radiosum* (Blue River, Oklahoma) sperm produced 5 early embryos, of which only 2 developed pigmentation, the test with *Percina caprodes* males from the same locality failed. Seven reciprocal experiments were set up with percid eggs from Blue River females, one *E. spectabile* and six *E. radiosum.* Six had some development and 58 of 192 gastrulated embryos produced pigmentation, but none showed any sign of circulatory development. Clearly these hybrids were more successful than most other interfamilial tests and approached that of the atherinid-cyprinodont tests.

A series of other intrafamilial tests were done with *Etheostoma* or *Hadropterus* eggs. It is not surprising that all 7 tests with the ostariophysines, *Moxostoma poecilurum, Notropis cornutus, Notropis umbratilis, Notemigonus crysoleucas,* and *Opsopoedeus emiliae* failed to gastrulate or that 3 crosses with the "black race" of *Gasterosteus aculeatus* (Chehalis, Washington) did not gastrulate. Five of 17 tests with *Aphredoderus sayanus* sperm had 1 or more eggs gastrulate. The males were from a stock obtained at Douglass, Texas. The successful combinations were essentially the same ones as the failures, indicating that the data are representative of the interfamilial combination. Two sets of *E. asprigene* (Douglass, Texas) eggs each had 2 eggs gastrulate and develop eye pigmentation. Two of them formed a heart that beat irregularly, but had no visible cells in the tubes. Many erythrocytes were present on the yolk mass anterior to the head. Another embryo had no heart beat but died breaking the egg shell.

Two sets of *H. scierus* (San Marcos and Pedro Creek, Texas) had 2 and 3 eggs gastrulate. Only 3 developed recognizable heads. Three additional embryos from an *E. spectabile* (San Marcos, Texas) × *A. sayanus* cross that developed pigmented eyes were sacrificed in an unsuccessful attempt to analyze the cytology. The putative hybrids were diploid but chromosome markers were not noted.

Four of 11 sets of *Etheostoma* eggs exposed to *Elassoma zonatum* sperm had gastrulation. All but one involved *E. spectabile* eggs. The 2 successful sets from Shoal Creek, Missouri, females had 6 gastrulated eggs, 5 had eye pigmentation, and 1 a functional heart beat and flow. All died at the time the maternal controls hatched. The 2 successful tests with Blue River, Oklahoma, females (*E. radiosum* and *E. spectabile*), each had 1 embryo that developed eye pigmentation.

The failure of 2 sets of *G. aculeatus* eggs exposed to *A. sayanus* sperm indicates that *A. sayanus* sperm will not fertilize all teleost eggs.

DISCUSSION

Most of the intrafamilial hybrid experiments substantiate those previously reported, i.e., teleost hybrids are relatively easily produced and if the parental morphology is similar the hybrids are easily reared. Drewry had evidence of a genetic block to the development of hybrids between *F. notatus* or *F. olivaceus* and other members of that genus. Because he had few tests (26 fertilized eggs), it might be possible that his results were due to chance. We had 26 fertilized eggs in the least studied reciprocal (*F. olivaceus* or *F. notatus* egg) and 22 tests with the reciprocal. Not only did the results confirm those of Drewry, they also showed a distinct difference between the reciprocals. Because most of our "standard *Fundulus*" in these tests were of the *F. kansae—F. zebrinus* type, it may be that the difference between reciprocals may relate only to those combinations. It is possible, however, that we have a second difference in reciprocal hybrid survival in funduline fishes. It is amply evident, however, that *F. notatus* and *F. olivaceus* are quite distinct from other species of *Fundulus*. Hybridization tests have clearly showed that gametes from *Adinia xenica* and *Lucania parva* are more compatible with gametes from typical *Fundulus* than are those of *Fundulus notatus* or *F. olivaceus*. Therefore, the genus should be expanded to include the members of *Lucania* and *Adinia*, or *F. notatus* and *F. olivaceus* should be separated from the other *Fundulus* species and placed in the genus *Zygonectes*.

The failure of 10 tests between *Fundulus parvipinnis* and 7 other species of *Fundulus* indicates that this species is quite distinct. The reasonable success of hybrids between *F. parvipinnis* and the *Crenichthys-Empetrichthys* complex suggests a possible relationship that makes biogeographic sense. The hybrids of all west coast Fundulines have earlier developmental blocks when crossed with an east-coast representative than when crossed with another western type. Perhaps the Fundulines had an east-west primary separation. The western types then diverged into a coastal (*F. parvipinnis* precursor) and a desert spring (*Crenichthys, Empetrichthys*) type. Because *F. parvipinnis* occupied a "typical *Fundulus*" environment, it retained "typical *Fundulus*" morphology, while *Crenichthys* and *Empetrichthys* occupied clear warm spring waters and became superficially distinct.

Assuming that the cyprinodonts have lost spinous fin rays, it seems that hybrids between soft-rayed and spiny-rayed fishes die at or before gastrulation. The consistent failures indicate a uniform distant relationship and perhaps a treelike phylogeny rather than a bushy type suggested by Greenwood *et al.* A treelike phylogeny is also indicated by hybrid development to late embryonic stages in almost all crosses between two spiny rayed types. If we placed *Aphredoderus* and *Etheostoma* in separate superorders than the hybrid success is incongruous; in contrast, if we follow Regan and make *Aphredoderus* a relic of a group ancestral to other perciforms, the phylogeny would agree with the hybridization data.

The success of most interfamilial spiny rayed hybrids is quite similar. Only two types of combinations usually survive to hatching. The cyprinodont-atherinid hybrids and hybrids among percids, serranids, and centrarchids. Recent classifications place each unit in a suborder.

In the future, hybrid survival tests may aid in determining other family group relationships.

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This paper is dedicated to Dr. George S. Myers because of his inspired teaching of systematic ichthyology.

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A REVISION OF THE FISHES OF THE GENUS *NOTOTHENIA* FROM THE NEW ZEALAND REGION, INCLUDING MACQUARIE ISLAND[1]

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INTRODUCTION

While preparing a revision of the southern and Antarctic fishes of the genus *Notothenia*, it became evident that the taxonomy of the species found in the New Zealand region is confused. In the most recent review (Parrott, 1958), five species are identified as occurring there. Of these, only four are valid, only three of the four are found in the New Zealand region, and the nomenclature of the three is entirely confused. This should not reflect upon Parrott, for he followed Boulenger, Waite, Regan, and Norman. For these reasons it is timely to present new descriptions and a new key for the New Zealand species together with a clarification of the nomenclatural confusion which has surrounded them.

I include Macquarie Island in this paper because two of the three species of *Notothenia* recorded from there also occur in New Zealand waters. Further, *Notothenia coriiceps* is included in the key to the species because it is widely distributed in the Southern Ocean, is known from the Kerguelen Islands, and eventually also may be found at Macquarie Island; a description of it is not given.

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I have not included *Notothenia cornucola* in this revision because I do not believe it occurs at New Zealand. This species was early recorded from New Zealand waters (Günther, 1860; p. 262; Hutton, 1872; p. 26; 1873; p. 262) and continues to be included in lists of New Zealand fishes although no specimens identified as *N. cornucola* have been found for nearly 100 years. The most recent reference is Parrott (1958), who admits that its occurrence is doubtful, although he includes it in his key to the New Zealand species of *Notothenia*. Considering that specimens of *N. cornucola* are encountered most commonly in littoral and shallow inner sublittoral areas (for example, among and under the rocks of the beaches near Punta Arenas, Chile, at low tide), it seems likely that if the species actually occurred in the New Zealand region it would be well known there. Norman (1937b; p. 86) reviewed the evidence and concluded that it ". . . is very slender." The specimen recorded by Günther was probably mislabeled, and Hutton's 1872 record is probably based upon that of Günther. Hutton's 1873 record from the Chatham Islands was probably based upon specimens of *N. angustata*. This species has recently been collected there (Moreland, 1957) and I have seen the specimens (see the section on material examined under *N. angustata*). Further, Hutton's (1873) statement that the upper lateral line ". . . extends to the end of the second dorsal, . . ." agrees best with my observations of *N. angustata* rather than with *N. magellanica*, the species to which Norman believed Hutton referred. For these reasons I have included Hutton's 1873 reference to *N. cornucola* in the synonymy of *N. angustata*. I have not included the listings of *N. cornucola* Richardson found in the lists and catalogues of New Zealand fishes because, in that form, they refer to a species which I believe does not occur in New Zealand.

Several check lists of New Zealand fishes have been prepared at various times, some of which I have not seen. The most important are those by Gill (1893), which reviews in detail the earlier works, and by Phillipps (1927b) which refers to earlier lists. For lists that I have seen, I have included the references to *Notothenia* species in the synonymies according to my present interpretations of the names used. For example, the name *Notothenia microlepidota* is listed under that species even though during that period the name was used in reports on collections for specimens properly called *N. angustata*.

MUSEUM ABBREVIATIONS

In preparing my descriptions I have utilized specimens from the collections of museums whose names are abbreviated in the lists of material examined as follows.

BMNH: British Museum (Natural History), London.
CM: Canterbury Museum, Christchurch, New Zealand.
DM: Dominion Museum, Wellington, New Zealand.
MACN: Museo Argentino de Ciencias Naturales, Buenos Aires.

MLP: Museo de La Plata, La Plata, Argentina.

NMV: Naturhistorisches Museum, Vienna.

PM: Muséum National d'Histoire Naturelle, Paris.

SAM: South Australian Museum, Adelaide.

SU: Division of Systematic Biology, Stanford University, Stanford, California.

USC-*Eltanin*: material collected by the University of Southern California Antarctic Biological Research Program from the USNS *Eltanin*.

USNM: United States National Museum, Washington, D.C.

ZIL: Zoological Institute, Leningrad.

ZMB: Zoologisches Museum, Humboldt-Universität, Berlin.

MEASUREMENTS AND COUNTS

All measurements were made in a straight line with calipers, and are presented in the descriptions as thousandths of the standard length unless otherwise specified. All were made on the left side unless there was a deformity or loss which necessitated using the right side. Lateral line and pectoral fin counts were usually made on both sides. Those measurements which are not usually made, or which have been made differently in the past, are defined in the following alphabetical list.

Anal to Pelvic Distance: from base of pelvic spine to origin of anal fin.

Body, Depth of: measured at origin of anal fin.

Body, Width of: measured at thickest part of body above origin of anal fin.

Dorsal Interspace: distance between base of last spine of first dorsal fin and first ray of second dorsal fin.

Dorsal to Anal Distance: distance between origins of second dorsal and anal fins.

Dorsal to Caudal Distance: distance between last ray of second dorsal fin and midbase of caudal fin.

Head, Depth of: measured at vertical through cheeks.

Head, Length of: measured from tip of snout (upper jaw) to posteriormost edge of opercular flap.

Head, Width of: distance between cheeks.

Pectoral Fin, Length of: measured from base of uppermost ray to tip of posteriormost extending ray.

Pectoral to Pectoral Distance: distance between upper ends of bases of pectoral fins.

Pelvic Fin, Length of: measured from base of pelvic spine to tip of posteriormost extending ray.

Post Orbital Distance (*Postorbital Part of Head*): measured from posterior margin of orbit to posteriormost edge of opercular flap.

Standard Length: measured from tip of upper lip to midbase of caudal fin.

Upper Jaw, Length of: measured from tip of upper lip to posterior end of maxillary.

The counts for the caudal fin include all the branched rays plus 1 additional ray above and below, *i. e.*, the branched rays plus 2. The last ray elements in the second dorsal and anal fins are counted separately. The scales in a lateral longitudinal series are counted from the upper end of the base of the pectoral fin to the base of the caudal fin. Gill raker counts are given as follows: 6–9 + 0–1 + 12–17 = 18–26. This means that there are a total of 18–26 gill rakers, of which 6–9 are on the upper limb, none or 1 at the angle, and 12–17 on the lower limb. On each arch, except occasionally the fourth arch, there are 2 rows of gill rakers, one projecting anteriorly and the other posteriorly. These are called, respectively, the anterior and posterior series. The lateral lines and their counts as well as the terminology of the cephalic canals have already been described (DeWitt, 1962).

GENUS *NOTOTHENIA* RICHARDSON

A formal diagnosis of the genus will be presented elsewhere. The following characters serve to distinguish it from other genera of New Zealand marine fishes. The nostrils are tubular and single on each side; the New Zealand species have the hind margin of the tube extended into a flap. The gill membranes are joined to each other and to the isthmus, forming a free fold across the isthmus. The vomer and palatines are edentulous. Two dorsal fins are present, the first composed of 3–8 spines which are usually soft and flexible, the second long and composed of soft rays. The anal fin is similar to the soft dorsal fin. The pectoral fins have broad, almost vertical, slightly curved bases. The body is scaled; the head is nearly naked in the New Zealand species. The scales may be ctenoid or nonctenoid, with both types usually present. Two lateral lines are present on the body, one high near the bases of the dorsal fins, the other on the midside in the region of the caudal peduncle. In the New Zealand species the head is somewhat depressed, and the interorbital space and the top of the head are broad and flat.

KEY TO THE SPECIES

1a. Lateral scales 78–99; middle lateral line 24–37; upper lateral line 61–75; 15–19 gill rakers on lower limb of first gill arch; total number of gill rakers on first arch 24–30 .... *N. microlepidota*, p. 325.
1b. Lateral scales 73 or less; middle lateral line 23 or less; upper lateral line 30–61; 8–15 gill rakers on lower limb of first gill arch; total number of gill rakers on first arch 15–23 .... 2.
2a. (from 1b). Pectoral rays 21–24 .... *N. rossii*, p. 312.
2b. Pectoral rays 16–19 .... 3.
3a. (from 2b). Second dorsal fin with 35–41 rays; anal fin with 26–32 rays .... *N. coriiceps.*
3b. Second dorsal fin with 27–31 rays; anal fin with 22–26 rays .... 4.

4a. (from 3b). Upper lateral line with 36–48 tubular scales; total number of scales in upper and middle lateral lines 45–57; length of caudal peduncle 37.0–45.5 percent of head length; preoperculo-mandibular canal not connected with the temporal canal; dorsal surface of head without prominent ridges .... *N. magellanica*, p. 303.

4b. Upper lateral line with 45–61 tubular scales; total number of scales in upper and middle lateral lines 59–76; length of caudal peduncle 25.5–34.5 percent of head length; preoperculo-mandibular canal connected dorsally with the temporal canal; in larger specimens prominent ridges present on top of head extending from above each eye posteriorly onto temporal region .... *N. angustata*, p. 318.

Notothenia magellanica (Forster).

Gadus magellanicus Forster, in Bloch and Schneider, 1801: 10–11 (original description; type locality seas about Tierra del Fuego; no types preserved, description based upon notes taken from fresh specimens and an unpublished rough drawing); Forster, 1844: 361–362 (description); Richardson, 1846: 61 (listed in footnote, see under *Lota magellanica*, below).

Notothenia magellanica Richardson, 1844: 9 (counts with reference to illustration: "Icon. ined. Bibl. Banks. fig. 178," catalogued in British Museum (Natural History) in Banksian MSS. no. 6 & 7); Gill, 1862: 520 (listed).

Lota magellanica Richardson, 1846: 61 (possibly a mistaken generic assignation[2]); Gill, 1862: 520 (listed).

Notothenia magellanicus Günther, 1860: 260 (listed).

Notothenia magellanicuz Delfin, 1899a: 21 (listed).

Notothenia macrocephalus Günther, 1860: 263 (original description; type locality Falkland Islands; type in British Museum); Gill, 1862: 520 (listed); Cunningham, 1871: 470 (color notes); Perugia, 1891: 618–619 (description); Smitt, 1897; 9–12, pl. 3, figs. 23–26 (description, scales); Boulenger, 1900: 53 (listed).

Notothenia maoriensis Haast, 1873: 276, pl. 16 (original description; type locality near Lyttleton Harbour, New Zealand; present location of type unknown, probably lost); Hutton, 1876: 212–213 (description); Hutton, 1890: 279 (listed); Gill, 1893: 118 (listed); Waite, 1907: 29 (listed); Frost, 1928: legend for pl. 17, fig. 15 (otolith).

Notothenia antarctica Peters, 1876: 837 (original description; type locality Accessible Bay, Kerguelen Island; type in Zoologisches Museum, Humboldt-Universität, Berlin).

Notothenia antarcticus Studer, 1879: 131 (listed; color notes).

Notothenia hassleriana Steindachner, 1876: 69–70, pl. 6, left-hand figures (original description; type localities Puerto Bueno and Port-Gallant, both in Strait of Magellan; types in Naturhistorisches Museum, Vienna); Steindachner, 1898: 303 (listed).

Notothenia arguta Hutton, 1879: 339 (original description; type locality Campbell Island; type in British Museum); Hutton, 1890: 280 (listed); Gill, 1893: 118 (listed); Waite, 1907: 30 (listed).

Notothenia macrocephala Günther, 1881: 20 (listed); Vaillant, 1888: 27, pl. 3, figs. 2a–d (listed, illustrations); Boulenger, 1902: 186 (listed); Steindachner, 1903: 207 (listed); Dollo, 1904: 86 (listed, distribution); Lönnberg, 1907: 10 (listed, color notes); Regan, 1913: 277 (description, distribution); Hussakof, 1914: 89 (listed with counts); Waite,

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[2] In his description of *Lota breviuscula*, Richardson compares *L. breviuscula* with several other species, among which is "*Lota magellanica* of Forster." In a footnote he lists the species and gives some data for each. Here Forster's species is listed as *Gadus magellanicus*, with the following counts: B. 6; D. 5–31; A. 25; C. 14; P. 17; V. 6. These counts are identical with those given in Forster (in Bloch and Schneider, 1801: 11; 1844: 362) and Richardson (1844: 9) under *Gadus magellanicus*, except that Richardson does not give an anal fin count. It seems obvious that both *Lota magellanica* and *Gadus magellanicus* refer to the same fish, but the reason for the use of *Lota* is unclear to me.

1916: 66–69, pl. 3, fig. 2 (description, illustration); THOMPSON, 1916: 431–433 (description); REGAN, 1916: 378–379 (distribution); PHILLIPPS, 1921: 123 (listed); THOMPSON and ANDERTON, 1921: 94 (listed, synonymy); RENDAHL, 1925: 6 (listed); PHILLIPPS, 1927a: 13 (listed); PHILLIPPS, 1927b: 44 (listed); FROST, 1928: 454–455, pl. 17, fig. 15 (otolith); NORMAN, 1937b: 88–90 (description, illustration, distribution); NORMAN, 1938: 27 (distribution); OLIVER SCHNEIDER, 1943: 110 (listed, illustration); MACDONAGH and COVAS, 1944: 235–236 (description, distribution); FOWLER, 1945: 128–129 (listed); HART, 1946: 339 (pelagic young); FOWLER, 1951: 314 (key); ANDRIASHEV and TOKAREV, 1958: 199 (listed); ANDRIASHEV, 1959: 5 (vertebral count); BLANC, 1961: 124 (description); KENNY and HAYSOM, 1962: 252 (habitat, food); SLACK-SMITH, 1962: 14 (color notes, habitat, food).

MATERIAL EXAMINED. USNM 77329: Sandy Point (Punta Arenas), Strait of Magellan, 53°10′S., 70°55′W. (1; 183 mm.).

USNM 88755: Municipal jetty (Port Stanley?), Falkland Islands (1; 193 mm.).

USNM 88756: Mullet Creek, Falkland Islands, 51°44′S., 57°53′W. (2; 51.9 and 55.3 mm.).

USNM 171000: Kainan Bay, Ross Sea, Antarctica, 78°14′S., 161°55′W. (1; 229 mm.).

SU 59880: Macquarie Island (3; 48.0–169 mm.).

SU 59882: Macquarie Island (2; 139 and 168 mm.).

BMNH 1860.2.20.2: Falkland Islands (1, a skin; holotype of *N. macrocephala*).

BMNH 1886.11.18.28: Campbell Island, from Otago Museum, Dunedin, New Zealand (1; 150 mm.; type of *N. arguta*).

ZMB 21626: Deutsche Tiefsee-Expedition Station 123, 49°07′S., 08°40′E.; bottom depth 4418 m.; presumably taken at surface in a plankton net, 22 November, 1898 (1; 80.2 mm.).

NMV 59926: Port Gallant (Puerto Gallant), 53°40′S., 71°58′W., field no. 1203a (1; 86.0 mm.; lectotype of *N. hassleriana*).

NMV 65389: Puerto Bueno, 50°59′S., 74°12′W., field no. 1203b (1; 87.0 mm.; paralectotype of *N. hassleriana*).

MACN 1859: Punta Colnet (Cabo Colnett, 54°43′S., 64°20′W.), 17 fathoms (1; standard length not measured).

MACN 2673a: Bahia Tethis (Tierra del Fuego), (1; 155 mm.).

ZIL (no number): Transvaal Cove, Marion Island, about 2 meters (2; 189 and 216 mm.).

ZIL (no number): Scotia Sea, 60°38′S., 44°08′W., bottom depth 287 m.; depth of capture 0–60 m.; gear Isaacs Kidd trawl; at *Academician Knipowich* Station 85 (1; 261 mm.).

CM (no number): South Island, New Zealand, probably near Dunedin (1; 137 mm.).

I have also examined specimens deposited in New Zealand museums (all uncatalogued) from the following localities. DM: Campbell Island, from Camp and Garden coves after tidal wave. CM: Campbell Island; Tucker Cove, Campbell Island; Penguin Harbour, Campbell Island; Perseverance Harbour, Campbell Island; Macquarie Island, 17 fathoms.

Description. Body evenly curved both dorsally and ventrally from head to base of caudal fin; compressed posteriorly, becoming broader and more rounded toward head; greatest depth of body at about origin of second dorsal fin; depth of body 208–282, its width 122–150; pectoral to pectoral distance 144–225; dorsal to anal distance 237–306. Caudal peduncle longer than deep, its length 107–135, its depth 93–102; dorsal to caudal distance 104–138. Head slightly shorter than average for genus, its length 280–320; its width, 146–248, about equal to its depth, 198–224. Vertebrae 16–18 + 28–30 = 45–47.

Snout very bluntly rounded from dorsal view; from lateral view it rises steeply from tip of upper jaw to a point a little above and anterior to nostrils, where it becomes abruptly less steep; its length 82–102. Tubes of nostrils short, with posterior rim raised into a flap which may be folded over opening; placed 52–79 from tip of snout, 17–29 from orbit and 52–75 apart. Eyes placed high on sides of head, but below dorsal profile; diameter of orbit 58–96. Interorbital region very broad and flat, its least width 88–134; all of top of head, from posterior part of snout to occipital region, nearly straight and rising slightly posteriorly; length of postorbital part of head 141–176.

Jaws short but wide, maxillary extending posteriorly to about vertical from pupil of eye; length of upper jaw 94–115. Teeth in each jaw in two almost uniserial bands; those in outer bands much larger and more numerous than those of inner bands and extend full length of jaws; inner bands confined to anterior ½ or less of jaws. The numbers of teeth vary, for in some individuals the bands are almost entirely uniserial, whereas in others they may become essentially double for part of their length. Oral valves extend most of length of each jaw, the lower broadest; their exposed surfaces covered with coarse papillae, especially close behind inner bands of teeth. Tongue fleshy and densely covered with short, slender papillae which may be covered by a mucous coating and appear as low rounded papillae.

Anterior gill rakers of first gill arch nondentigerous, or occasionally with 1 to a few spines, the larger ones flattened, arranged 3–6 + 1 + 9–13 = 14–19. Posterior gill rakers of first arch dentigerous, arranged 0–1 + 0–1 + 10–15 = 12 – 16. Gill rakers of remaining arches all dentigerous; 1–11 in posterior series of fourth arch. Branchiostegal rays 6; pseudobranchiae curved ventralward posteriorly.

First dorsal fin 3–6, originating 306–343 from tip of snout, from just behind to just in advance of upper end of base of pectoral fin; lower than second dorsal fin, second or third spine longest, 67–99. Second dorsal fin 29–31, originating 396–437 from tip of snout, 25–65 behind base of last spine of first dorsal fin; length of sixth ray 125–171, of sixth from last ray 87–105. Membrane behind last spine of first dorsal fin may reach to base of first ray of second dorsal fin. Anal fin 22–26, originating 513–606 from tip of snout, below bases of rays 8–10 of second dorsal fin; length of sixth ray 103–134, of sixth from last ray 82–98. Caudal fin 14–16, its length 165–242; its posterior margin changes shape considerably with size, being deeply forked in very small individuals and becoming emarginate or even slightly rounded in larger specimens.

Pectoral fins 16–18, their length 222–275, extending posteriorly to above bases of rays 1–8 of anal fin; width of their bases 81–88. In larger specimens (100 mm. or more) the upper rays are longest and cause the posterior margin to be obliquely truncate or slightly falciform; the lower posterior margin is rounded. Pelvic fins rather short, their length 166–216, third rays longest, not reaching posteriorly to base of anal fin; inserted 232–312 from origin of anal fin, not entirely to entirely in advance of bases of pectoral fins.

Upper lateral line 36–46, separated from origin of second dorsal fin by 6–10 scale rows, ending below rays 3–6 from last of second dorsal fin; middle lateral line 5–14. The pores of the cephalic canals are small and often difficult to see, but are otherwise normal. Preoperculo-mandibular canals with 10–11 pores; infraorbital canals with 8–9 pores; supraorbital canals each with 4 pores and sharing a median coronal pore; temporal canals with 6 pores; supratemporal canal with 3–4 pores.

Most scales on body nonctenoid, 47–64 in a lateral longitudinal series, 23–28 rows around caudal peduncle; ctenoid scales present in area of sides covered by appressed pectoral fins. These latter have a single row of weak teeth along the posterior margin which is vertical and straight and may be recessed into the scale. There may be also a few weak projections on other scales of the body. Scales extend onto base of caudal fin and exposed bases of pectoral fins. Medial bases of pectoral fins, including small portions of body posterior to bases, naked; a small scaleless area also present on exposed side just anterior to base of rays. Head nearly entirely naked; small patches of scales present behind eyes, on uppermost part of operculum, and at postero-lateral parts of top of head. Round fleshy papillae cover remainder of top of head, and are present around lower and posterior parts of eyes, on snout, opercles, and sometimes on skin covering posterior parts of maxillaries.

The color patterns of preserved specimens seem to vary considerably. Most of the specimens examined show no striking patterns anywhere, being darker above (bluish-grey to warm brown) shading to paler ventrally. The vertical fins are dusky, with pigment on both rays and membrane in the dorsal and anal fins, but mainly on the rays in the caudal fin. The pectoral fins are more or less dusky, being darkest in the more recently caught specimens. However, the 2 specimens from Marion Island in the collection of the Zoological Institute in Leningrad have a strikingly different coloration. Overall they are brown, darker above, lighter below, with small spots and mottlings, more or less distinct, on the upper parts of the body. There are very clear spots and vermiculations on the top and sides of the head, including, in the larger specimen, most of the snout and the upper medial part of the upper lip. Rather irregular spots and stripes are present on the dorsal and caudal fins, and there is faint spotting of the upper pectoral rays in the larger specimen. This spotted coloration is very similar to that found on most specimens of *N. angustata*. Norman (1937b) adds the following: ". . . more or less distinct longitudinal stripes or series of spots on the sides; traces of oblique stripes below eye; . . . soft dorsal dusky, sometimes reticulated, and with a narrow pale margin. The young are more silvery, especially on the lower parts of head and body, and the fins are much paler." Waite (1916) gives a good description of specimens from Macquarie Island: "The general color is olive grey, the lower parts yellow; the markings are black and somewhat irregular, but two oblique bands may be traced below the eye; a branch from the upper one crossing the lower part of the opercle; the rest of the upper parts and sides of the head bear irregular spots and lines; six or seven bands cross the back to below the lateral line, whence they break and form blotches alternating with the bands. The first dorsal is dark and clouded; the second has a dark intramarginal band and a white edge; diagonal bars cross the lower portion, and the clouding leaves lacunae in the membrane; the anal is sooty, but the tips of the rays are lighter; the other fins are also sooty but without markings."

In life the colors appear to be striking, as several authors have noted them. The back may be dark brown, dark grey-green, blue-grey, or rich golden-brown, passing to golden-yellow, cream, or reddish on the belly (the 189 mm. specimen in the Zoological Institute, Leningrad, was orange ventrally in life). The branchiostegal membranes may be bright orange-red or orange-yellow. The underparts of the head may be white, or the throat and jaws may be bright orange-red. The dorsal fins are blue-grey, the other fins grey (Cunningham, 1871; Lönnberg, 1907; Norman, 1937b; Studer, 1879).

The existence of pelagic juveniles in this species, which have been collected some distance from land over great depths, explains satisfactorily the wide distribution of the species and the apparent lack of differentiation between the many seemingly isolated populations. In their general coloration they resemble closely the pelagic young of *N. coriiceps* and *N. rossii*, species which also have wide distributions.

Antarctic specimens. Among the *Notothenia* material which I have examined are 2 large specimens captured well within the Antarctic Zone (Norman, 1938; Andriashev, 1965) which appear to belong with *N. magellanica*. One, USNM 171000, is from the Ross Sea and the other, in the Zoological Institute in Leningrad, is from the Scotia Sea. Both were collected from near the surface over fairly deep water. These 2 specimens thus present a problem with respect to both habitat and distribution. Information from the literature indicates that, except for the pelagic juveniles, *N. magellanica* is a near shore bottom fish, living among kelp, and that it can be captured with traps, hand lines and seines. Its distribution is primarily Subantarctic, extending into the edge of the Antarctic Zone only at Kerguelen and Macquarie islands. Further, very few species are known to inhabit both the Subantarctic and Antarctic zones. For these reasons the pelagic habit and high Antarctic localities of these 2 specimens suggest that they represent a different species. However, for nearly every character examined they show no differences from Subantarctic material of *N. magellanica,* and it may be that the observed differences are products of their large size. Also, since *N. magellanica* is known to penetrate into the edge of the Antarctic Zone, it may prove to be one more species which inhabits both the Subantarctic and high Antarctic for at least part of the year. For the present, then, I shall consider these specimens as possible representatives of a differing population of *N. magellanica* of unknown taxonomic rank.

Table 1 presents the pertinent measurements and counts taken from the Antarctic specimens together with the ranges of the measurements expressed as thousandths of the Standard Length. Comparison of these data with those taken from the subantarctic material shows that the Antarctic specimens have smaller eyes, a shorter distance between the tip of the snout and the nostrils, a greater distance between the nostrils and the edge of the orbit, a wider interorbital space, a shorter upper jaw, a deeper body, a greater distance between the origins of the second dorsal and anal fins, shorter pectoral and pelvic fins, and more rows of scales about the caudal peduncle.

Besides the above differences, the lowermost gill rakers in the anterior series of the first gill arch are dentigerous and appear similar to those of the posterior series; the caudal fin is distinctly emarginate and each lobe is pointed. Most striking, however, are the presence of ctenoid scales over most of the body. Those covered by, and just above and below, the appressed pectoral fins are strongly ctenoid, while those posteriorly on the sides of the body, anteriorly along the back, especially anterior to the first dorsal fin, and anterior to bases of pectoral fins are more weakly ctenoid. All of the scales on the belly, even anterior to the pelvic fins, are ctenoid.

There are no obvious markings on the body or head. Top and sides of head and upper parts of body a dark grey-brown or bluish black; body shading to paler below, head becoming paler more abruptly along ventral edges of cheeks and opercles, and on lower jaw; the Scotia Sea specimen is very pale orange-pinkish below. First dorsal fin uniformly black; membranes of second dorsal

TABLE 1. *Measurements (in mm.) and counts from two Antarctic specimens of* Notothenia magellanica, *with ranges of measurements expressed as thousandths of the Standard Length.*

Observation	USNM 171000	ZIL Specimen	Range
Measurements			
Standard Length (SL)	229	261	
Length of head (HL)	64.3	68.8	253–281
Width of head (HW)	51.6	—	215
Orbital diameter (O)	12.2	10.1	39–53
Length of snout (Sn)	19.8	22.1	85–86
Snout to nostril distance (Sn-N)	11.1	10.5	40–48
Nostril to nostril distance (N-N)	16.3	18.4	71
Interorbital width (IO)	32.5	35.6	136–142
Length of postorbital part of head (PO)	37.1	—	162
Length of upper jaw (JL)	21.2	24.0	92–93
Length of caudal peduncle (CPL)	27.7	34.9	121–134
Depth of caudal peduncle (CPD)	22.1	21.9	84–96
Dorsal to caudal distance (D-C)	28.6	—	125
Depth of body (BD)	72.6	70.1	269–317
Pectoral to pectoral distance (P-P)	50.2	—	219
Second dorsal to anal distance (D_2-A)	86.7	—	379
Snout to first dorsal (Sn-D_1)	70.5	70.8	271–308
Snout to second dorsal (Sn-D_2)	91.7	99.9	383–400
Snout to anal (Sn-A)	126	141	540–550
Anal to pelvic distance (A-V)	71.5	83.5	312–320
Length of caudal fin (CL)	46.7	48.5	186–204
Length of pectoral fin (PL)	49.9	57.0	218
Length of pelvic fin (VL)	35.8	39.8	152–156
Length of sixth ray of second dorsal fin	30.4	—	133
Length of sixth ray of anal fin	26.4	—	115
Counts			
First dorsal fin (D_1)	4	4	
Second dorsal fin (D_2)	31	29	
Anal fin (A)	25	25	
Caudal fin (C)	16	16	
Pectoral fin (P)	16	16	
Lateral scales (LatSc)	52	53	
Scale rows between lateral line and origin of second dorsal fin (LL-D_2)	10	—	
Scales around caudal peduncle (ScArCP)	30	32	
Upper lateral line (ULL)	37	44 & 45	
Middle lateral line (MLL)	10	2	
Branchiostegal rays (Br)	6	—	
Preoperculo-mandibular pores	10	12 & 10	
Infraorbital pores	8	9 & 8	
Supraorbital pores	4	4	
Temporal pores	6	6	
Supratemporal pores	3	3	
Anterior gill rakers, first arch	4+1+10=15	4+1+11=16	

fin black, the rays pale hyaline, creating the effect of white stripes on a black field. Membranes of anal fin dusky basally, clear hyaline toward margin, the rays pale. Caudal fin dusky, especially along upper and lower edges of rays. Pectoral fins dusky along upper and posterior margins, paler centrally and below; pelvics dusky.

Distribution. *Notothenia magellanica* has been recorded from the Magellanic region; Kerguelan, Macquarie, Aukland, and Campbell islands; and from the South Island of New Zealand. In addition it is recorded here for the first time from Marion Island and 2 localities well within the Antarctic Zone. Except for pelagic juveniles and the 2 far southern records, the species appears to inhabit only very shallow water, as all records (where the information is given) state that specimens were secured by traps, hand lines, or seines. The *Discovery* obtained a few juveniles with dip nets and tow nets from or near the surface in open waters. Kenny and Haysom (1962) state that the species lives among kelp near the shore at Macquarie Island, and Forster (in Bloch and Schneider, 1801; 1844) states that about Tierra del Fuego it lives near the shore among sea weed.

In the Magellanic region *N. magellanica* appears to be restricted to the west coasts of Tierra del Fuego and Patagonia, and the Falkland Islands, a pattern similar to that of several other Subantarctic species. It is probable that adults everywhere are associated with rocky and protected areas near shore.

Discussion. Although Norman (1937b) listed *Gadus magellanicus* Forster (in Bloch and Schneider, 1801) with a sign of interrogation under *Notothenia macrocephala* Günther, he considered Forster's description to be equally applicable to *N. macrocephala* and *N. microlepidota* (*non N. microlepidota* of Hutton, but equals *N. angustata* of Hutton; see discussions under both species). His reasons for this position were that the unpublished drawing of the species by Forster is a rough sketch which, while definitely representing a *Notothenia*, is not of sufficient detail to identify the species, and that the anal fin is described as having 25 rays, a number common to both species. Through the courtesy of Mr. A. C. Wheeler of the British Museum (Natural History) and the Trustees of the British Museum I have been able to obtain a photograph of Forster's drawing which is reproduced here (fig. 1). Although the drawing is obviously unfinished, it shows definitely that *N. macrocephala* is a synonym of *Gadus magellanicus*. The pectoral fin is drawn with an oblique posterior margin and with the upper rays longest, the snout is separated from the top of the head by an abrupt rounding above the nostrils, and the caudal fin is emarginate. These characters are diagnostic for the present species.

Norman (1937b) also lists *Notothenia porteri* Delfin as a synonym of *N. magellanica*, but a careful reading of the description demonstrates that the name is a synonym of *N. angustata*. A full discussion is presented under that species.

Figure 1. *Notothenia magellanica.* Reproduction of J. G. A. Forster's unpublished drawing of *Gadus magellanicus*, by permission of the Trustees of the British Museum (Natural History).

A final problem has been the location and designation of the types of *N. maoriensis*, *N. arguta*, *N. hassleriana*, and *N. antarctica*.

It would appear that the type of *N. maoriensis* has been lost. In 1965 Miss M. Büchler (now Mrs. M. Darby), then Assistant Zoologist in the Canterbury Museum at Christchurch, New Zealand, informed me that an old register, dating back to the early part of this century or even into the last century, contains the following entry:

> "*Notothenia maoriensis* Haast, Trans. N. Z. Inst. vol. 5, p. 276 *N. coriiceps* Hutton, Cat. Fishes N. Z.: 32 (*nec* Richardson) Stuffed (Type lost, originally stuffed)."

Miss Büchler made a thorough search through the fish collection and catalogues and the above entry was the only positive result. Therefore it seems fairly certain that the type is no longer in existence.

A number of fishes, some of which are types, were presented to the British Museum in the 1880's by the Otago Museum in Dunedin, New Zealand. Among them is a specimen labelled as the type of *Notothenia arguta.* Its total length is about 179 mm., which is close to the length of 7¼ inches (equals 184 mm.) given by Hutton in the original description. Dr. D. R. Simmon of the Otago Museum informed me (letter dated 8 April 1964) that "although N. arguta is entered as a name in the register . . . there is no record of a specimen being held by this museum." I therefore conclude that the British Museum specimen is indeed the type.

Notothenia hassleriana was described from an unknown number of specimens collected at 2 localities in the Strait of Magellan. I have examined 2 specimens

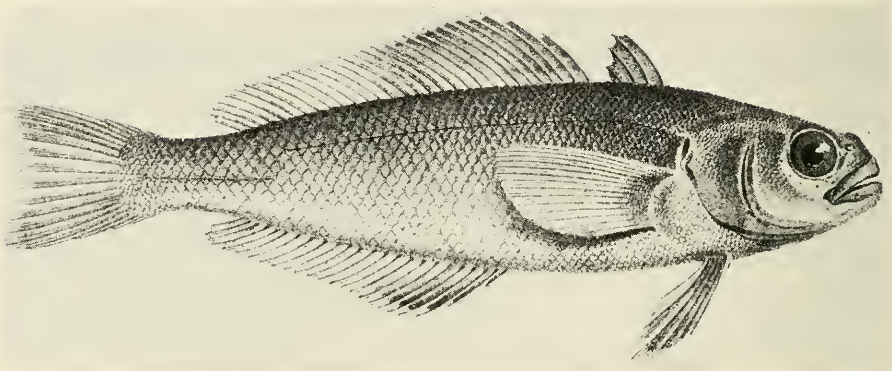

Figure 2. *Notothenia magellanica*, from Steindachner, 1876.

labeled as types, one each from the 2 localities. It is possible that these 2 specimens are all that Steindachner had, for Dr. P. Kähsbauer of the Naturhistorisches Museum in Vienna indicated in letters dated 7 October and 7 November, 1964, that these were all he could find. In any event, the specimen from Port Gallant (register number 59926) is very similar to the illustration published by Steindachner and reproduced here (fig. 2), and I designate this specimen as the lectotype.

Notothenia antarctica was described from a single specimen, 35 cm. long, collected by Dr. Studer during the voyage of the SMS *Gazelle* from Accessible Bay, Kerguelen Island. Dr. C. Karrer of the Zoologisches Museum of Humboldt University in Berlin has written that a specimen identified as *N. antarctica* of the proper size, from the above locality and collected by the *Gazelle* is in the fish collection there. Although it is not labeled as the type, it is undoubtedly the specimen Peters used for his description. Professor Kurt Deckert of the same museum had earlier written that although the register of the fish collection listed the type of *N. antarctica*, he had been unable to find it.

Notothenia rossii Richardson.

Notothenia rossii Richardson, 1844: 9–10, pl. 5, figs. 1 & 2 (original description and illustration; type locality unknown, but probably the Kerguelen Islands (Regan, 1916); type lost); Günther, 1860: 263 (description); Norman, 1937a: 61, 64 (description, separation from *N. coriiceps*); Norman, 1938: 25 (description, illustration, distribution); Blanc, 1951: 495 (listed, food); Blanc, 1954: 191 (listed); Blanc, 1958: 137 (listed, illustration); Blanc, 1961: 123–124 (description); Bellisio, 1966: 69, foto 40 (listed, illustration).

Notothenia rossi Regan, 1913: 240, 276–277 (description); Andriashev and Tokarev, 1958: 199 (juvenile listed).

Macronotothen rossii Gill, 1862: 521 (listed).

Notothenia marmorata Fischer, 1885: 53–55 (original description; type locality South Georgia, probably at about 54°31′S., 36°05′W.; types (2 specimens remain of original

Table 2. *Measurements (in mm.) and counts from the types of* Notothenia macrocephala, N. arguta *and* N. hassleriana. *Abbreviations are as in table 1, with the addition of body width (BW), anterior gill rakers of first gill arch (AntGR) and longest pelvic rays (LongVR). Where two measurements or counts are given, the second is taken from the right side.*

Observation	*N. macrocephala*: BMNH 1860.2.20.2 (Type)	*N. hassleriana*: NMV 59926 (Lectotype)	*N. hassleriana*: NMV 65389 (Paralectotype)	*N. arguta*: BMNH 1886.11.18.28 (Type)
SL	—	86.0	87.0	150
HL	84	24.5	25.4	45.4
O	16	5.7	6.1	9.5
Sn	—	7.5	7.1	13.4
Sn-N	—	4.9	4.5	8.7
N-N	—	4.9	5.2	9.9
IO	36	8.6	9.0	17.6
PO	—	13.1	13.9	23.9
JL	—	9.0	8.6	16.4
CPL	32	10.5	10.3	16.7
CPD	—	8.3	8.4	14.7
BD	—	21.6	22.3	38.7
BW	—	10.5	12.3	22.1
P-P	—	14.8	17.6	30.9
Sn-D_1	—	27.5	27.4	49.0
Sn-D_2	—	36.7	36.3	63.8
Sn-A	—	45.8	45.8	77.5
A-V	—	26.7	24.6	40.5
CL	—	18.4	18.0	29.4
PL	—	21.0	20.1	38.1
VL	—	16.8	16.8	29.8
AntGR	—	$5+1+11=17$	$5+1+10=16$	$6+1+11=18$
D_1	—	4	5	4
D_2	31	30	31	30
A	24	24	24	24
C	—	16	16	16
P	17	16 & 17	16 & 16	17
LongVR	—	3	3	3
LatSc	49	51	54	50
LL-D_2	—	7	6	7
ScArCP	—	27	24	24
ULL	38	41 & 42	40 & 38	38 & 36
MLL	11	9 & 11	10 & 11	9 (?) & 10

3) in Hamburgischen Zoologischen Staatsinstituts und Zoologischen Museums, Hamburg).

Notothenia macrocephala marmorata Lönnberg, 1905: 34–36, 53 (description, spawning); Lönnberg, 1906: 94–95 (description, spawning, food).

Notothenia coriiceps var. *macquariensis* Waite, 1916: 64–66, pl. 5, fig. 3 (original description and illustration; type locality Macquarie Island; lectotype in South Australian Museum, Adelaide); Regan, 1916: 378 (differentiation from *N. coriiceps*); Norman, 1937a: 60–61 (synonymized).

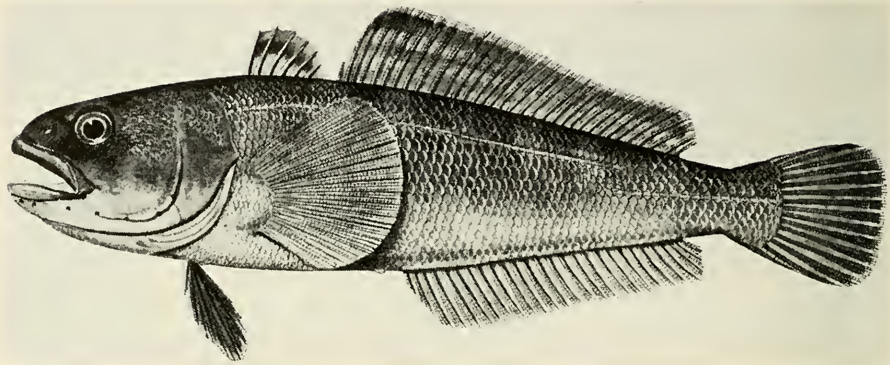

Figure 3. *Notothenia rossii*, from Waite, 1916.

Notothenia rossii marmorata Nybelin, 1947: 22–26 (differentiation from *N. r. rossii,* description, distribution); Nybelin, 1951: 23–27 (description, differentiation from *N. r. rossii,* spawning); Olsen, 1954: 373–382 (description, growth, food, habits); Ruud, 1954: 849 (oxygen capacity of blood); Olsen, 1955: 88 (biology compared to Channichthyids); Ladiges, Wahlert, and Mohr, 1958: 165 (designation of lectotype); Andriashev, 1959: 5 (vertebrae).

Notothenia rossii rossii Andriashev, 1959: 5 (vertebrae).

Material examined. SU 67031: washed up on beach, Macquarie Island (1; 461 mm.; partly eaten and eviscerated).

SAM (uncatalogued): Macquarie Island (1; 342 mm.; lectotype of *N. coriiceps macquariensis*).

The following material has been examined for purposes of comparison with the above Macquarie Island specimens.

BMNH 1937.7.12.563–4: Jetty (probably Government Jetty, Grytviken), South Georgia (2; 129 & 143 mm.).

USNM 107158: Stromness Harbour, South Georgia (1; 208 mm.).

USNM 179080: King George Island, South Shetland Islands (1; 274 mm.).

USC-*Eltanin* Station 671: South-west of South Georgia Island, 54°41′S., 38°38′W.; 220–320 m.; 10-foot Blake trawl (1; 432 mm.).

Description

Body less deep than *N. magellanica*, not becoming much deeper than head; ventral profile curves more evenly than dorsal profile, which rises most steeply in the snout; body compressed posteriorly, but becomes somewhat depressed anteriorly. Length of head 319–323, its width 234–292, its depth 204; depth of body 213, its width 138, dorsal to anal distance 235; pectoral to pectoral distance 219–228; length of caudal peduncle 103–104, its depth 85–91; dorsal to caudal distance 105–109. Vertebrae $20 + 31 = 51$.

Snout rises steeply in a smooth curve from lateral view, its length 86–95. Nostrils short tubes with the posterior margin raised into a point, placed 53–63 from tip of snout, 24–25 from orbits, and 63–67 apart. The mouth appears larger than in *N. magellanica,* but the upper jaw extends posteriorly only under anterior edge of pupil; length of upper jaw 130–138; lower jaw projects slightly beyond upper jaw. Eyes directed laterally, placed just below dorsal profile of head; diameter of orbit 51–58. Interorbital region broad and almost flat, both from lateral and frontal views, its width 102–105. Length of postorbital part of head 174–186.

Teeth in both jaws in 2 bands; outer band a single row of somewhat enlarged, evenly spaced, canine-like teeth extending almost full length of jaw, becoming slightly smaller anteriorly and absent near symphysis; inner band lies immediately behind outer row, broad anteriorly, becoming narrow posteriorly, extending posteriorly only ⅓ to ½ length of jaw (upper jaw) or as far as outer row (lower jaw). Tongue free anteriorly, fleshy, but not soft. Oral membranes extend most of length of jaws, papillose only along anterior edges.

Larger gill rakers in anterior series of first gill arch flattened, nondentigerous, and not very elongate, arranged 6 + 0–1 + 13–14 = 20. Posterior gill rakers of anterior gill arch dentigerous distally on anterior face, arranged 1 + 1 + 11 = 13 (SAM specimen); gill rakers of remaining arches similar. Branchiostegal rays 6; pseudobranchiae curved ventralward posteriorly.

First dorsal fin 5–6, lower than second dorsal fin, length of longest spine 39–60; its origin 301–332 from tip of snout, from slightly behind to slightly in advance of upper end of base of pectoral fin. Second dorsal fin 32–33 (Waite, 1916, gives 33–34), its origin 406–451 from tip of snout, 31–51 from base of last ray of first dorsal fin; first ray short, heavy and unbranched but segmented; length of sixth ray 101–102, of sixth from last ray 70–86. Anal fin 27–28, its origin 558–562 from tip of snout, beneath bases of rays 8–10 of second dorsal fin; length of sixth ray 81–92, of sixth from last ray 69–77. Caudal fin 14–16, its length 154–173, its posterior margin truncate.

Pectoral fins 22–23, their length 215–223, reaching posteriorly to above base of first ray of anal fin or not reaching to anal fin; middle portion of posterior edge truncate, upper and lower portions rounded; uppermost ray very short, about 48. Pelvic fins inserted 237–330 from origin of anal fin, entirely in advance of bases of pectoral fins; their length 157–160, third, or third and fourth rays longest, not at all reaching to anal fin.

Upper lateral line of body with 40–57 tubular scales, dipping slightly above upper end of base of pectoral fin, ending posteriorly below about fifth to ninth from last rays of second dorsal fin, and separated by about 6–7 scale rows from origin of second dorsal fin. Middle lateral line with 15–17 tubular scales, originating below or a little behind end of upper lateral line and extending a short distance onto base of caudal fin. Cephalic lateral line system normal in pattern, but pores very small and difficult to see. Preoperculo-mandibular canals with 10 pores, not connected to temporal canals; infraorbital canals with 8–9 pores; supraorbital canals with 4 pores and sharing a coronal pore; temporal canals with 6 pores; supratemporal canal with 3 pores.

Scales in lateral longitudinal series 55–57; 28–29 around caudal peduncle. Scales nonctenoid except for those in area of side of body covered by appressed pectoral fin and a little posteriorly which are weakly ctenoid; scales present everywhere on body except medial (posterior) base of pectoral fin and area immediately adjacent, and an arc along lateral base of pectoral fin; scales extend onto proximal part of caudal fin and onto lateral proximal part of pectoral fin; scales small on belly, ventral area anterior to pelvic fins and on back anterior to first dorsal fin. Scales absent on head except for about upper ½ of cheeks behind eyes, about upper ¼ of operculum, and 2 small patches on each side, one in front of the other, on posterolateral corners of top of head. Head only very slightly rugose, with small raised vermiculations, the most prominent radiating from eyes. Low ridges present, probably associated with parietal and pterotic bones.

Color (in alcohol) of the SAM specimen is dark grey-brown with some blue above, becoming lighter, somewhat yellowish below. Second dorsal fin with dark longitudinal bands, 3 anteriorly, 2 posteriorly, rather irregular anteriorly. The SU specimen is brownish black above, lighter on belly. The second dorsal is marked with somewhat irregular brownish bands which extend posteroventrally in anterior part of fin and more or less parallel with back in posterior part of fin. Anal fin dusky except for a pale margin; caudal fin irregularly and indistinctly mottled. Two faint stripes on head, one extending along edge of upper jaw, the other extending from posteroventral edge of eye to angle of preopercular.

Subspecies. *Notothenia marmorata* Fischer, described from South Georgia, has long been considered a synonym of *N. rossii* since comparison of material from Kerguelen and Macquarie islands with that from the region of the Scotia Sea has shown that the two populations are very similar. Nybelin (1947, 1951) was the first to call attention to differences between specimens from the two regions, and he resurrected the name "*marmorata*" as a subspecies of *N. rossii.* Unfortunately, very little material has been reported from the Kerguelen-Macquarie region (Richardson, 1844; Waite, 1916; Blanc, 1951, 1954, 1961). The most reliable published information is that by Richardson; Waite's 1916 paper contains numerous errors, and his methods of counting differ in some instances from those now in practice; the data given in the papers by Blanc seem to have been copied from reports on Antarctic material and cannot be used. For these reasons the data presented above, although obtained from only 2 specimens, are important additions to our knowledge of the species.

Combining my observations with those of Richardson, it seems possible that

TABLE 3. *Measurements* (*in mm.*) *and counts from two specimens of* Notothenia rossii *from Macquarie Island. Abbreviations are as in table 2. Where two measurements or counts are given, the second is taken from the right side.*

Observation	Lectotype	SU 67031	Observation	Lectotype	SU 67031
SL	342	461	A-V	98.1	152
HL	109	149	CL	52.7	79.8
O	17.5	26.8	PL	73.5	103
Sn	32.5	39.7	VL	54.9	72.3
Sn-N	21.6	24.4	AntGR	6+1+13	6+0+14
N-N	22.8	29.1		=20	=20
IO	36.0	47.1	D_1	6	5
PO	59.5	85.7	D_2	33	32
JL	44.4	63.4	A	28	27
CPL	35.1	48.1	C	16	14
CPD	31.0	39.3	P	22 & 22	23
BD	72.3	—	LongVR	3	3 and 3 & 4
BW	47.1	—	LatSc	57	55
P-P	74.9	105	LL-D_2	7	6
Sn-D_1	103	153	ScArCP	28	29
Sn-D_2	139	208	ULL	57 & 54	40
Sn-A	191	259	MLL	17 & 17	15

the Kerguelen and Macquarie material differ from the Scotia Sea material in having a longer snout (86–95 vs. 75–86), a broader interorbit (102–105 vs. 87–100), a longer upper jaw (130–138 vs. 106–123), a greater distance between the tip of the snout and the origin of the anal fin (558–562 vs. 472–547), fewer rays in the second dorsal fin (32–33 vs. 34–35), fewer vertebrae (51 vs. 52–53), and different coloration. It may be that the proportional differences are due to size, as the 2 Macquarie Island specimens examined are larger than nearly all of those seen from the Scotian region, but the counts and color differences seem to be reliable. In color, specimens from the Scotian region have the sides of the body covered by a series of irregular lines and blotches, with sometimes a dark arc at the base of each pectoral fin and spots on top of the head. The second dorsal is marked in much the same manner as in the Macquarie specimens, but the bands are much more distinct.

For the above reasons I believe there is good evidence for following Nybelin in recognizing as subspecies two populations, one, *N. rossii rossii,* inhabiting the Kerguelen and Macquarie islands, and the other, *N. rossii marmorata*, inhabiting the islands of the Scotia Ridge system, including the South Shetland Islands.

DISCUSSION. In his original description of *N. coriiceps* var. *macquariensis,* Waite stated that the type was in the South Australian Museum, but he did not specifically designate either of the 2 specimens upon which his description was based. I therefore select the specimen from the South Australian Museum listed under material examined as the lectotype. The second specimen, now presumably in the Australian Museum, Sydney, becomes a paralectotype. I do not know whether the lectotype is the specimen illustrated by Waite, but selecting the specimen in the South Australian Museum accords with Recommendation 74D of the International Code which suggests that a lectotype be selected from the material in the institution containing the largest number of types from the collection worked upon by the original author.

Notothenia angustata Hutton.

Notothenia coriiceps (*non* Richardson) HUTTON, 1872: 26 (brief description); THOMPSON and ANDERTON, 1921: 94 (listed).

Notothenia cornucola (*non* Richardson) HUTTON, 1873: 262–263 (brief description).

Notothenia angustata HUTTON, 1875: 315–316 (original description; type locality Dunedin Harbour; type in Otago Museum); HUTTON, 1876: 213 (an almost verbatim reprint of the previous paper; localities given as Dunedin and Bluff harbours); HUTTON, 1879: 339 (listed, synonymy); HUTTON, 1890: 279 (listed); GILL, 1893: 118 (listed); WAITE, 1907: 30 (listed).

Notothenia parva HUTTON, 1879: 339 (original description; type locality Auckland Islands; types in Dominion, Otago and British Museums); HUTTON, 1890: 280 (listed); GILL, 1893: 118 (listed); WAITE, 1907: 30 (listed).

Notothenia porteri DELFIN, 1899b: 118–120 (original description; type locality Talcahuano, Chile; type (or types) possibly in the old natural history museum in Valparaiso, Chile).

Notothenia microlepidota (*non* Hutton) BOULENGER, 1902: 185 (listed); WAITE, 1909: 590–594 (description, illustration); REGAN, 1913: 277–278 (description); WAITE, 1916: 69 (listed); REGAN, 1916: 379 (synonymy); THOMPSON AND ANDERTON, 1921: 94 (listed); MACDONAGH, 1936: 428–429 (synonymy); NORMAN, 1937b: 90–91 (description, synonymy, distribution); FOWLER, 1951: 314 (key); MORELAND, 1957: 34 (listed); PARROTT, 1958: 110–111 (description, variation).

Notothenia latifrons THOMPSON, 1916: 434–435, pl. 3, fig. 1 (original description and illustration; type locality Sandy Point (Punta Arenas), Strait of Magellan; holotype in U.S. National Museum).

Notothenia macrocephala (*non* Günther) FOWLER, 1926: 283 (description).

Notothenia patagonica MACDONAGH, 1931: 100 (original description; type locality among the rock ledges of Bahia del Fondo, Golfo San Jorge, Santa Cruz (province), Patagonia (Argentina); holotype in Museo de La Plata); MACDONAGH, 1934: 84–91, pl. 10, figs. 2 & 3, pl. 11, figs. 1 & 2, pl. 12 (description, illustrations, scales, systematics).

MATERIAL EXAMINED. BMNH 1886.11.18.29: Auckland Islands; from the Otago Museum (1; 71.7 mm.; lectotype of *N. parva*).

BMNH 1886.11.18.30: Dunedin, New Zealand (1; 238 mm.).

BMNH 1936.7.7.4: among the rocky ledges of Bahia del Fondo, Golfo San Jorge, Santa Cruz (province), Patagonia (Argentina) (1; 230 mm.; paratype of *N. patagonica*).

USNM 39670: New Zealand (1; 182 mm.).

USNM 176391: Huiches Island, Chile (45°10′30″S., 73°33′W.) (1; 332 mm.).

MLP 12–XII–30–1: same data as for BMNH 1936.7.7.4 (1; 315 mm.; Holotype of *N. patagonica*).

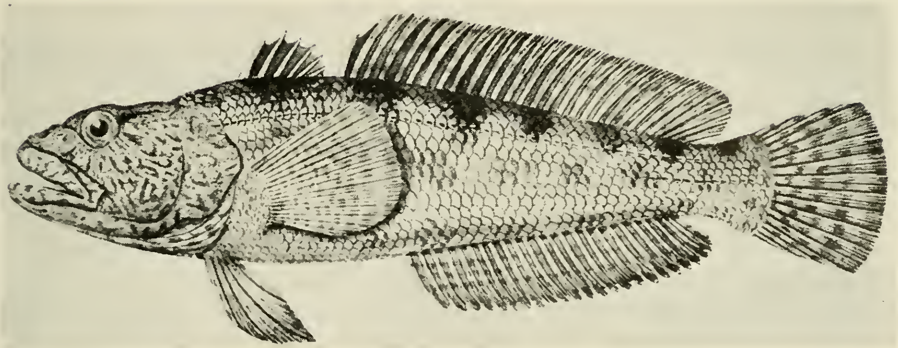

Figure 4. *Notothenia angustata*, from Waite, 1909.

CM (uncatalogued): Ranui Cove, Auckland Island (2; 56.2 and 85.8 mm.).

Selected measurements and counts were taken from the following specimens, all deposited in the Dominion Museum, New Zealand. 2864: Campbell Island (1); 2897: Oreti Beach, Southland (1); 3124: Campbell Island (1); 3332: outer Ranui Cove, Auckland Island (7); uncatalogued: Waitangi, Chatham Island, 43°36.2′S., 176°48.5′W. (3); uncatalogued: Glory Bay, Pit Island, Chatham Islands, shore, 43°47′S., 179°30′W. (1).

Material in the Canterbury Museum (all uncatalogued) from the following localities was also examined. Tucker Point, Port Ross, Auckland Island, under stones (2); west coast of Campbell Island (1); Tucker Cove, Campbell Island, among kelp at low tide (1); Auckland Islands (2); Laurie Harbour, Auckland Island (1); Ranui Cove, Auckland Island (1).

Description. Larger specimens more than usually compressed posteriorly; caudal peduncle distinctly deeper than long. Smaller specimens more cylindrical; caudal peduncle may be longer than deep. In region of bases of pectoral and pelvic fins, body becomes broader and less deep; the head appears depressed and small, although its measured length is similar to those for other species. Dorsal and ventral profiles about equally convex, or the ventral profile, at least of head, may be a little more convex than dorsal profile. Length of head 302–345, its width 187–281, its depth 181–187; depth of body 197–259, its width 140–188; dorsal to anal distance 229–288, pectoral to pectoral distance 189–266; length of caudal peduncle 92–117, its depth 92–125; dorsal to caudal distance 89–125. Vertebrae 17–18 + 27–29 = 44–46.

Snout broad and flattened, its length 84–98, longer than diameter of orbit. In lateral view the snout appears short, but its breadth causes its measured length to be larger. A pair of ridges, through which the supraorbital canals extend, separate the medial and lateral parts of the snout. These ridges curve around the posterior and medial sides of the nostrils and extend anteriorly to end at the edge of the groove behind the upper lip. In larger specimens the medial portion of the snout is flat and somewhat raised; in smaller specimens the ridges are little developed and the snout is more evenly rounded. The nasal tubes lie in shallow depressions, placed 52–66 from tip of snout, 17–30 from orbit, and 53–64 apart. The posterior half of each tube is raised into a pointed flap which can be used to constrict or close the nasal opening.

Eyes rather small, diameter of orbit 45–82, placed entirely within upper half of side of head, either above or extending slightly below line between tip of snout and upper end of base of pectoral fin, not projecting into dorsal profile of head. Interorbital region very broad, its width 81–104. Ridges of supraorbital canals, described above for snout, are continued through interorbital region on each side above eyes; these ridges are clearly visible on the small specimens. Medial portion of interorbital space flat and covered with elongate or finger-like papillae.

Supraorbital ridges continue onto postorbital part of head as ridges of temporal canals, and extend to above operculum. Upper surface of head behind eyes almost flat, covered with papillae like those of interorbital region; posterior limit of papillae follows posterior line of head medially, but overlies posttemporal bone laterally. Length of postorbital part of head 167–198.

Mouth broad, somewhat oblique, lower jaw projecting slightly; length of upper jaw 123–150, maxillary extending under anterior ¼ to ⅓ of eye; width of jaws 176–180. Teeth all conical, arranged in 2 bands in each jaw. Outer bands uniserial, composed of enlarged, almost canine-like teeth; inner bands broader, especially anteriorly, composed of smaller and more slender teeth. Inner band of lower jaw extends only along anterior ½ of jaw; that of upper jaw extends about full length of jaw. Outer bands of both jaws extend about full length of jaws, that of upper jaw being slightly longer than inner band.

Gill rakers in anterior series of first gill arch short, blunt, somewhat flattened obliquely to long axis of arch and bearing teeth distally; arranged 5–7 + 0–1 + 11–15 = 17–22; in smaller specimens those near angle may be more elongate, bearing teeth along upper edges. Gill rakers of posterior series of first gill arch dentigerous and only slightly flattened at right angles to long axis of gill arch, arranged 0–1 + 0–1 + 10–11 = 11–13; gill rakers of remaining arches similar. Branchiostegal rays 6.

First dorsal fin 4–7, its origin 289–329 from tip of snout, above or slightly in advance of upper end of base of pectoral fin; second spine longest, its length 62–102. Second dorsal fin 27–30, its origin 400–457 from tip of snout and 17–75 from base of last spine of first dorsal fin; length of sixth ray 111–162, of sixth from last ray 97–122. Anal fin 22–26, its origin 505–577 from tip of snout, originating below bases of sixth to eighth rays of second dorsal fin; length of sixth ray 96–138, of sixth from last ray 85–105. Caudal fin 14–16, its length 157–219, its posterior margin very slightly rounded, almost truncate.

Pectoral fins 17–19, their length 193–240, not extending to origin of or reaching to above first four rays of anal fin, their posterior margins rounded; width of their bases 80–97. Pelvic fins placed 262–346 from origin of anal fin, entirely in advance of bases of pectoral fins, their length 174–217, third or fourth rays longest, not reaching posteriorly to origin of anal fin.

Upper lateral line 45–61, terminating from below fourth from last ray to slightly behind posterior end of base of second dorsal fin, separated from origin of latter by 6–7 scale rows. Middle lateral line 9–18, extending a short distance onto base of caudal fin. Cephalic lateral line canals of normal pattern, the pores very small and difficult to see. Preoperculo-mandibular canals with 9–10 pores, connected to temporal canals; infraorbital canals with 8–10 pores; supraorbital canals each with 4 pores and sharing a median coronal pore; temporal canals with 5–6 pores; supratemporal canal normally with 3 pores, but in 1 specimen the canal is incomplete across the head and consists of a short tube on each side extending dorso-medially from the temporal canals, each with a single pore at its end.

Most scales on body ctenoid, 49–60 in a lateral longitudinal series, 27–31 rows around the caudal peduncle. Parrott (1958) records 61–69 scales in a lateral longitudinal series, but none of the specimens I have examined had counts that high; MacDonagh (1931) gives a lateral scale count of 68 for the holotype of *N. patagonica*, but I count only 60; Thompson (1916) records 67–73 lateral scales. Since Thompson's counts were made along the lateral line, and above it, from the angle of the operculum to the base of the caudal fin, higher counts would be expected. It is probable that the other high counts were made in a similar manner. Nonctenoid scales present on belly and area anterior to bases of pectoral fins; a few may be found along bases of dorsal and anal fins. Scales extend onto basal parts of caudal fin and, except for a narrow naked crescent at bases of pectoral rays, onto lateral bases of pectoral fins. Scales absent directly in front of bases of pelvic fins, but medially they extend to area covered by fold of branchiostegal membrane across isthmus.

Head almost entirely naked; a few scales, some of which may be ctenoid, present at posterolateral corners of head above temporal canals and on either side of supratemporal canal; a larger patch, some being ctenoid, present on upper part of operculum; a still larger patch, all nonctenoid, present on upper part of cheek behind eye; a few scattered scales may be present below eye.

Ground color of BMNH specimen 1886.11.18.30 brown, somewhat lighter, perhaps originally white or yellowish, on belly. Head somewhat darker and greyish above. No prominent markings present on body. Sides of head with darker vermiculations creating a marbled appearance; these markings continued onto lateral parts of snout, lips, lower jaw, and faintly onto branchiostegal rays. All vertical fins more or less uniformly brownish-dusky; second dorsal fin with indistinct and irregular darker brown markings on rays; anal fin with 1 or 2 series of darker markings on rays, tending to form horizontal lines. Rays of pectoral fins with brown spots, arranged to form bars on left side, but irregular on right side; pelvic fins with faint marbling similar to that on sides of head.

The USNM specimen from New Zealand is nearly entirely a uniform dark grey-brown. The larger of the 2 Canterbury Museum specimens has on the body irregular light areas over a dark background. The head is uniformly dark above and on the snout, but on each cheek is a series of 4 light lines, partially broken into spots, which radiate from the ventral and posterior parts of each eye; irregular light spots are present on the operculum. The vertical fins are generally dark; the second dorsal fin has 1 to 3 light spots along its rays creating horizontal lines, most distinct anteriorly and basally; the anal fin shows light areas, irregularly arranged anteriorly, horizontally arranged posteriorly; tips of rays of second dorsal and anal fins pale. The pectoral fins show only faint barring and spotting. The smaller specimen is essentially the same as the larger, but the light areas on the sides of the head are larger and less broken.

Little has been recorded of life colors. Hutton (1875; p. 316) gives "Variable in color from dark olivaceous black to olive-green, slightly mottled with blackish on the back; lips speckled with white; axil of pectorals yellow; caudal and dorsal blackish." In his description of *N. porteri* Delfin (1899b; pp. 119–120) gives some color notes for the South American representatives of the species. The color of the iris is reddish yellow and the conjunctiva is green speckled with greenish yellow spots. The cheeks are described as hoary, with a scaled appearance due to the coloration, which probably refers to the dark vermiculations described above, which do sometimes look like scales. Most of the body is a greenish brown, with blackish overtones above, becoming paler ventrally; there also may be 1 or 2 longitudinal bands. Rays of pectoral fins with yellow spots, largest basally; the axil is yellow. Membranes of dorsal and anal fins dusky green, with spots of two shades of greenish yellow. Caudal fin greenish brown with a pale vertical band.

DISTRIBUTION. I can find no essential differences between the New Zealand and South American material and I therefore concur with Norman (1937b; p. 91) that specimens from the two areas represent the same species. Such a broad distribution is not surprising when one considers the broad distributions of other closely related species (*N. coriiceps*, *N. rossii*, and *N. magellanica*), all of which have characteristic pelagic young. Although no pelagic juveniles of this species have been found, it is probable that they do exist. Night-light fishing in the waters east of New Zealand might prove fruitful, for many pelagic juveniles of the other three species have been obtained in this manner.

Discussion. The use of the specific name "*angustata*" for this species and the inclusion of *Notothenia porteri* in its synonyny represents a radical departure from the interpretations of all workers since Hutton's time. My reasoning is as follows.

Probably no one took the trouble to read Delfin's description carefully, for the number of spines and rays in the dorsal and pectoral fins, and the color description, which have been abstracted and brought together above, clearly indicate that the species cannot be *N. magellanica* (D_1 4–6; D_2 28–30; P 18–19 in *N. porteri* vs. D_1 3–6; D_2 29–31; P 16–18 in *N. magellanica*).

The realization that something was amiss in the interpretations of Hutton's work by later authors came as a result of attempting to place the various early names applied to New Zealand nototheniids with the 5 species recognized from the area by Parrott (1958). Although it became clear that Hutton had himself confused species, certain important discrepancies were found between his descriptions of *N. angustata* and *N. microlepidota* and the species to which the names were applied. These include fin ray counts, scale counts, color, and shape of the caudal fin. I concluded that the name *Notothenia angustata* should apply to the species which has been called *N. microlepidota* by all authors since Hutton's time, and that the latter name should apply to the species which have been called *N. colbecki* and *N. filholi* (see discussion under *N. microlepidota*). The confusion can probably be traced back to the 1880's, when a number of fishes were given to the British Museum by the Otago Museum, including some type material. Among these fishes is a specimen identified as *N. microlepidota* which, although never labeled as such, was presumed to be the type (see Norman, 1937b; p. 89). I have examined this specimen (BMNH 1886.11.18.30) and it does belong with the species described here. Boulenger (1902; p. 185) was the first to apply the name *N. microlepidota* to the present species and, because he gave in the same paper an excellent description of the true *N. microlepidota* under the new name *N. colbecki*, all later authors followed him.

In an effort to obtain further and better evidence to support my belief that Hutton's species had been confused, I wrote to the Otago Museum in Dunedin, New Zealand. Dr. D. R. Simmon of that institution was kind enough to locate the *Notothenia* material in the museum and to discover that the types of *N. angustata* and *N. microlepidota* are probably there. Although there are no data which demonstrate that the Otago Museum specimens definitely are the types, the circumstantial evidence is very strong. In his 1876 paper, which redescribes both *N. angustata* and *N. microlepidota,* Hutton stated that the types of both species were in the Otago Museum. Further, the lengths given by Hutton are close to those measured by myself on the stuffed specimens, my measurements being greater for both species (*N. angustata*: Hutton's length "about 14.5 inches," equals 368 mm.; my measurement, TL = 407 mm.; *N. microlepidota*:

Hutton's length "about 17 inches," equals 432 mm.; my measurement 492 mm.). Mr. P. O'Brian, the preparator at the Otago Museum, stated that the process of stuffing tends to lengthen specimens slightly, and this may account for the apparent greater size of the stuffed specimens. There are other discrepancies between the original accounts and my own data, the most serious being the pectoral count of 18 for *N. microlepidota* (I counted 21 rays). This count is difficult to make on large specimens, however, because of thick investing skin, and I can only conclude that Hutton's count is in error. The same may be said for my scale counts, which were made with difficulty because of the heavy lacquer with which the specimens are coated. Other differences between Hutton's published accounts and my own observations include dorsal and anal fin ray counts.

Whether one believes, as I do, that the specimens in the Otago Museum are the types, or because of the above discrepancies one believes that they are not, the interpretations of Hutton's species by Boulenger, Waite, Norman, and Regan are untenable. *Notothenia angustata* is described as having "a bony ridge over each eye extending back to the posterior margin of the praeoperculum," the "Caudal rounded," the "Lips speckled with white," 19 rays in the pectoral fin and 52–58 scales in a lateral longitudinal series. The supraorbital ridges, rounded caudal fin and number of rays in the pectoral fin clearly distinguish it from *N. magellanica* and demonstrate that it is the same as the *N. microlepidota* of the above authors. Hutton described *N. microlepidota* as having 91 scales in a lateral longitudinal series, 12 scale rows between the origin of the second dorsal fin and the upper lateral line, and a truncate caudal fin. These characters are all incompatible with the species which has been called *N. microlepidota* and show its identity with *N. colbecki* and *N. filholi* (see discussion under *N. microlepidota*). Finally, the name "*microlepidota*" certainly refers to the small and numerous scales implied by the high counts given in the original description, and which is most inappropriate if the conventional interpretation of the 2 species is accepted. Table 4 presents the data for the types of *N. angustata* and *N. microlepidota*, together with those for the types of other species synonymized with them.

I have seen the holotype of *N. latifrons* (USNM 76854), but it is not in good condition and I did little with it. Thompson's description of the species seems good, and since the upper lateral line count of 51–56 is diagnostic for this species I again concur with Regan (1916) and Norman (1937b) that *N. latifrons* belongs in the synonymy of *N. angustata*.

Notothenia parva was described from 4 specimens ranging in size from 3 to 3½ inches in length (equals 76–89 mm.). I have been able to locate three of these specimens, which are now deposited in 3 different institutions: the British Museum, the Dominion Museum, and the Otago Museum. Since the specimen in the British Museum is not mounted in gelatine or on a glass plate and is the most accessible, I designate it as the lectotype, the two others thereby becoming paralectotypes.

The only remaining nomenclatural problem concerning this species is the identity of *N. maoriensis* Haast, which has priority over the name "*angustata*." However, it is not possible to determine without any doubt whether the original description applies to *N. magellanica* or to the present species. Characters which indicate an identity with *N. magellanica* are the first dorsal fin with only 3 spines, the lack of any mention of supraorbital ridges on the head, and the dark coloration and lack of any speckling on the head. Characters which indicate an identity with *N. angustata* are scales present below the eye, the posterior end of the upper lateral line ending below the last ray of the second dorsal fin, and the shape of the pectoral fin as shown in the figure published with the original description. The illustration might constitute conclusive evidence except that it is a relatively crude drawing and contains some obvious errors which indicate it was not made with care. In the description the second dorsal fin is said to have 29 rays; the drawing shows only 27, and the membranes are drawn in a manner not found in any specimens belonging to *Notothenia*. The pelvic fins are drawn with a spine and 6 rays with the first ray longest; I have never examined a specimen of *Notothenia* with 6 pelvic rays, and the third or fourth rays are longest, never the first. For these reasons I cannot trust the shape shown for the pectoral fin. Further, large specimens of *N. magellanica* have a number of low papillae below and behind the eyes, many of which are broad and flattened and appear similar to scales. It is possible that these were mistaken for scales by Haast.

To conclude, there is enough doubt concerning the identity of *N. maoriensis* to make me follow Regan and Norman in placing it with *N. magellanica*.

Notothenia microlepidota Hutton.

Notothenia microlepidota Hutton, 1875: 316 (original description; type locality Dunedin and Moeraki (45°23′S., 170°52′E.), New Zealand; holotype in Otago Museum, Dunedin); Hutton, 1876: 213 (virtual reprint of 1875 original description); Hutton, 1879: 339 (listed with counts); Hutton, 1890: 280 (listed); Gill, 1893: 118 (listed); Waite, 1907: 30 (listed); Fowler, 1945: 130 (listed).

Nototoenia filholi Sauvage, 1880: 228 (original description; type locality Campbell Island; types in Museum National d'Histoire Naturelle, Paris); Filhol, 1885: 345 (reprinting of Sauvage's description).

Notothenia filholi Dollo, 1904: 127 (listed); Vaillant, 1907: 22–23 (redescription of syntypes; correction of errors made by Sauvage); Regan, 1913: 278 (description from Vaillant and Sauvage); Phillipps, 1927a: 13 (listed); Phillipps, 1927b: 44 (listed); Blanc and Hureau, 1962: 341–342 (disposition of syntypes).

Notothenia colbecki Boulenger, 1902: 185, pl. 16 (original description and illustration; type locality Campbell Island; types in British Museum); Waite, 1907: 30 (listed); Waite, 1909: 594–595 (description); Regan, 1913: 278 (description); Waite, 1916: 70 (listed); Regan, 1916: 378 (distribution); Rendahl, 1925: 6 (listed); Phillipps, 1927a: 13

TABLE 4. *Measurements (in mm.) and counts from the types of* Notothenia angustata, N. microlepidota *and of some specimens bearing names considered as synonyms of them. Abbreviations are as in table 2. Where two measurements or counts are given, the second is taken from the right side, except for LongVR, where two figures indicate two rays are equally long.*

Observation	*N. angustata:* (Type)	*N. parva:* BMNH 1886.11.18.29 (Lectotype)	*N. patagonica:* MLP 12-XII-30-1 (Holotype)	*N. patagonica:* BMNH 1936.7.7.4 (Paratype)	*N. microlepidota:* (Type)	*N. filholi:* PM A2384 (Paralectotype)	*N. filholi:* PM A2384 (Lectotype)	*N. colbecki:* BMNH 1901.11.8.72–74 (Paralectotype)	*N. colbecki:* BMNH 1901.11.8.72–74 (Paralectotype)	*N. colbecki:* BMNH 1901.11.8.72–74 (Paralectotype)	*N. colbecki:* BMNH 1901.11.8.70–71 (Lectotype)	*N. colbecki:* BMNH 1901.11.8.70–71 (Paralectotype)
SL	348	71.7	315	230	424	126 (about)	151 (about)	111	102	73.1	331	196
HL	118	23.3	96.3	75.4	144	—	43.5	33.5	31.5	22.8	105	62.5
O	—	5.7	14.2	12.4	—	9.0	9.2	6.8	6.8	5.6	16.9	11.7
Sn	—	6.0	28.5	22.5	—	—	12.6	9.2	8.7	5.9	30.7	17.2
Sn-N	—	3.7	18.3	13.9	—	—	7.7	5.6	5.2	3.5	19.6	10.5
N-N	—	4.1	17.2	13.9	—	—	7.8	5.8	5.5	4.2	20.8	12.2
IO	36.3	5.8	26.6	22.4	45.2	9.6	11.1	9.0	8.2	5.8	34.0	19.2
PO	—	12.1	—	44.0	—	20.7	23.3	18.0	16.6	11.5	61.3	35.0
JL	—	9.2	43.2	34.6	—	—	15.7	11.7	11.8	8.5	39.0	22.2
CPL	—	7.4	31.0	24.2	—	17.2	—	13.9	13.2	9.9	42.2	24.1
CPD	—	7.3	29.1	24.6	—	10.4	—	8.8	8.6	5.9	30.0	15.5
BD	—	15.1	61.0	52.6	—	25.4	—	21.4	21.1	13.3	76.6	39.2
BW	—	10.5	48.4	39.4	—	14.9	—	15.3	14.0	8.4	62.8	26.1
P-P	—	13.6	—	61.1	—	17.4	—	18.9	17.7	10.6	85.7	39.4
Sn-D_1	—	23.1	91.1	71.7	—	—	44.5	35.0	32.8	23.9	106	61.3
Sn-D_2	—	32.8	126	102	—	—	—	50.4	46.7	33.7	154	89.2
Sn-A	—	37.8	171	116	—	—	—	58.5	54.1	37.1	177	108

Table 4. (*continued*)

Observation	*N. angustata:* (Type)	*N. parva:* BMNH 1886.11.18.29 (Lectotype)	*N. patagonica:* MLP 12-XII-30-1 (Holotype)	*N. patagonica:* BMNH 1936.7.7.4 (Paratype)	*N. microlepidota:* (Type)	*N. filholi:* PM A2384 (Paralectotype)	*N. filholi:* PM A2384 (Lectotype)	*N. colbecki:* BMNH 1901.11.8.72–74 (Paralectotype)	*N. colbecki:* BMNH 1901.11.8.72–74 (Paralectotype)	*N. colbecki:* BMNH 1901.11.8.72–74 (Paralectotype)	*N. colbecki:* BMNH 1901.11.8.70–71 (Lectotype)	*N. colbecki:* BMNH 1901.11.8.70–71 (Paralectotype)
A-V	—	20.4	93.8	67.4	—	38.4	—	31.3	30.0	19.5	104	53.5
CL	—	14.1	—	39.4	—	—	—	19.2	19.0	15.8	57.4	36.0
PL	—	17.2	60.8	46.6	—	27.0 & 26.5	28.7	23.2	21.1	17.0	66.2	38.2
VL	—	15.6	55.0	41.2	—	21.3	23.6	20.1	19.1	—	54.4	34.3
AntGR	—	6+0+13 = 19	6+1+12 = 19	5+1+13 = 19	—	—	—	9+1+18 = 28	—	—	8+1+19 = 28	9+1+19 = 29
D_1	6	7	6	5	6	6	6	8	7	7	7	7
D_2	28	29	29	29	29	29	about 27	27	27	27	27	27
A	25	25	24	24	23	about 24	23	23	23	24	23	23
C	—	15	—	16	14	14	14	about 14	14	14	14	14
P	19	18 & 17	18 & 18	18 & 17	21	20	21	20	20	20 & 21	20 & 20	20 & 20
LongVR	4	3 & 4	—	3 & 4	2 & 3	3	3	3	3	—	3	3
LatSc	52	51	60	59	about 80	about 90	about 87	98	96	89	88	84
LL-D_2	—	7	—	6	—	—	10	10	10	11	11	10
ScArGP	—	28	31	28	—	—	—	40	45	43	39	41
ULL	52 & 55	54 & 52	55 & 53	59 & 56	about 71	73	72	70	71	75 & 74	67 & 67	74 & 72
MLL	12	14 & 14	16 & 12	12 & 12	—	about 30	about 30	28 & 32	35 & 32	36 & 37	34 & 34	32 & 32

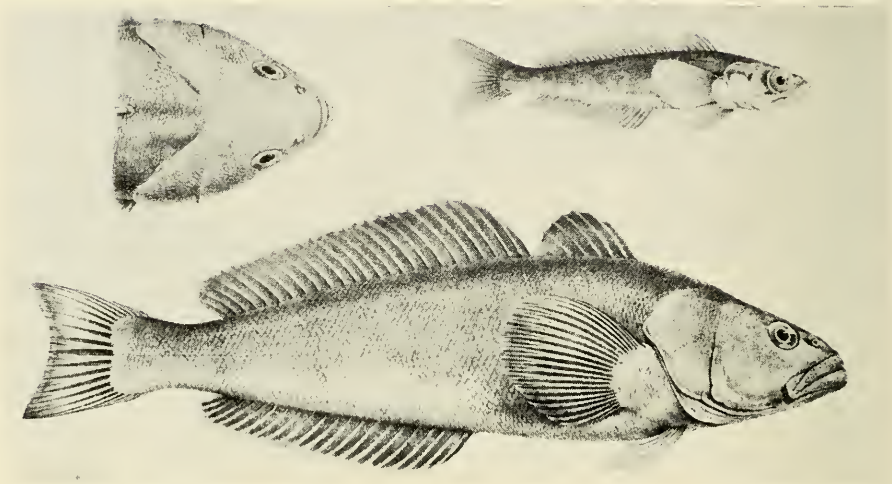

Figure 5. *Notothenia microlepidota.* Lateral view and top of head of adult, and lateral view of young; from Boulenger, 1902.

(listed); Phillipps, 1927b: 44 (listed); Norman, 1938: 27 (distribution); Parrott, 1958: 112–113 (description).

Material Examined. PM A2384: Campbell Island (2; about 126 and 151 mm., not in good condition; paralectotype and lectotype, respectively, of *N. filholi*).

BMNH 1901.11.8.70–71: Campbell Island (2; 196 and 331 mm.; paralectotype and lectotype, respectively, of *N. colbecki*).

BMNH 1901.11.8.72–74: Campbell Island (3; 73.1–111 mm.; paralectotypes of *N. colbecki*).

DM 2734: Campbell Island (4; 111–141 mm.).

The following New Zealand material was also examined, but not used for descriptive purposes.

In the Dominion Museum: 1413, Tucker Cove, Campbell Island (1); 2084, off Big South Cape Island (1); 3123, off rocks in N. W. Bay, Campbell Island (1); 3333, outer Ranui Cove, Auckland Island (2).

In the Canterbury Museum (uncatalogued): Campbell Island (3); Perseverance Harbour, Campbell Island, from throat of Shag (1); Perseverance Harbour, Campbell Island (1); Penguin Harbour, Campbell Island (1); Auckland Islands (2).

Description. Body fusiform, compressed throughout, including head (except in largest specimen); dorsal and ventral profiles nearly evenly curved throughout, a little more strongly so anteriorly, dorsal profile sometimes slightly more convex than ventral profile; caudal peduncle distinctly longer than deep. Length of head 288–341, its width 126–247, its depth 164–182; depth of body 182–232, its width 115–190, pectoral to pectoral distance 138–254, dorsal to anal distance 196–254; length of caudal peduncle 123–137, its depth 79–91; dorsal to caudal distance 124–144. Vertebrae 18 + 27–28 = 45–46.

Snout smoothly rounded from both lateral and dorsal views, rising from tip of upper jaw at about same angle as top of head; its length 81–100. Nostrils tubular, elliptic in cross section, each with its hind margin raised into a flap ending in a rounded point; nostrils placed 48–69 from tip of snout, 17–23 from orbit, and 52–63 apart.

Eyes directed laterally, placed high on head, above a line between tip of snout and upper end of base of pectoral fin, but not protruding into dorsal profile of head; diameter of orbit 51–77. Interorbital space broad and nearly flat, only very slightly convex, its width 66–103. Length of postorbital part of head 154–185.

Mouth oblique, lower jaw projecting slightly in front of upper jaw; length of upper jaw 104–128, maxillary extending posteriorly under first third of eye. Teeth in upper jaw may be described for convenience as being in 2 bands; outer band a uniserial row of enlarged, spaced (canine-like) teeth, extending only along anterior half of jaw; inner band composed of smaller, more closely spaced teeth, slightly broadened anteriorly, becoming a uniserial row posteriorly; inner teeth become slightly larger posterior to point where outer row ends. Teeth in lower jaw may be described as occurring in a single band, somewhat broadened anteriorly, with outermost teeth largest, and becoming a uniserial row of enlarged teeth in posterior two-thirds of jaw, the teeth becoming smaller posteriorly. Oral valves extend nearly entire length of jaws; they may be covered with papillae or not. Tongue rounded and free anteriorly, with a slight depression in its upper surface, and covered with scattered low papillae.

Gill rakers in anterior series of first gill arch slender and elongate, arranged 6–11 + 0–1 + 15–19 = 24–30; those on lower limb near angle slightly flattened on ventral edge, those further below flattened dorsoventrally, those on upper limb more cylindrical; all bear a few to many teeth, those on lower limb near angle with fewest. Posterior gill rakers of first arch short and blunt, somewhat flattened dorsoventrally, and bearing teeth; arranged 1–3 + 1 + 14–15 = 17–19. Branchiostegal rays 6.

First dorsal fin 6–8, its origin 295–338 from tip of snout, from above upper end to just in advance of bases of pectoral fins; its height relatively low, length of longest spine 86–110. Second dorsal fin 25–29, its origin 413–467 from tip of snout, 28–48 from base of last spine of first dorsal fin; highest anteriorly, length of sixth ray 105–130, of sixth from last ray 75–79. Anal fin 21–24, its origin 507–570 from tip of snout, below bases of rays five to seven of second dorsal fin; highest anteriorly, length of sixth ray 88–111, of sixth from last ray 76–87. Caudal fin 14, its length 173–216, its posterior margin distinctly emarginate, almost forked. Although the sample counted is small, the apparent lack of variation in the number of principal rays may be due to the emarginate shape of the fin, in which the principal unbranched rays are nearly as long as the longest branched rays and form most of the upper and lower edges of the fin.

Pectoral fins 20–21, their length 190–232, not reaching to, or extending as far as, above fourth ray of anal fin, the posterior margin rounded; width of their bases 66–88. Pelvic fins placed 251–314 from origin of anal fin, entirely in advance of bases of pectoral fins; their length 156–197, third ray longest, not reaching posteriorly to origin of anal fin.

Upper lateral line with 61–75 tubular scales, ending below last few rays of second dorsal fin or extending a short distance posterior to it, separated from origin of second dorsal fin by 9–11 scale rows. Boulenger (1902; p. 185) gives a range of 59–71, but his counts are low in every case. Table 4 presents my counts from the same specimens (see under discussion), which range from 67–75. Middle lateral line with 24–37 tubular scales, originating below ninth to fifteenth rays of second dorsal fin, and extending onto base of caudal fin.

Cephalic lateral-line canals normal in pattern except that preoperculo-mandibular canals are joined to temporal canals. The pores are small and difficult to find. Preoperculo-mandibular canals with 9–10 (usually 9) pores, connected to temporal canals at areas of second pores of latter canals; infraorbital canals with 9–11 (usually 10) pores; supraorbital canals each with 4 pores and sharing a median coronal pore; temporal canals with 6 pores; supratemporal canal with 2–4 (usually 3) pores.

Scales everywhere small, 84–98 in a lateral longitudinal series, with 37–45 rows around caudal peduncle; on body ctenoid except dorsally anterior to first dorsal fin, anterior to bases of pectoral fins, on ventral surface anterior to pelvic fins, and sometimes on lower sides of body between pelvic fins and anterior few rays of anal fin. A few nonctenoid scales may be found scattered among the ctenoid scales, especially at base of caudal fin, and the number of ctenae may be reduced to one. Scales extend onto basal parts of caudal fin and, except for a naked arc at bases of rays, onto exposed proximal portions of pectoral fins.

Most of head naked; 2 patches of scales, some of which are ctenoid, present on each side at posterolateral corners of head, one just anterior to supratemporal canal, the other in triangle formed by temporal canal, supratemporal canal and very weak ridge of posttemporal bone. An elongate patch of nonctenoid scales present on uppermost part of operculum; a patch of similar scales present on upper and anterior part of cheek, extending ventrally and anteriorly in a narrowing arc around posterior and ventral margins of eye. Upper portions of head, including snout, lips, and naked parts of cheeks, as well as other parts in lesser degree, covered with scattered and low papillae or ridges, the most marked being on top of head and anterior parts of lower lip and jaw.

Ground color of body (in alcohol) uniformly brownish or greyish, becoming lighter ventrally; lower half of body may be somewhat silvery (this probably reflects the method of initial fixation). Both dorsal fins dusky to deep brown; anal fin pale to brown; pectoral fins slightly brownish basally; pelvic fins a little dusky distally; caudal fin slightly dusky. Upper surface of head and tip of lower jaw dark, head otherwise becoming lighter ventrally; lower halves of operculum and cheek may be silvery. Indistinct and irregular dark areas may be present on top of head; a dark patch may be present behind eye at level of upper end of preopercular. Two dark lines may be present on lower parts of cheek, one extending from edge of upper jaw above end of maxillary posteriorly and ventrally towards lower margin of preopercular, the other extending from ventral margin of eye towards angle of preopercular. A third line, extending from posteroventral edge of eye to upper end of preopercular, may be present, and the dark patch behind the eye mentioned above may represent this line.

Juvenile specimens are somewhat silvery in color and, although there are no striking color changes between the young and adults as seen in *N. rossii*, the silvery color may indicate that the young of this species are also pelagic in habit.

Little has been recorded of life colors. Hutton (1875) gives "Purplish brown above, greyish below; throat, gill-membranes, axil of pectorals, and opercles yellowish." Parrott (1958) notes that a specimen from Auckland Island was dark olive-green with dark red bands on the dorsal and ventral fins.

Distribution. *Notothenia microlepidota* is known only from the New Zealand region, including Macquarie Island. Its habits are apparently similar to those of *N. angustata*, specimens having been captured primarily with hooks and lines close to shore.

Discussion. Since the nomenclature and synonymy used for this species are totally different from those used by previous authors, some explanation of the present usage is desirable. My first suspicion that the names *N. filholi* and *N. colbecki* represented the same species was entertained upon reading the account by Filhol (1885; pp. 343–346) of his fishing efforts at Campbell Island. He stated that *N. filholi* was the most common fish encountered there. Boulenger later described *N. colbecki*, also from Campbell Island, and it subsequently was found to be very common there, whereas *N. filholi* was never recorded again. Boulenger's description is good and it was accompanied by an excellent figure; *N. colbecki* was therefore easily recognized by subsequent workers. Sauvage's description, on the other hand, is not only brief, but contains a number of important errors (see Vaillant, 1907; p. 22, footnote), and no illustration was prepared. Thus *N. filholi* was never again recognized, although the name continued to be included in keys and check lists because of the unusual counts which Sauvage had given. Vaillant (1907) corrected Sauvage's errors, but his redescription and discussion has been disregarded. Regan (1913), apparently not knowing what to believe, gave the data of both Sauvage and Vaillant; later authors followed Sauvage.

Through the courtesies of Dr. Maurice Blanc of the Museum National d'Histoire Naturelle, Paris, and of Mr. A. C. Wheeler and Dr. P. H. Greenwood of the British Museum (Natural History) I have been able to examine 2 syntypes of *N. filholi* and 5 syntypes of *N. colbecki.* Although the specimens of *N. filholi* are not in good condition, I was able to take some counts and measurements from them. These are presented in table 4 together with the more complete data from the specimens of *N. colbecki.* There is no doubt that they all represent the same species, and the data from them have been incorporated into the above description.

I have related already the probable cause of the confusion attending Hutton's species *N. angustata* and *N. microlepidota* (see discussion section under *N. angustata*). Although there is some doubt whether the specimen in the Otago Museum thought to be the type of *N. microlepidota* is indeed the type, since there are no records or catalogues dating back to the 1870's, the original description leaves no doubt that Hutton's species is the same as both *N. filholi* and *N. colbecki.* The supposed type is now stuffed, and while its total length is somewhat greater than that recorded by Hutton, it is sufficiently near Hutton's figure that the difference can be accounted for by the process of stuffing. The counts taken from the specimen are presented in table 4 for direct comparison with those from the types of *N. filholi* and *N. colbecki*, and show conclusively that the specimen, whether type or not, represents the same species as the others.

A final matter is the selection of lectotypes from the type series of *N. filholi* and *N. colbecki.* As the lectotype of the former name I choose the specimen of 151 mm. standard length (Paris Museum number A2384) listed above in the material examined. This is as nearly as I can tell the specimen which Vaillant used for his table (1907; p. 23) and is probably the specimen referred to by Sauvage in his original description when he gave a length of 350 mm. (corrected to 150 mm. by Vaillant, 1907; see also Blanc and Hureau, 1962; pp. 341–342). For the lectotype of the name *N. colbecki* I choose the specimen of 331 mm. standard length (British Museum number 1901.11.8.70–71) listed above in the material examined. This is the largest of the specimens which remain of the type series, and is probably the specimen used for the figure of the adult published with the original description (there is some doubt because the legend for the plate states that the figure has been reduced to ⅛, which would mean the specimen was a little over 500 mm. in standard length; if the above specimen was used for the illustration the reduction is about ½). Boulenger also gives in his description a total length of 380 mm., which corresponds well with both Norman's (1938; p. 27) and my measurements (385 and 388 mm., respectively) for the largest specimen in the series, and indicates that this specimen was considered as the type. Only 5 of the original 12 specimens of the type series remain, and they are undoubtedly the 5 specimens Boulenger used for his table of counts and measurements (Boulenger's total lengths: 380, 230, 130, 120 and 85; my measurements: 388, 232, 130, 121 and 89).

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PROCEEDINGS
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Festschrift for George Sprague Myers

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HOW MANY RECENT FISHES ARE THERE?

By

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It is a pleasure to dedicate this paper to Professor George S. Myers on the occasion of his 65th birthday. His interests in ichthyology have ranged widely and the topic of this paper seems especially appropriate, not least because he has been interested in this particular problem himself.

Estimates of the number of species of Recent fishes in the current ichthyological literature range from a low of 15,000–17,000 to a high of 40,000. Presented below is a brief list of some.

SOME PAST ESTIMATES OF NUMBER OF RECENT FISH SPECIES

Bailey (1960) gave 15,000 to 17,000, of which about 45 are Agnatha and about 575 are Chondrichthys. His estimate was apparently based on a group approach.

Marshall (1965) mentioned that, "We know more than twenty thousand living kinds, but our inventory is by no means complete." He gave no basis for his estimate.

Norman (1963) gave 25,000, with no mention of how the figure was reached.

Myers (1958) stated there are, ". . . .33,000 or more living species of teleosts." No mention of method of estimation was given.

Schultz and Stern (1948) gave a figure of 40,000; however, Schultz (1965) later lowered his estimate to 32,000. No basis was given for either figure.

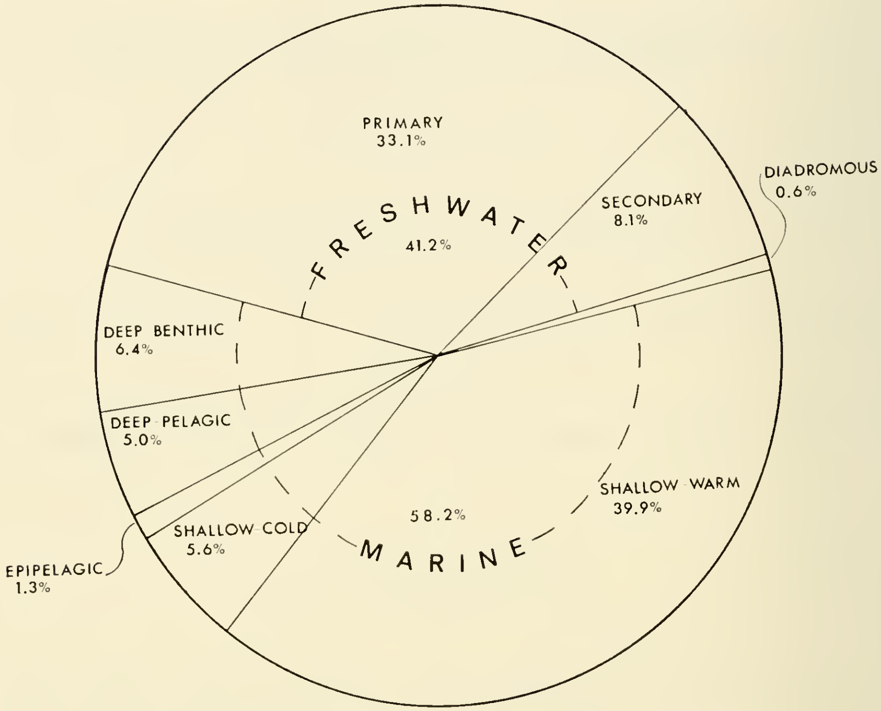

Figure 1. Percentages of Recent fish species living in various habitats.

MY ESTIMATE OF NUMBER OF RECENT FISH SPECIES

The wide range of figures suggests that a rational estimate, as opposed to an educated guess, is difficult for any one ichthyologist. With this in mind I compiled a list of fish families and began to solicit estimates from specialists and to consult recent revisions. Seven years have gone by since the initiation of the project, and this seems an appropriate time and place to present the results of my canvas. For the several groups for which neither colleagues nor recent revisions could supply information, I was obliged to consult several large faunal works and interpret the results in what I hope was a judicious manner.

Estimates are intended to be of the number of living species rather than described ones. Although approximately 75 to 100 species of Recent bony fishes are described each year (Zoological Record), we lack comparable information on how many species are placed in synonymy annually.

The final results of the present survey are: Agnatha about 50; Chondrichthyes 515 to 555; Osteichthyes 19,135 to 20,980. The figures given for bony fishes are two minimums rather than a maximum and a minimum. Most specialists who volunteered a single figure gave it as a minimum. Many colleagues, however, gave a range. The first figure, 19,135, is the sum of single estimates and the lower figures of ranges; therefore, it represents a bare minimum. The second figure is the sum of single estimates and the upper figures of ranges; therefore, it is a combination of minimum and maximum estimates.

I have attempted an ecological analysis of the data for Osteichthyes. The figures used for calculating percentages are averages of high and low estimates.

(1) Primary freshwater (Myers, 1949) 6650. *33.1 percent.* Approximately 6200 of this group belong to the Ostariophysi.

(2) Secondary freshwater (Myers, 1949) 1625. *8.1 percent.* Most of the species in this group belong to the families Cichlidae, Cyprinodontidae, and Poeciliidae.

Total freshwater 8,275. *41.2 percent.* If this astonishingly high percentage is valid it must be a reflection of the degree of isolation possible in the freshwater environment.

(3) Diadromous (including Complementary of Myers, 1949) 115. *0.6 percent.* As the systematics and life histories of tropical shore fishes become better known it seems likely that at least some species will be shifted from category 4 to this group.

(4) Marine shore and continental shelf to depths of approximately 200 meters—warm water 8000. *39.9 percent.* Perciform fishes and their derivatives are the major component of this category. Particularly important are percoid, blennioid, and gobioid fishes. Among nonperciforms, eels probably contribute the most species.

(5) Marine shore and continental shelf to depths of approximately 200 meters—cold water 1130. *5.6 percent.* A factor that may contribute to the substantially smaller size of this fauna as compared with that of group 4 is the smaller area occupied. Also, much of the region has had long-term, unstable climatic conditions so that many of the species must be fairly recent in their present habitats. There is no doubt, however, that a high degree of endemism prevails. Important components of this group are Gadidae, Zoarcidae, northern blennioids, and scorpaeniform fishes.

Total marine shore and continental shelf to 200 meters 9,130 *45.5 percent.*

(6) Continental slope and deep sea benthic below 200 meters 1280. *6.4 percent.* Important components of this group are Macruridae, and species of Brotulidae, Zoarcidae, Apodes, and Scorpaeniformes. Contrary to the opinion of Greenwood *et al.* (1966), I do not believe that this group or group 8 contains a great number of unknown species. Fishes of these groups occupy a vast amount of space; however, conditions are relatively so stable and uniform that niches are correspondingly few.

(7) Epipelagic (high seas) above 200 meters 255. *1.3 percent.* Important

groups in this category are Scombroidei and Synentognathi. These fishes are mostly mobile, living in an environment that offers few niches. The small number of species is scarcely remarkable.

(8) Deep pelagic below 200 meters (including mesopelagic and bathypelagic) 1010. *5.0 percent.* Clupeiform and myctophiform fishes are the chief constituents of this category. Probably more space is occupied by this group than by any other, yet the number of species is small. The environment is poor in niches and in energy; it is surprising that the fauna is not smaller.

SOME CONCLUSIONS

The number of species in any one of the 8 categories seems to be chiefly related to the degree of isolation possible. Certainly tropical reefs, great river deltas, and major river drainages have contributed a great variety of habitats and ecological niches which are reflected in the high percentage of species found in freshwater and along tropical shores.

The most important regions economically (though not necessarily in terms of biological productivity) are the cooler water shelf areas and the epipelagic, both regions with relatively few species.

A final conclusion concerns the freshwater fishes. In view of the high percentage of fishes found in freshwater and man's increasing modification of this environment throughout the world, it is vital that research be drastically increased on the basic systematics of freshwater fishes while this is still possible.

ACKNOWLEDGMENTS

It is a pleasure indeed to acknowledge the cooperation that I have received from my colleagues. Whatever value this paper may have is due to their contributions. I thank R. Bailey, P. Bănărescu, R. Behnke, F. Berry, J. Böhlke, R. Bolin, M. Bradbury, J. Briggs, W. Burgess, D. Caldwell, B. Collette, E. Crossman, W. Davis, H. DeWitt, W. Eschmeyer, J. Garrick, R. Gibbs, W. Gosline, D. Greenfield, P. H. Greenwood, M. Grey, R. Haedrich, E. Herald, L. Knapp, E. Lachner, R. Lavenberg, N. B. Marshall, H. McCully, R. McDowall, G. Mead, A. G. K. Menon, G. Miller, G. S. Myers, T. Nalbant, N. Parin, J. Randall, W. Richards, L. Rivas, C. R. Robins, R. Rofen, D. Rosen, R. Rosenblatt, L. Schultz, W. B. Scott, V. Springer, R. Suttkus, A. N. Svetovidov, W. R. Taylor, J. Tyler, E. Trewavas, B. Walker, V. Walters, A. Wheeler, N. Wilimovsky, and L. Woods.

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DESCRIPTION OF A NEW SUBSPECIES OF *RHABDOPHIS AURICULATA* IN THE PHILIPPINES, WITH COMMENTS ON THE ZOOGEOGRAPHY OF MINDANAO ISLAND

By

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During recent investigations on the snakes of the Philippine Islands, a study begun more than 15 years ago under the guidance of Professor George S. Myers, it became apparent that the island of Mindanao is inhabited by two clearly distinguishable populations of the diminutive natricine snake, *Rhabdophis auriculata*. That the two populations of this species occupy different but contiguous parts of Mindanao make this discovery the more interesting, inasmuch as it helps shed further light on the paleogeography of the island.

The type specimen of *Rhabdophis auriculata*, a species described by Günther in 1858, was collected by Hugh Cuming, its locality being given simply as "Philippine Islands." Miss Alice G. C. Grandison of the British Museum kindly examined Günther's type, compared it with the figure published by Boulenger (1893, pl. 17, fig. 1) [fig. 1], prepared a sketch [fig. 2] of the color pattern at the angle of the jaw, and responded that Boulenger's figure could well have been based on the type specimen. With Miss Grandison's sketch at hand, and after examining Boulenger's figure with care, I do not doubt that Günther's type is based on a specimen drawn from the eastern Mindanao population. I have seen specimens from Davao Province that closely approximate the Günther type, and

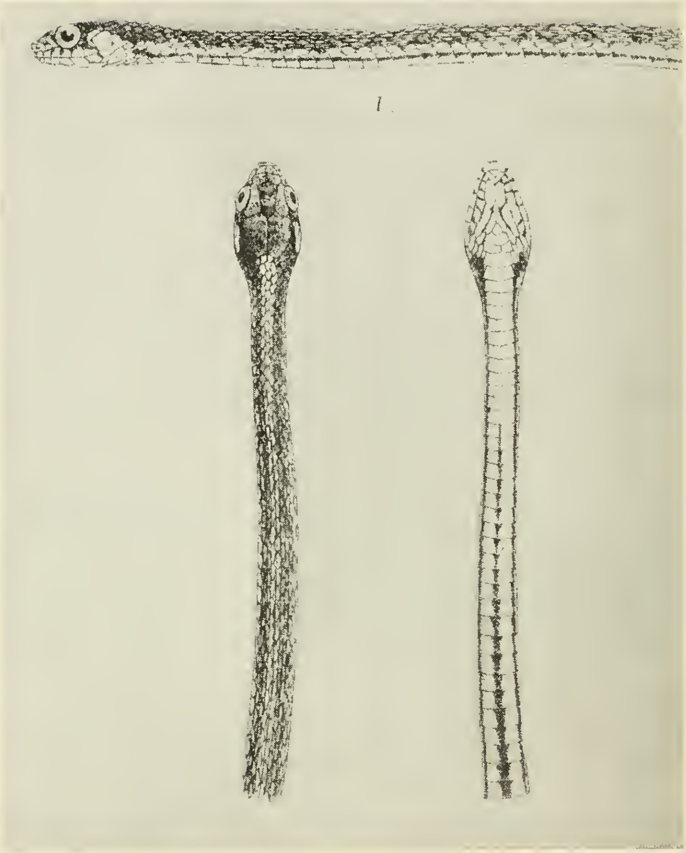

Figure 1. Figure of *Rhabdophis auriculata* published by Boulenger (1893).

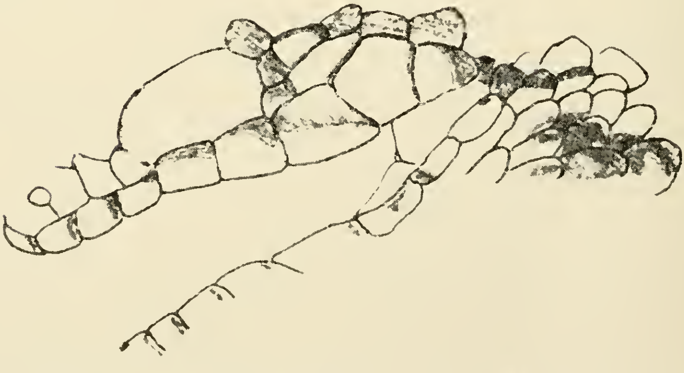

Figure 2. Sketch of scale and color pattern at angle of jaw on left side of holotype.

therefore, to insure stability of nomenclature, restrict the type locality of *Tropidonotus auriculatus* Günther to Mt. Apo, Davao Province, Mindanao Island.

Specimens of *Rhabdophis auriculata* from Zamboanga del Norte, Zamboanga del Sur, Misamis Occidental, and Bukidnon provinces of western Mindanao [fig. 3] differ from animals from the Davao-Agusan region in color pattern. These animals are referred to a new taxon, named in honor of Professor Myers, who has for many years concerned himself with the zoogeography of the Philippines, especially Mindanao Island:

Rhabdophis auriculata myersi Leviton, new subspecies.

(Figures 4–6.)

Tropidonotus auriculatus, Boulenger, 1893, Cat. Snakes British Mus., vol. 1, p. 261 (part; Mindanao [Pasanaca, Zamboanga City]).

Natrix auriculata, Taylor, 1922, Philippine Jour. Sci., vol. 21, p. 294 (Basilan [Port Holland]); 1923, Philippine Jour. Sci., vol. 22, p. 542 (Basilan, Mindanao [Zamboanga City]).

Diagnosis. Maxillary teeth 27–32, last 3 or 4 enlarged but not separated by diastemata from others; head short, distinct from neck; scales in 17 longitudinal rows on anterior third body, reducing to 15 at about level of 80th ventral plate; usually 3 labials bordering orbit; ventrals 143–162; subcaudals 80–93; hemipenes extending to end of 6th subcaudal plate, forked at end of 4th-mid 5th plate; sulcus forked; proximal portion opposite sulcus with longitudinal plicae, portion bordering sulcus spinose; 2 large basal spines present; distal forks uniformly spinose; ventrolateral black stripe extending forward to suture of 8th and 9th labials, continuing as diagonal stripe to corner of eye; lateral light stripe extending uninterrupted (rarely interrupted at angle of jaw by black spot on 8th upper labial) along side of body to anterior temporals. Measurements (of largest male and largest female, in mm.): ♂ s-v 342, tail 138; ♀ s-v 388, tail 165.

Holotype. CAS-SU 23391, an adult male, taken near Masawan, approximately 14 km. southeast of Buena Suerte, New Piñan, on west side of Dapitan Peak, Misamis Occidental Province, Mindanao Island, at an altitude of 4700 feet (1433 m.) on 13 April 1959 by Dr. Angel Alcala (figs. 4–5).

Paratypes (61). MINDANAO: Misamis Occidental Province: *West side of Dapitan Peak*: Masawan area, approximately 14 km. southeast of Buena Suerte, New Piñan, 26 March–20 April 1959 (CAS-SU 23372–23374, 23392–23394, 23397 [elev. 4400 ft. (1340 m.)]; 23375 [elev. 4400–4500 ft. (1340–1370 m.)]; 23376–23380, 23390 [elev. 4500 ft. (1370 m.)]; 23381–23382 [elev. 4700 ft. (1430 m.)]; 23383 [elev. 4300 ft. (1310 m.)]). Approximately 2 km. east of Masawan and 15 km. southeast of Buena Suerte, New Piñan, 5 April 1959 (CAS-SU 23384 [4700 ft. (130 m.)]). Approximately 12 km. east of Masawan, 6 April 1959 (CAS-SU 23387 [elev. 5500 ft. (1670 m.)]). Ap-

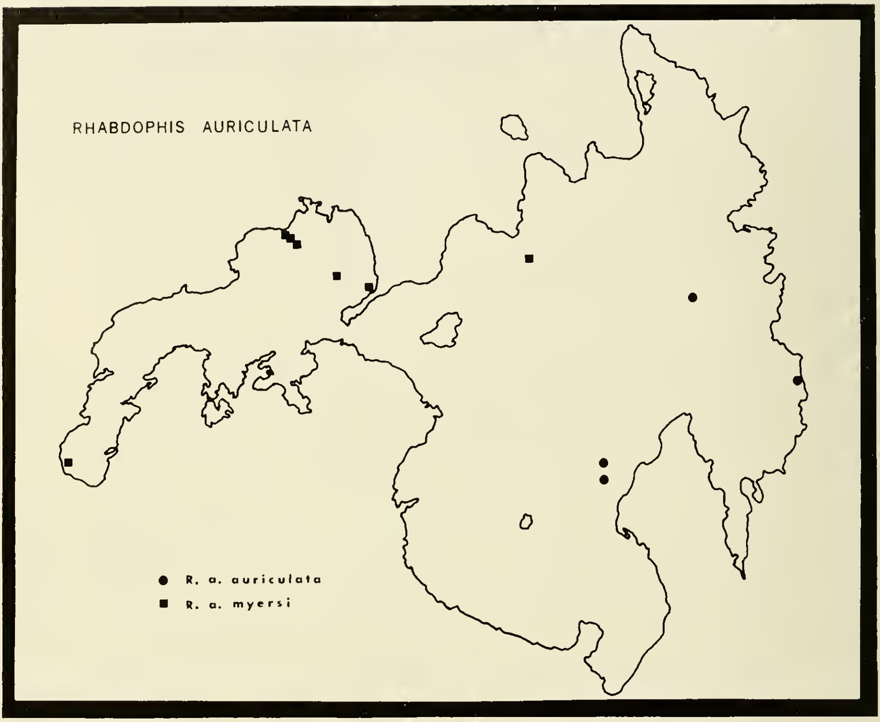

FIGURE 3. Known distribution of *Rhabdophis auriculata* on Mindanao Island.

proximately 2 km. southeast of Masawan and 16 km. southeast of Buena Suerte, New Piñan, 12 April 1959 (CAS-SU 23389 [elev. 4800 ft. (1460 m.)]). Approximately 2–3 km. southeast of Masawan, 19 April 1959 (CAS-SU 23395–23396 [elev. 5000–5200 ft. (1520–1580 m.)]). Ridge 11–12 km. southeast of Buena Suerte, New Piñan, 22 April 1959 (CAS-SU 23398 [elev. 4000 ft. (1220 m.)]). Bank of Dapitan River, 11–12 km. southeast of Buena Suerte, New Piñan, 23 April 1959 (CAS-SU 23399 [elev. 4000 ft. (1220 m.)]). Bank of Dapitan River, approximately 13 km. southeast of Buena Suerte, 25 April 1959 (CAS-SU 23400 [elev. 4200 ft. (1280 m.)]). ZAMBOANGA DEL NORTE PROVINCE: *West side of Dapitan Peak*: Gumay area, approximately 6 km. southeast of Buena Suerte, New Piñan, 28-29 April 1959 and 4–8 May 1959 (CAS-SU 23401, 23403–23404, 23419 [elev. 2500 ft. (760 m.)], 23402 [elev. 2400 ft. (730 m.)], 23426–23427 [elev. 2300 ft. (700 m.)]). Dapitan River area, approximately 1 km. southeast of Gumay and 7 km. southeast of Buena Suerte, New Piñan, 30 April–1 May 1959 (CAS-SU 23405–23413, 23415–23416 [elev. 2300 ft. (700 m.)], 23414 [elev. 2400 ft. (730 m.)]). Gumay Creek, approximately 6 km. southeast of Buena Suerte, 2–6 May 1959 (CAS-SU 23417, 23422

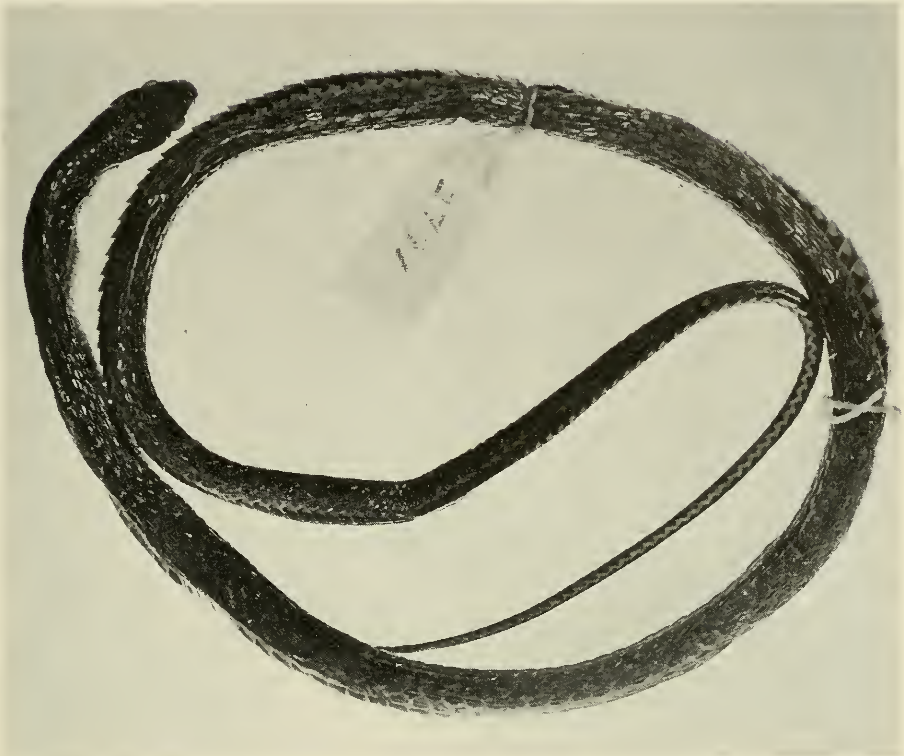

Figure 4. Holotype of *Rhabdophis auriculata myersi* Leviton (dorsal view).

[elev. 2300 ft. (700 m.)]). Bank of Dapitan River, approximately 2 km. southeast of Gumay and 8 km. southeast of Buena Suerte, New Piñan, 4 May 1959 (CAS-SU 23418 [elev. 2500 ft. (760 m.)]). Approximately 7 km. southeast of Buena Suerte, New Piñan, 5 May 1959 (CAS-SU 23420–23421 [elev. 2700–2800 ft. (820–850 m.)]). Approximately 10 km. southeast of Buena Suerte, New Piñan, 6 May 1959 (CAS-SU 23423–23425 [elev. 3500 ft. (1070 m.)]). Gumay, approximately 5–6 km. southeast of Buena Suerte, New Piñan, 26 March 1959 (CAS-SU 23371 [elev. 2500 ft. (760 m.)]). Gumay Creek, approximately 0.5 km. southwest of Gumay and 6 km. southeast of Buena Suerte, New Piñan, 8 May 1959 (CAS-SU 23428 [elev. 2400 ft. (730 m.)]). *Mt. Malindang*: Masawan, April-May 1956 (CAS-SU 19362–19364 [elev. 3500–4500 ft. (1067–1372 m.)]). Between Masawan and Gandawan, April 1956 (CAS-SU 19535). MISAMIS OCCIDENTAL AND ZAMBOANGA DEL NORTE PROVINCES BOUNDARY: *West side of Dapitan Peak*: Approximately 4 km. northwest of Masawan and 10 km. southeast of Buena Suerte, New Piñan, 9–11 April 1959 (CAS-SU 23385–23386 [elev. 3400 ft. (1040 m.)], 23388 [elev. 3500 ft. (1070 m.)]).

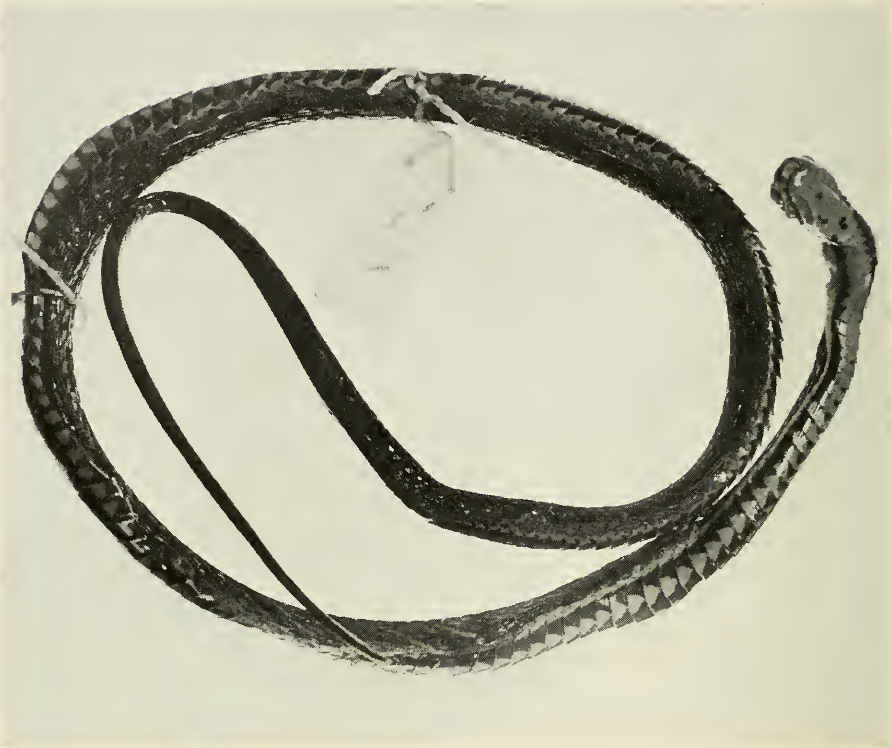

FIGURE 5. Holotype of *Rhabdophis auriculata myersi* Leviton (ventral view).

ADDITIONAL MATERIAL EXAMINED (30). BASILAN: Abung-Abung, 5–25 October 1921 (CAS 60332–60339). Port Holland, 5–25 October 1921 (CAS 60468). BOHOL: Cantaub Sitio, Sierra Bullones, 30 April 1955 (CAS-SU 18895). MINDANAO: BUKIDNON PROVINCE: Del Monte Plantation, 22 August 1940 (CAS-SU 12396). ZAMBOANGA DEL NORTE PROVINCE: Catagan, 15 May 1906 (USNM 37390). Katipunan, 30 km. up the Dicayo River (FMNH 68905–68906). Miatan, Katipunan (FMNH 68916–68917). ZAMBOANGA DEL SUR PROVINCE: San Ramon, 10 July 1929 (FMNH 14948). Zamboanga City, 23 September–6 October 1920 (CAS 62023–62029). PHILIPPINE ISLANDS: (FMNH 68909, USNM 37415–37418).

DESCRIPTION OF HOLOTYPE. Measurements (in mm.): snout-vent 318; tail 122; ventrals 157; subcaudals 82. Anal plate divided; 8 upper labials, 3–5 bordering orbit; nasal shield divided below nostril only; loreal 1; preocular 1; postoculars 3; temporals 2 + 3; dorsal scales reduce 17 (–4[89/91])15; hemipenes extend to end of 6th subcaudal plate, forked at middle of 5th plate; sulcus forked; forked portions spinose; half of proximal portion spinose on other

Table 1. *Comparison of ventral counts for samples of* Rhabdophis auriculata.

Locality	*Sex*	*Mean ± S.D. ± S.E.*	*Range*	*Number*
Mindanao				
Zamboanga del Norte[1]	♂	154.9 ± 2.6 ± 0.5	150–160	29
	♀	154.6 ± 2.5 ± 0.4	150–162	33
Zamboanga del Sur	♂	152.2 ± 2.3 ± 1.0	149–146	5
	♀	153.5	153–154	2
Bukidnon	♀	148	—	1
Davao	♂	150.9 ± 3.1 ± 0.6	143–155	28
	♀	152.7 ± 3.5 ± 0.7	146–160	28
Agusan	♂	150.5	149–153	4
	♀	150.5	147–154	4
Basilan	♂	146.7	143–150	3
	♀	152.2 ± 3.1 ± 1.3	147–157	6
Bohol	♂	148	—	1
Luzon	♀	145	—	1

[1] Based on a large sample from the Buena Suerta area, on Mt. Dapitan, along the boundary between Misamis Occidental and Zamboanga del Norte provinces.

side of sulcus; walls opposite sulcus with longitudinal plicae; 2 very large basal spines present on either side of sulcus. Color pattern as described in diagnosis; black ventrolateral stripe extending uninterrupted to meet lower postocular stripe; black midventral stripe originating on 24th ventral.

Variation. There is scarcely any variation in head and body scutellation beyond that already reported for ventral and subcaudal counts. Only two of

Table 2. *Comparison of subcaudal counts for samples of* Rhabdophis auriculata.

Locality	*Sex*	*Mean ± S.D. ± S.E.*	*Range*	*Number*
Mindanao				
Zamboanga del Norte[1]	♂	86.3 ± 3.1 ± 0.6	80–92	25
	♀	86.3 ± 2.8 ± 0.5	82–93	28
Zamboanga del Sur	♂	85.4 ± 2.4 ± 1.1	82–89	5
	♀	86.5	83–90	2
Davao	♂	79.7 ± 3.9 ± 0.8	71–86	22
	♀	80.5 ± 2.9 ± 0.6	73–87	26
Agusan	♂	82.3	81–85	4
	♀	81.7	73–87	3
Basilan	♂	83.7	80–86	3
	♀	83.4 ± 1.9 ± 0.8	80–86	5
Bohol	♂	84	—	1
Luzon	♀	78	—	1

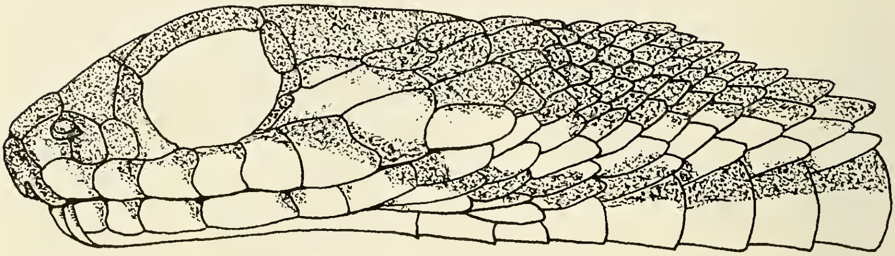

Figure 6. Side view of head of CAS-SU 19362, *Rhabdophis auriculata myersi* (drawn by Marilyn Kramer).

87 specimens had 9 upper labials on both sides, one had 7 on both sides, one had 7 on one side, 8 on the other, and one had 9 and 8 labials. In most specimens there were 2 anterior temporals; however, in more than ⅔ of the sample the upper anterior temporal is divided by a vertical suture; 3 posterior temporals are usually present, only eight specimens have 2, and three have 2 on one side, 3 on the other. No variation was observed in numbers of preoculars, postoculars, or loreals. The nasal shield was carefully scrutinized under high magnification of a binocular stereoscopic microscope, and in no instance was I able to detect a suture in the shield above the nostril; a vertical suture was always present, extending from below the nostril to the lower border of the shield. Therefore, the nasal is only partially divided.

The color pattern is remarkably stable, too. The dorsal ground color, in preserved specimens, is dark brown to black. There is a prominent middorsal light streak originating just behind the parietals and most distinct on the anterior fourth of the body. A lateral white stripe extends the length of the body along the outer edges of the ventrals to the neck, then angles forward onto the upper anterior temporals, ending just behind the postoculars [figure 6]. This stripe becomes narrower and less distinct posteriorly. It extends uninterrupted onto the side of the head, there being no squarish black spot on the neck behind the angle of the jaw as in the typical form [figure 7] connecting the dorsal ground color with the ventrolateral black stripe. This latter stripe, formed by black spots on the ventrals, extends forward, usually uninterrupted, onto the suture of the 8th and 9th lower labial and thence meets the lower postocular black bar which extends onto the 7th upper labial. Occasionally the stripe is interrupted for one scale width immediately behind the 8th lower labial. Otherwise it extends posteriorly along the sides of the ventrals, broadening and usually coalescing with the black middorsal stripe which originates on the 4th to 23rd ventral, extends posteriorly, becoming broad and joining the lateral black stripes. The

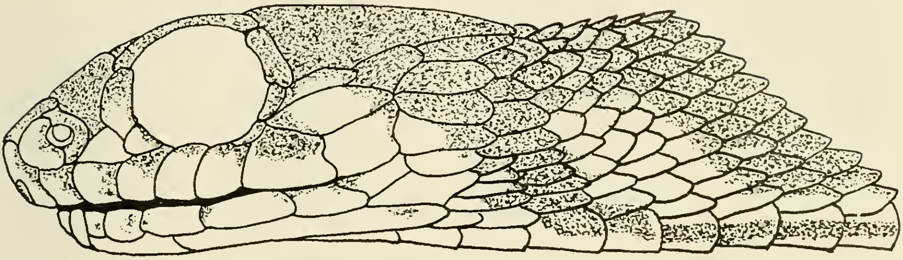

Figure 7. Side view of head of CM 2592, *Rhabdophis a. auriculata* (drawn by Marilyn Kramer).

venter is thus posteriorly almost entirely black except for a series of paramedial white spots, sometimes forming stripes.

Ecological notes. The sample from Davao Province is large and is made up of both young and adult specimens. The smallest gravid female measured 299 mm. snout-vent length; young with umbilical scars still evident, though almost completely closed, measured up to 200 mm., although most animals above 150 mm. in snout-vent length showed no visible signs of the scar. The young, defined here arbitrarily as those with some evidence of an umbilical scar or less than 200 mm. in snout-vent length, were collected mostly during the months of October and November 1946 by members of the Hoogstraal Expedition to Mindanao. The fact that young animals measuring from 104 to 200 mm. were collected during this period suggests that some egg laying takes place almost year round. However, 11 of the 19 young measured between 104 and 125 mm., suggesting further that there is probably a peak reproductive period during late spring or early summer. Gravid females were collected in June and July as well as during the October-November period previously mentioned. At least two specimens of *R. a. myersi* from northern Zamboanga, collected in April, were also gravid. Since most of the animals from the Zamboanga Peninsula were collected during April and early May, and those from Basilan in late October, this would add weight to my argument, based on the survey of the Davao sample, that a peak in egg laying takes place in late spring, possibly late May or June. Six of the sample measured less than 150 mm. snout-vent length, the smallest being a young female, 121 mm. from snout to vent. The rest of the sample divides up as follows: 150–199 mm. snout-vent, 19 specimens; 200–249 mm., 8; 250–299 mm., 13; 300–349 mm., 6; 350–399 mm., 6; and 400 and over, 1.

Only amphibian remains were found in the gut, mostly frogs, though in two cases there were tadpoles, and in three, masses of gelatinous frog eggs. In three specimens of *R. a. auriculata* from Davao Province, the frogs were identified as *Oreophryne*, a small terrestrial species found in southern Mindanao living in moss growing on logs or trees, under bark or in leaf axils (Inger, 1954, p. 447). Two specimens of *R. a. myersi* from near Buena Suerte had identifiable frog remains in the gut, one referable to *Rana magna* and the other to *Ansonia muelleri*. It is not too surprising that these frogs are eaten by *R. auriculata*, considering the diminutive size of the snake and of the frog, adults of which measure from 17.2–21.7 mm. (Inger, 1954, p. 447).

The snakes for which we have adequate data are found at elevations from 2800 to about 6400 feet (850–1950 m.) in the mountains of Davao Province (Mt. McKinley and Mt. Apo regions). In like manner, specimens of *R. a. myersi* from the northern part of the Zamboanga Peninsula were taken largely between 2300 feet and 4500 feet (700–1370 m.). The type and those of the paratypic series for which data are available were taken from beneath rocks in dry river beds, while others were collected in brush or among other vegetation, usually near water courses, even if dry at that time of year (late September through November). A Basilan series of *R. a. myersi* collected by Taylor at Abung-Abung appear to come from near sea level. Also Taylor obtained a series from Zamboanga City, at or near sea level. However, the hills immediately behind Abung-Abung may in fact have been the source of these specimens. The Bunawan, Agusan Province, series collected by Taylor in 1921 was taken in the Agusan River valley, in the vicinity of water, usually from beneath leaves or logs at the edge of a small swamp (Taylor, 1922, p. 90). This locality lies below 500 feet. Since Taylor's data seem quite reliable, the vertical distribution of *R. auriculata* is more than 600 feet, this being true for both nominal forms.

Rhabdophis auriculata auriculata (Günther).

Tropidonotus auriculatus GÜNTHER, 1858, Cat. Col. Snakes British Mus., p. 80 (type locality: Philippine Ids. [restricted here to Mt. Apo, Davao Province, Mindanao]; type in British Museum). PETERS, 1861, Monatsb. Akad. wiss. Berlin, 1861, p. 687 (Samar). MÜLLER, 1883, Verh. Naturf. Ges. Basel, vol. 7, p. 286. BOETTGER, 1886, Ber. Senckenberg Naturf. Ges., p. 108; 1898, Kat. Rept. Samml. Senckenberg Naturf. Gesell., Schlangen, p. 28 (Leyte). FISCHER, 1885, Jahrb. Hamburg wiss. Anst., vol. 2, p. 80 (Süd-Mindanao). BOULENGER, 1893, Cat. Snakes British Mus., vol. 1, p. 261, pl. 17, fig. 1 (part; "Philippines" [type specimen]).

Natrix auriculata, GRIFFIN, 1911, Philippine Jour. Sci., sec. D, vol. 6, p. 257 (part; distribution compiled). TAYLOR, 1922, Snakes Philippine Ids., p. 89, pl. 4, figs. 2–4 (Mindanao [Bunawan, Agusan], Samar).

DIAGNOSIS. See *Rhabdophis a. myersi* except as follows: ventrals 143–160; subcaudals 71–87; ventrolateral black stripe extends forward to side of neck, does not extend onto throat, does not meet dark lower postocular diagonal stripe; light lateral stripe usually interrupted on side of neck behind angle of jaw by squarish black spot joining black ventrolateral stripe to dark dorsal color. Measurements (of largest male and largest female, in mm.): ♂ s-v 352, tail 123; ♀ s-v 372, tail 140.

Table 3. *Variation in head scutellation in* Rhabdophis auriculata auriculata.

Preoculars	1 – 1[3](42)	2 – 2(3)	2 – 1(2)	1 – 2(3)			
Postoculars	3 – 3(41)	3 – 2(2)	4 – 3(1)	4 – 4(1)	3 – 4(1)	2 – 3(1)	2 – 2(3)
Upper labials	8 – 8(46)	7 – 7(1)					
Temporals	2 + 3[4](25)	2 + 2(12)	2 + 3/2 + 2(5)	2 + 2/2 + 3(4)			
	1 + 3/2 + 3(1)	1 + 2(1)	2 + 1(1)	2 + 2 + 3(1)			

[3] First number is count on right side, second number is for left side.

[4] 2 + 3 indicates anterior + posterior temporals for both sides; 2 + 3/2 + 2 are counts for right and left sides.

Range. *Leyte*[2]. *Mindanao*: Agusan Province (Bunawan); Cotabato Province (Burungkot); Davao Province (Mt. Apo [Baclayan, Todaya], Mt. McKinley). *Samar*[2]. *Luzon*[2].

Material examined (86). LUZON: (CAS 15231). MINDANAO. Agusan Province: Bunawan (CM 2590–2598). Cotabato Province: Burungkot (FMNH 53345 [elev. 1500 ft. (460 m.)]). Davao Province: Baganga River (USNM 34734–34735). Mt. Apo (FMNH 15016; 53322–53323 [elev. 2800 ft. (850 m.)]; 53326 [elev. 5500 ft. (1670 m.)]; USNM 34713 [2 July 1904; elev. 4000 ft. (1220 m.)]; 34719 [3 July 1904; elev. 5000 ft. (1520 m.)]; 34712, 34714–34718, 34720–34727, 34770–34771 [June-July 1904; elev. 6000 ft. (1829 m.)]; 34728–34734). Todaya, Mt. Apo, November 1946 (FMNH 53316–53321, 53324–53325, 53329–53344 [elev. 2800 ft. (850 m.)]). Baclayan, Mt. Apo, 11 November 1946 (FMNH 53327–53328 [elev. 6500 ft. (1980 m.)]). Mt. McKinley, 8 August–19 September 1946 (FMNH 53299–53314 [elev. 3000–6400 ft. (910–1950 m.)], 53315 [elev. 6300 ft. (1920 m.)], 53346 [elev. 3400 ft. (1040 m.)]).

Variation. Variation among the specimens examined is minimal. Ventral and subcaudal counts are summarized in tables 1 and 2. Variations in head scutellation are summarized in table 3.

In color pattern in the typical form, variation is limited also. The light mid-dorsal stripe is present in 76 percent of the sample. However, its presence or absence is not correlated with distribution, sex, or age group. The ventrolateral stripe is usually joined to the dorsal color by a vertical or almost vertical black bar on the neck behind the angle of the jaw in 83 percent of the sample. In 10 percent the vertical bar does not contact the dorsal pattern, being separated by about one-half of a scale width. In only four animals—one from Burungkot, Cotabato Province, one from Mt. McKinley, and two from Mt. Apo, Davao Prov-

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[2] Specimens from Leyte and Samar were reported by Boettger (1898, p. 28) and Peters (1861, p. 687) respectively. The specimens on which these records were based are probably extant, Peters' at the Berlin Museum, Boettger's at Senckenberg, and should be examined. I have not done so.

The Luzon specimen is in the collection of the California Academy of Sciences, CAS 15231. Formerly it was in the Museo Santo Tomas and sent to the Academy around 1909 by Dr. J. C. Thompson, who said it probably came from Luzon. Indeed, the specimen may have originated on Luzon, but confirmation is needed. The specimen has an interrupted light lateral stripe and therefore is most similar to the eastern Mindanao population.

ince—is the bar absent. In most animals the ventrolateral stripe stops well short of the commissure of the mouth, being separated from the subpostocular blotch or stripe by at least 1 and usually 2 to 4 scales.

Remarks. *Rhabdophis auriculata* is an unusually small natricine. I hesitate to venture an opinion on its relationships now, inasmuch as I haven't seen several Bornean forms such as *Rhabdophis sarawacensis* (Günther) with which, based on available descriptions, it seems to agree. Although *R. auriculata myersi* is readily separable from *R. a. auriculata* on the basis of color pattern alone, an examination of data for ventral and subcaudal counts is revealing (table 1). A comparison of the Zamboanga-Misamis sample with the eastern Mindanao samples does not indicate a statistically significant level of difference in these counts, yet inspection of the means and ranges, especially of subcaudal shields, suggests the populations do indeed differ, though there is a substantial overlap. Perhaps most interesting is the fact that in subcaudal counts both Basilan and Bohol samples agree with the western Mindanao population, and though this is not confirmed by similar close agreement of ventral counts, even here the counts are well within the range of the western Mindanao sample. Of course, in color pattern both Basilan and Bohol samples are readily referrable to the typical subspecies.

A further instructive comparison brings out the fact that the means and ranges of subcaudal counts for the Davao-Cotabato and Bunawan samples and the counts for the one specimen from Luzon are lower than for the typical form.

Mindanao has long been of considerable interest to biogeographers concerned with the Philippine fauna and flora. Unquestionably it has served as a principal route for faunal and floral movements to the northern islands. Also it has had a complex post-Miocene history, which is still not completely unraveled. To the extent that we must deal with the matter here, it is sufficient to note that a substantial body of evidence, particularly in the form of coral reefs and numerous terraces, indicate clearly that, during the early and mid-Pleistocene, and possibly during the Pliocene, too, the island was divided into at least five and possibly seven smaller islands (fig. 8). These islands have been detailed by Dickerson (1928, pp. 85–87, fig. 19). Inger (1954, p. 453), in a paleographic map portraying the probable land areas during the lower Miocene based on Umbgrove (1938), suggests that even at that date Mindanao was probably not a single island, but rather a series of at least four island masses. The distribution of certain elements of the flora and fauna (see Merrill, 1928, p. 290; Cook, 1928, p. 269; Dickerson, 1928, p. 295) suggests at least a division between the Zamboanga Peninsula and the rest of Mindanao. Further, these authors suggest a greater faunal and floral similarity between the Cotabato-Agusan-Surigao regions than between Cotabato and Zamboanga. This probably indicates that the Pleistocene islands depicted by Dickerson, i.e. Cotabato, Agusan, and Surigao, were connected by emerging

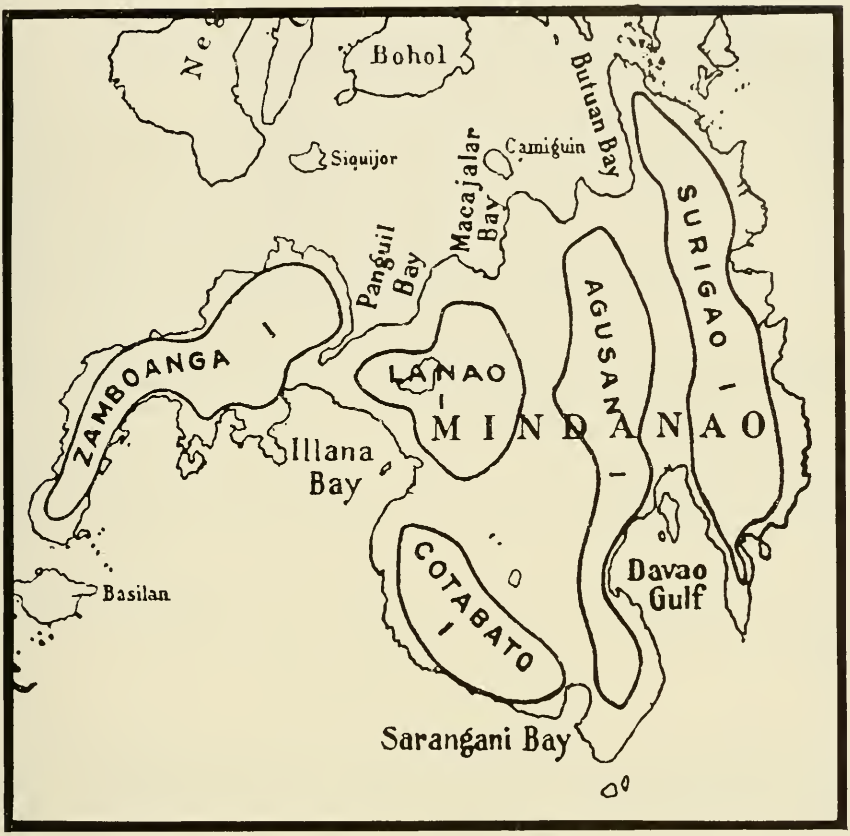

FIGURE 8. "Some probable Pleistocene islands in Mindanao," from Dickerson (1928, p. 86, fig. 19).

subaerial valleys before the Panguil-Illana Isthmus connecting the Zamboanga Peninsula with the Bukidnon-Lanao region emerged.

In an earlier paper I pointed out that the populations of *Cyclocorus nuchalis* from eastern and western Mindanao differed significantly from one another (Leviton, 1967). This was a clue that suggested that in all probability other species of snakes might show similar patterns which could be related to the Plio-Pleistocene paleogeographic history of Mindanao. A careful study of *Rhabdophis auriculata* on Mindanao would seem to confirm this supposition. Populations of this species from Cotabato and Davao are most similar to the Surigao-Agusan populations I have seen and quite distinct from animals from the Zamboanga Peninsula. Samples of *R. auriculata* from Bukidnon and Lanao provinces, on the other hand, are indistinguishable from those from the Zamboanga Peninsula and Basilan Island, raising the possibility that western Mindanao, composed of the "Pleistocene islands" of Lano and Zamboanga, were joined to one another and separated from the eastern complex of islands until fairly late in the Pleistocene by a persistent Macajalar-Illana Bay seaway.

Indeed, it may have been the persistence of this seaway that prevented any significant eastward movement of the Lanao freshwater fishes. Significantly, only one species of *Puntius* is known from eastern Mindanao, *P. binotatus*, a Bornean species. Of course the seaway no longer exists and certainly there has been sufficient time for faunal movements throughout the island. Terrestrial animals can move with greater freedom than those that must wait for stream-capture in order to go from one drainage basin to another, so it is not surprising to find, for example, a paucity of species of cyprinid fishes in eastern Mindanao, though many forms are known from Lake Lanao and several from the Zamboanga Peninsula. On the other hand, many subspecies of frogs are widely distributed throughout Mindanao, Samar, and Leyte. This distribution is obviously a more recent development, probably a late Pleistocene phenomenon. Indeed, it is becoming more apparent that several faunal movements and radiations can be identified in Mindanao and are correlated with its post-Oligocene geological history.

Quite clearly, a more extensive and careful study of populations of animals and plants on Mindanao, especially the montane forms, should give us considerable insight into the late geological history of that region.

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The writer wishes to express his appreciation for the loan of specimens to Mr. Neil B. Richmond and Dr. Clarence J. McCoy, Carnegie Museum; Dr. Robert F. Inger and Mr. Hymen Marx, Field Museum of Natural History; and Dr. James A. Peters, U.S. National Museum.

The following abbreviations are used: CAS—California Academy of Sciences; CAS-SU—California Academy of Sciences-Stanford University (for specimens formerly housed at Stanford University and registered in the Stanford catalogues); CM—Carnegie Museum; FMNH—Field Museum of Natural History; USNM—United States National Museum.

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A REINTERPRETATION OF THE TELEOSTEAN FISH ORDER GOBIESOCIFORMES

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An intensive effort to interpret relationships among the old group "Jugulares" (Linnaeus, 1758, p. 249; Jordan, 1923, p. 228; etc.) led to a consideration of the Callionymidae and Draconettidae. For reasons dealt with below, the conclusion was reached that these two families (I do not agree with Davis, 1966, that they should be combined) are specialized derivatives of the notothenioid section of the perciform suborder Blennioidei (Gosline, 1968). Since, however, the Draconettidae and Callionymidae are morphologically well differentiated from the notothenioids, it appears best to remove them from the Perciformes entirely. Investigation also suggested that the Gobiesocidae has evolved from the notothenioid section of the perciform suborder Blennioidei and in small part at least over the same route as the draconettids and callionymids. The Callionymidae, Draconettidae, and Gobiesocidae are therefore combined here in the order Gobiesociformes.

The systematic position of the Callionymidae and Draconettidae has never been the subject of direct investigation. Various views concerning the relationships of these two families have, however, been suggested. Boulenger (1904, p. 708) included both the Callionymidae and Gobiesocidae in his Division Jugulares, and under his account of the Gobiesocidae stated: "The position of the ventral fins suggests, at first glance, affinity with the Callionymidae, and a comparison of the skeletons of these two types has convinced me that they are really related to each other, though highly modified in different directions." (My own conclusions are essentially those of Boulenger.) Starks (1905, p. 302) in connection with his account of the gobiescoid *Caularchus* [=*Gobiesox*] *maeandricus* wrote: "The Callionymidae, however, possess some important characters not possessed by the Gobiesocidae, and these probably more than counterbalance the characters held in common." Regan in 1913 (pp. 144, 145) placed the Callionymidae and Draconettidae in the "Division Callionymiformes" of the perciform suborder Percoidei. He stated that the Callionymidae "may be related to the Pinguipedidae, but is much more specialized [a suggestion with which I also agree]. The Gobiesocidae differ in many characters of importance." Referring again to the Callionymidae, Starks (1923, p. 267) said: "The osteology shows, however, that this family on account of several rather extraordinary and unique characters should be segregated in a suborder coördinate in value with the Batrachoid fishes." Regan in 1929 also recognized the Callionymoidei as a perciform suborder. The most recent comment on the systematic position of the Draconettidae and Callionymidae is that of Briggs and Berry (1959, p. 125). They summarized as follows: "Considering the paucity of our knowledge about these two families and their relationships with other percomorph groups, we see no present need for setting them aside in a separate suborder. Their morphology is no more peculiar than that of several other families that are traditionally retained without subordinal recognition within the vast assemblage of the Percomorphi."

The best and most complete account of the anatomy of the Gobiesocidae remains that of Guitel (1889). However, Guitel draws no conclusions regarding gobiesocid relationships within the Acanthopterygii. Since the days of Starks (1905)[1] and Regan (1909) the family has generally been allocated to an order of its own. In his monograph of the family, Briggs (1955, p. 7) wrote: "The Xenopterygii [=Gobiesociformes] seems to be most closely allied to the Haplodoci (batrachoids) but there is also some resemblance to the Callionymoidea. The order may be considered a highly specialized derivative of some still unknown primitive percomorph stock." McAllister (1968, p. 165) also suggests a gobiesocid-batrachoidid relationship. Apparently on the assumption that such exists Greenwood *et al.* (1966, pp. 389, 397) have assigned the Gobiesociformes to the superorder Paracanthopterygii, thus separating the group superordinally from the callionymoids.

Under the circumstances, it first seems advisable to discuss the possible relationship between the gobiesocoid and batrachoid fishes. Though both groups hold certain characteristics in common, *e.g.*, the usually scaleless body, the flattened head, anterior pelvics, incomplete circumorbital series, etc., it is my pro-

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[1] Starks (1905, p. 292) attributed the creation of ordinal status for the gobiesocids to Gill, but neither Briggs (1955, p. 7) nor I have been able to find where Gill recognized more than subordinal rank for this family.

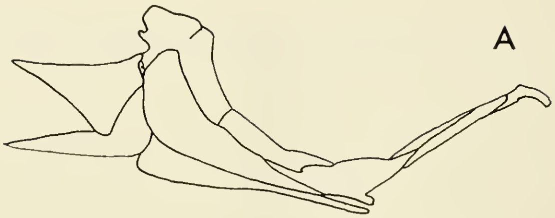
visional view that these similarities are the result of convergence. The batrachoid fishes differ from the Gobiesociformes, *i.e.*, Callionymidae, Draconettidae, and Gobiesocidae, in the following features:

In the batrachoid fishes the pelvic fins are fairly close together, small, and with 2 or 3 soft rays that are usually held out at an angle from the abdominal surface; in the Gobiesociformes the pelvic fins are wide apart, well developed (though highly specialized in the Gobiesocidae), and of 4 or 5 soft rays that are normally held flat against the body surface. In the batrachoids the upper hypurals have a peculiar intervertebral-like basal articulation with the rest of the caudal skeleton (Regan, 1912, fig. 2B); in the Gobiesociformes there is no such articulation. In the batrachoids the ascending process of the premaxillary has a movable basal articulation with the toothed portion, and a separate articular process of the premaxillary is well developed (Monod, 1960, fig. 49); in the Gobiesociformes the ascending and articular processes of the premaxillary have merged or fused and are firmly attached to the toothed portion. In the batrachoids there is no median ethmoid ossification; in the gobiesociform fishes a median ethmoid ossification is always present. Finally, the batrachoids have a peculiar gas bladder (Sørensen, 1884); in the Gobiesociformes there is no gas bladder.

With regard to the postulated derivation of the Gobiesociformes from the superfamily Notothenioidae (containing the parapercids [=mugiloidids], cheimarrichthyids, trichonotids, nototheniids, etc., see Gosline, 1968) of the perciform suborder Blennioidei, the gobiesociform fishes have almost all of the diagnostic notothenioid characteristics despite their high degree of specialization along other lines.

Thus in the Gobiesociformes the head is always more or less flattened, sometimes greatly so. The circumorbital ring of bones is incomplete. The medial tabulars are apparently lacking. There is a basisphenoid bone in *Draconetta* but not in the Callionymidae and Gobiesocidae. Flanges from the parasphenoid do not extend up in front of the prootics excluding the prootics from the internal cranial border of the orbit. (When, as in some gobiesocids and callionymids, the parasphenoid does have an upward expansion, this extends up between the middle portion of the orbits, not in the form of a postorbital bar such as occurs for example, in the zoarcioid blennioids.) The pelvic fins are as noted above. (The Gobiesocidae, in which the pelvic fins form the anterior portion of the sucking disc, is the only group known to me in which such a disc extends well forward of the pectoral bases.) The pectoral actinosts are three or four in number. (The 3 broad plate-like actinosts of the Callionymidae are closely duplicated in such notothenioid families as the Nototheniidae.) The dorsal and anal rays are equal in number to the vertebrae between them. The caudal fin is rounded or brush-like, with fewer than 15 branched rays.

Additional notothenioid resemblances of the Gobiesociformes are as follows.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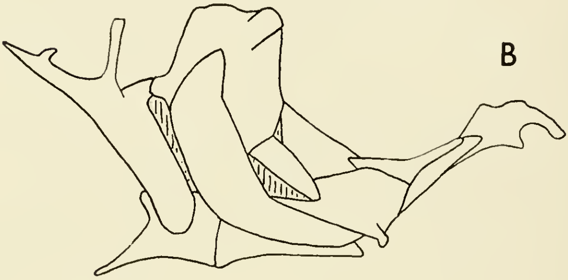
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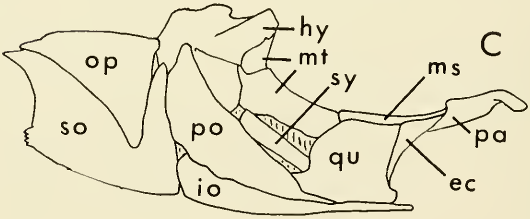
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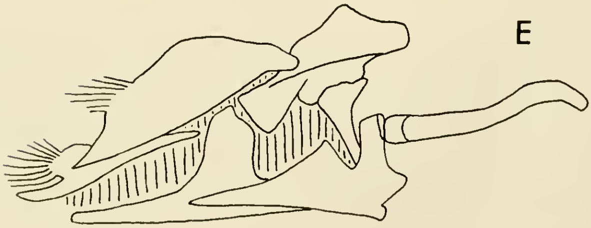
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The ventral sucking disc of the Gobiesocidae would seem to be to some extent foreshadowed in the ridges on the flat ventral surface of the nototheniold family Cheimarrichthyidae. The notothenioid genera *Prolatilus* and *Mugiloides* are the only members of the suborder Blennioidei known to me with the draconettid supraoccipital crest and with the body musculature extending well forward over the top of the cranium. Seven branchiostegal rays, said to be present in some members of the Gobiesocidae (Briggs, 1955) also occur in a number of notothenioids, but rarely elsewhere among the Blennioidei. Finally, the opercular peculiarities of *Draconetta* (fig. 1A) are largely duplicated in the notothenioid *Harpagifer* (fig. 1B) and would seem to be foreshadowed in the more generalized notothenioid *Parapercis* (fig. 1C).

The anatomical account of the draconettids, callionymids, and gobiesocids which follows is based primarily on alizarin-stained and dissected specimens from the following lots:

Callionymidae: *Callionymus flagris,* 125 mm. in standard length (U. S. National Museum no. 71082); *C. decoratus,* 50 mm. (University of Hawaii no. 2073); and *Pogonymus pogognathus,* 24 mm., paratype (UH 1626).

Draconettidae: *Draconetta acanthopoma,* 75 mm. (USNM 156956).

Gobiesocidae: *Gobiesox nigripinnis,* 70 mm. (USNM 131163), and *Trachelochismus pinnulatus,* 55 mm., an exchange specimen from New Zealand in the UH collections.

The external features of various other species of Callionymidae and Gobiesocidae in the U. S. National Museum were examined during tenure of a Smithsonian Research Associateship. I wish to express my deep obligation to the members of the Fish Division of that institution for help and facilities during that time and for sending me on loan the specimens of *Draconetta acanthopoma* listed above.

General features. The head and body of callionymids, draconettids, and gobiesocids are always scaleless, although Ochiai (1963, p. 66) finds "degenerate scales" partly surrounding the lateral line canal of the callionymid *Diplogrammus goramensis.* In callionymids the gill opening is a small hole; in *Draconetta* it is larger, but the gill membranes are broadly attached to the isthmus; and in the Gobiesocidae the gill membranes may be attached to or free from the isthmus (Briggs, 1955). The widely separate pelvic fin bases are entirely in front of the broad pectoral bases, which extend far down the sides; in some callionymids and

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Figure 1. Right suspensorium and opercular bones, external view, of A, *Draconetta acanthopoma*; B, *Harpagifer bispinis*; C, *Parapercis cephalopunctata*; D, *Callionymus flagris*; and E, *Gobiesox nigripinnis.* ec, Ectopterygoid; hy, hyomandibular; io, interopercle; ms, mesopterygoid; mt, metapterygoid; op, opercle; pa, palatine; po, preopercle; and sy, symplectic.

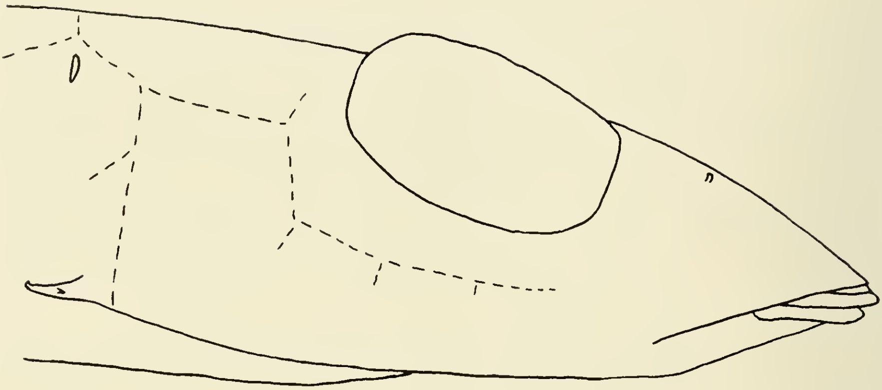

Figure 2. *Callionymus flagris.* Sketch of right side of head to show lateral line canals (dashed lines) that are not enclosed in head bones.

gobiesocids there is indeed a membrane extending from the innermost pelvic rays onto the outer surface of the pectoral fin. There is a short spinous dorsal in the Draconettidae and usually in the Callionymidae, but never in the Gobiesocidae.

Fin structure. The Gobiesociformes show a transitional series from the usual percoid condition with spines and branched rays to that of the Gobiesocidae where the only spinous element is the flat outer pelvic plate and all the soft rays are simple. The loss of the spinous dorsal in this series has already been noted. As for soft rays, in the callionymid genera *Yerutia* and *Synchiropus* all of the soft dorsal rays may be branched (Schultz, 1960, p. 399) and in large specimens of *Draconetta acanthopoma* all of the anal rays are branched, but elsewhere the dorsal and anal rays are mostly or all simple. In *Draconetta* and the callionymids examined, most of the pectoral and the 5 pelvic rays are branched. I count 8 branched caudal rays in *Draconetta acanthopoma,* 6 in *Callionymus flagris.*

The lateral line system. Those portions of the lateralis system enclosed in head bones will be dealt with below. Here, only the peculiar extension of the lateralis system in the Callionymidae will be mentioned. Such extensions occur on both the head (fig. 2) and body. In *Callionymus,* the system includes such peculiar features as a commissure across the top of the caudal peduncle. On the head of the same genus the canals behind the frontals all lie superficial to the skull bones, extending across the surface of the pterotic and forming a complete supratemporal commissure that is not contained in extrascapulars. Again the preopercular canal, instead of running up within that bone, exits from its lower limb, passes out superficially across the preopercular spine, and then up over the flesh behind the preopercle (fig. 2). None of the peculiarities mentioned are found in either the Draconettidae or the Gobiesocidae, although in the Draconettidae there are membranous extensions of the lateralis system.

Nasal apparatus. The nasal apparatus differs considerably among the gobiesociform fishes examined. It is most percoid-like in *Gobiesox nigripinnis* which has 2 nostrils, the anterior with a fringed flap and the posterior in a raised collar; these 2 nostrils lead into a nasal cavity, bordered mesially above by the nasal bone; the cavity contains a roundish nasal rosette. The nasal apparatus of *Callionymus flagris* is about the same except that there is only 1 nostril on each side. In *Draconetta acanthopoma* there are 2 tubular nostrils but no nasal bone; the nostrils lead into the two ends of a flattened, hollow, fleshy pad which seems to contain no specialized olfactory folds or lobes.

The circumorbital bones. The circumorbital series in the Gobiesociformes is always reduced to the lacrimal bone. Behind the eye in *Callionymus* and *Draconetta* a membrane-enclosed canal exits from the main lateralis canal and extends downward. In *Draconetta* this canal is short, ending behind the eye; in *Callionymus flagris* it extends forward below the eye towards the base of the lacrimal bone (fig. 2) but fails to connect with the lacrimal-enclosed canal.

Jaw structure. The peculiarity of the upper jaw protrusion of *Callionymus* has been described by van Dobben (1935, pp. 47, 48) and by Kayser (1962). In most percoids, the maxillary heads twist on their axes extruding the premaxillary articular processes before them like a squeezed cake of soap (van Dobben, 1935, pp. 10–13). In *Callionymus* the maxillary heads and associated cartilages and ligaments of the two sides form a ring around the long ascending processes of the premaxillaries. The ascending processes of the premaxillaries are free to move in and out within this ring. Upper jaw protrusion is entirely produced by the lowering of the mandible with the associated downward movement of the lateral end of the maxillary. Anatomically *Callionymus* is peculiar in having no articular processes on the premaxillaries lateral to their ascending processes.

The gobiesocids also have premaxillaries without articular processes (Guitel, 1889, pl. 25, fig. 16, and Briggs, 1955, figs. 74–81). In *Draconetta* there are long, narrow, articular processes that are all but fused to the ascending processes. So far as I determine from preserved specimens, *Draconetta* and most gobiesocids use the same peculiar method of upper jaw protrusion that *Callionymus* does. In at least the gobiesocid genus *Tomicodon,* however, the upper jaw does not appear to be protrusile.

Gill covers and suspensoria. With the extreme flattening of the head region that has taken place in the Callionymidae, Draconettidae, and Gobiesocidae, the operculum becomes squashed, so to speak, into a horizontally elongate structure. In at least some members of all three families, backwardly projecting spines are developed, but they are formed in different ways.

As already noted, the opercular apparatus of *Draconetta* (fig. 1A), with spinous opercles and subopercles, is essentially similar to that of the notothenioid *Harpagifer* (fig. 1B), although in *Harpagifer* an additional support for the opercle has been added by extending a vertical strut up to an abutment against the cranium. How the spinous arrangement in *Harpagifer* and *Draconetta* might have originated is suggested by the basal notothenioid *Parapercis* (fig. 1C). In *Parapercis* the opercle ends in the not unusual point; the subopercle has two structurally different sections, an upper, flap-like ossified membrane and a lower rigid plate ending posteriorly in a few serrations. Disappearance of the upper membranous portion of the subopercle and development of the lower would provide essentially the configuration of gill cover spines found in *Harpagifer* and *Draconetta.*

Now, if instead of developing the lower portion of the subopercle of *Parapercis,* the upper flap-like portion were enlarged, the lower eliminated, and the preopercle developed backward as a strong spine, the configuration found in *Callionymus* (fig. 1D) would result.

To arrive at the gobiesocid-type opercle (fig. 1E), one could hypothesize a form of *Callionymus* in which the subopercle loses its association with the interopercle and swings back onto the end of the opercle where it may form a spine in gobiesocids.

The changes in opercular structure just described are reflected in the interopercle. This bone, fairly long in *Parapercis* and longer in *Draconetta,* is pulled out into a long weakly ossified tendon in *Callionymus.* In *Gobiesox* the interopercle is wholly concealed by the preopercle and does not reach the subopercle at all but terminates in an abutment against the rear of the hyoid apparatus, as in the Blenniidae; the interopercle is, however, better developed in the more primitive *Trachelochismus,* where it nearly reaches the subopercle.

A last minor point about the gill cover structure of the Gobiesociformes should perhaps be made. In all three families those edges that are not rigid tend to have long, flexible bony fimbriae.

The "squashing" of the opercle would also seem to have had an effect on the suspensoria of callionymids, draconettids, and gobiesocids. The preopercles of the callionymids (fig. 1D) and gobiesocids (fig. 1E) have been extruded backward, so to speak, and the hyomandibular, preopercle, and quadrate have come to form the three points of a triangle. *Draconetta* (fig. 1A), however, has retained the usual configuration with the hyomandibular, preopercle, and quadrate all more or less in line. There is however no separate metapterygoid in the Draconettidae, Callionymidae, or Gobiesocidae.

The connection between the palatine and the posterior portion of the suspensorium has become rather tenuous. In *Draconetta* (fig. 1A) the palatine is attached to the quadrate by a long narrow strut composed of the ectopterygoid and mesopterygoid. In *Callionymus* (fig. 1D) these last two bones seem to have fused, but the strut is still present. In *Gobiesox* (fig. 1E) the palatine is only loosely connected with the rest of the suspensorium, the mesopterygoid is gone, and the minute ectopterygoid is only ligamentously attached to the palatine.

THE HYOID APPARATUS AND GILL ARCHES. The hyoid apparatus is close to,

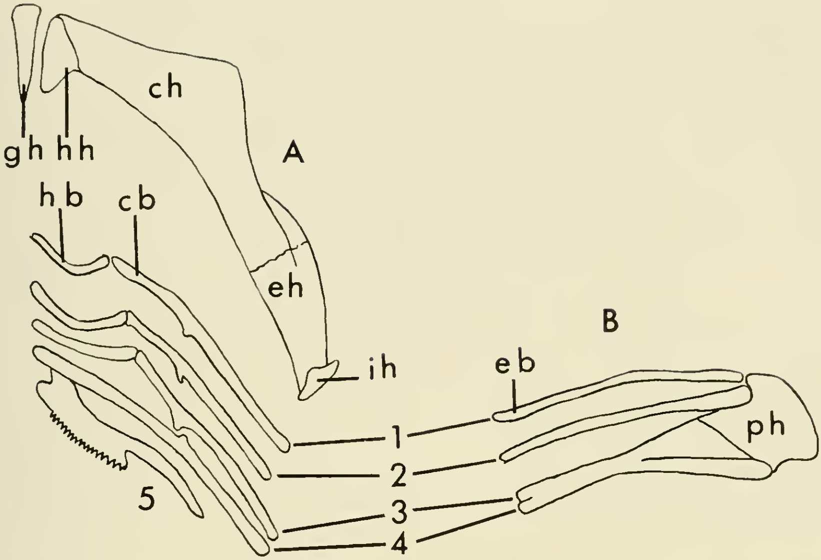

Figure 3. Hyoid and gill arches (1–5) in *Gobiesox nigripinnis*: A, hyoid arch and lower portions of the gill arches of the right side, from above; and B, the upper portions of the gill arches of the left side, from above. cb, Ceratobranchial; ch, ceratohyal; eb, epibranchial; eh, epihyal; gh, glossohyal; hb, hypobranchial; hh, hypohyal; ph, upper pharyngeal tooth plate.

and firmly connected by the anterior basibranchial with, the gill arches in *Callionymus*; in *Draconetta* and *Gobiesox* the hyoid arch is well separated from and unconnected with the other gill arches. In *Callionymus* and *Draconetta,* a well developed glossohyal extends forward from the hypohyals; in *Gobiesox* (fig. 3) the glossohyal is a small sliver of bone completely contained in the interspace between the hypohyals of the two sides. In *Draconetta* and *Callionymus* there are 6 branchiostegal rays on each side, in the gobiesocids 5–7 (Briggs, 1955, p. 9). In *Draconetta, Callionymus,* and *Gobiesox* there are 2 anterior branchiostegals attached to the inner surface of the hyoid arch; the other 4 close to its lower rim. In *Draconetta* and *Callionymus* the first 2 are short; in *Gobiesox* the first 3. In *Draconetta* 4 of the 6 branchiostegals are crowded back on the epihyal, in *Callionymus* 3, and in *Gobiesox* only 1 branchiostegal articulates with the epihyal.

Among gobiesociform families the first spicular pharyngobranchial seems to have completely disappeared and there are never more than 2 sets of pharyngeal teeth on either side above. In *Draconetta* and *Callionymus* epihyal 2 extends up to the relatively small and narrow anterior tooth patch, while epihyals 3 and 4 articulate with the broader, posterior pharyngeal tooth patch[2]; in these two genera epihyals 3 and 4 are closely but movably attached to one another. In *Gobiesox*

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[2] Starks (1905, p. 302) stated that *Callionymus* had "three superior pharyngeals on each side" but in 1923 (p. 269) he describes 2 upper pharyngeals of the same shape as noted here.

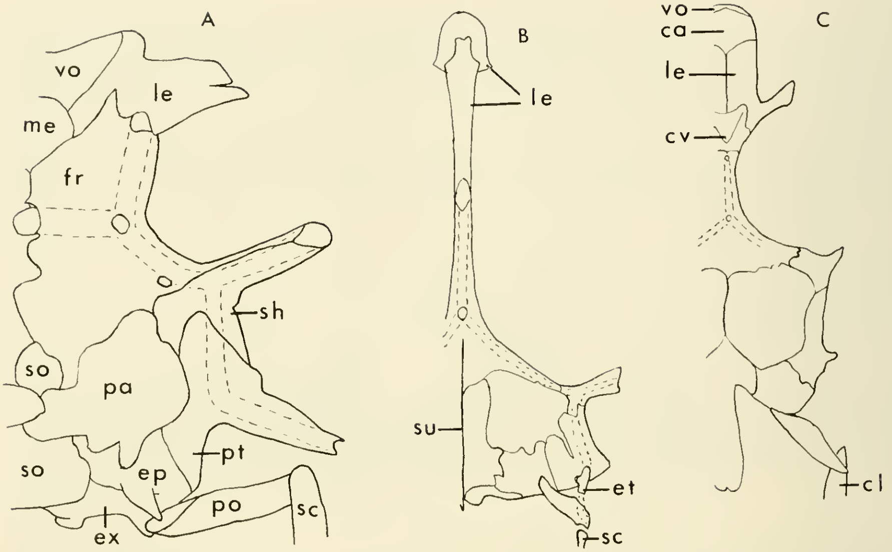

Figure 4. Cranium plus upper portion of pectoral girdle, right side, from above, of A, *Gobiesox nigripinnis;* B, *Draconetta acanthopoma* (only the upper surface of the rostral region is shown); and C, *Callionymus flagris.* Lateral line canals passing through cranial bones indicated by dashed lines. ca, Cartilage; cl, cleithrum; cv, cavity into which the ascending processes of the premaxillaries extend; et, lateral extrascapular; ex, exoccipital; fr, frontal; le, lateral ethmoid; me, mesethmoid; pa, parietal; po, posttemporal; pt, pterotic; su, supracleithrum; so, supraoccipital; st, sphenotic; su, supraoccipital crest; and vo, vomer.

(fig. 3) there are no chondrified or ossified basibranchials, and the gill arches are not interconnected below. Above, there is only 1 small pharyngeal tooth plate on each side; epihyals 2, 3 and 4 articulate with it, and epihyals 3 and 4 are rigidly united to one another.

Skull. In *Gobiesox* (which lives under rocks in the tidal zone) the head is broad with small eyes in strong laterally placed bony sockets. In *Callionymus* and *Draconetta* the eyes are close together on the top of the head. These differences are strongly reflected in the crania.

Lateral line and associated skull bones. In the Gobiesocidae the forward portion of the supraorbital canal on each side commences near the snout rim and passes back through the paired nasal and frontal bones. Between the wide-set eyes there is a complete, bone-enclosed frontal commissure (fig. 4A). In the Draconettidae and Callionymidae the narrow interorbital region has doubtless caused the fusion of the 2 supraorbital canals into a single median canal between the eyes (fig. 4B, C). Furthermore, in *Draconetta* the frontals themselves have fused into a single median bone. However, in the two species of *Callionymus* examined the frontals appear to be only partially fused, and in the callionymid *Pogonymus,* which has a somewhat broader interorbital area, I believe I can see a suture completely dividing the frontals. Anteriorly, the supraorbital canals of callionymids begin in the separate nasals as usual, but in *Draconetta acanthopoma* there are no nasal bones and the anterior median pore of the frontal canal is the anteriormost point in the supraorbital system. (In *Draconetta oregona* Davis, 1966, fig. 2, shows the supraorbital canals as separating ahead of the eyes and extending forward on each side to just behind the nostril. Perhaps these anterior extensions of the supraorbital system in *D. oregona* are represented by fine ridges of flesh running over the same areas in *D. acanthopoma.*)

Behind the frontals the lateral line canals of *Callionymus* lie superficial to the skull bones, as previously noted (fig. 1). In *Gobiesox* and *Draconetta* the temporal canals pass backward from the frontals through what appears to be the sphenotic and pterotic (fig. 4A, B). Passage of the lateral line through the pterotic is normal in fishes, but a canal in the sphenotic is not. Possibly the "sphenotic" canal of *Gobiesox* and *Draconetta* extends through a dermosphenotic which has become fused to the sphenotic. In *Draconetta* the lateral line canal passes back from the pterotic into a lateral tabular, where it gives off the membranous, incomplete supratemporal commissure, and then into the posttemporal, where it ends. In *Gobiesox* the lateral line canal ends in the pterotic; there is no tabular bone or posttemporal commissure.

Ethmoid region of the skull. The peculiarities of the ethmoid region of the cranium of *Callionymus* (Starks, 1923, pp. 267–268) and of *Draconetta* can, I think, have developed through a pinching together of the broader, more normal ethmoid area of the Gobiesocidae. In the Gobiesocidae the ethmoid overlaps the vomer in the usual percoid fashion but lies behind the level of the lateral ethmoids (Guitel, 1889, pl. 25, fig. 1). In the narrower-snouted draconettids and callionymids the mesethmoid is completely separated from the vomer by cartilage and by the medial bases of the two lateral ethmoids which meet (fig. 4C) or nearly meet on the midline. In *Draconetta* (fig. 5) the mesethmoid is above and behind the lateral ethmoid bases, but in the callionymids it is entirely behind them. In both families the mesethmoid forms part of the orbital border. In the callionymid *Pogonymus* the ascending processes of the premaxillaries extend up and back over the rostral surface as usual; here the mesethmoid does not extend down into the interorbital space. But in *Callionymus* the ascending processes are more horizontal and their tips extend back into a medial rostral cavity; here the mesethmoid has been pushed down and back, as it were, into the infraorbital space (Starks, 1923, pl. 4, fig. 5). The same sort of thing seems to have happened in the chaetodontid percoids, as Starks (1926, p. 301, footnote 35) has noted.

Upper surface of rear of skull. Major differences on the upper surface of the skull posteriorly have to do with the extent to which it is covered by the body musculature. In *Callionymus* the rear face of the skull drops away abruptly, and no musculature at all extends forward over its upper surface. The supraoccipital

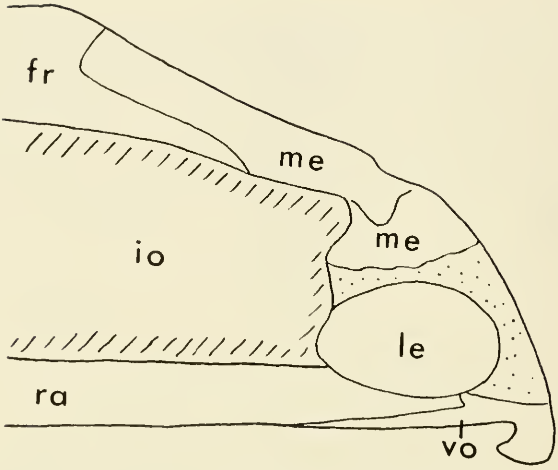

Figure 5. *Draconetta acanthopoma.* Lateral view of forward end of cranium with only the base of the lateral ethmoid indicated. Cartilage stippled. fr, Frontal; io, infraorbital fenestra; le, lateral ethmoid; me, mesethmoid; ra, parasphenoid; and vo, vomer.

extends back from the skull as a flat superficial cap (fig. 4C) the bottom of which forms a surface for muscular attachment. In *Gobiesox* the rear face of the skull slopes more obliquely and two large lateral lobes of musculature extend forward nearly to the rear borders of the eyes. The musculature does not extend forward over the central portion of the skull and there is no median crest. The flat supraoccipital bone (fig. 4A) in *Gobiesox* is pinched off into two parts by the overlapping parietals, but this is not true of at least certain other gobiesocid genera (see Guitel, 1889, pl. 25, fig. 1, and Starks, 1905, p. 283—Starks's *Caularchus* equals *Gobiesox* and his *Gobiesox* equals *Sicyases* according to Briggs, 1955). In *Draconetta* (fig. 4B) the musculature extends forward along either side of the midline to just behind the eye, and a median crest extends forward on the supraoccipital and even a short way on the fused frontals.

Sphenoid region of the skull. In *Draconetta* a pleurosphenoid and small basisphenoid bone are present; the two bones are, however, widely separated, the basisphenoid ending posteriorly in the membrane lining the orbits posteriorly. In neither *Callionymus* nor *Gobiesox* are pleurosphenoids or basisphenoids present.

As is true of all notothenioids, there is little upward extension of the parasphenoid into a postorbital bar, and the prootic borders the orbit in all the Gobiesociformes. In *Gobiesox,* however, the parasphenoid is considerably expanded anteriorly, forming a broad shelf below and between the orbits; this expansion is greater than that of the parasphenoid just behind the orbits.

Otic and occipital regions of the skull. In none of the Gobiesociformes examined is there an expanded auditory bulla. In *Draconetta* there is a triangular

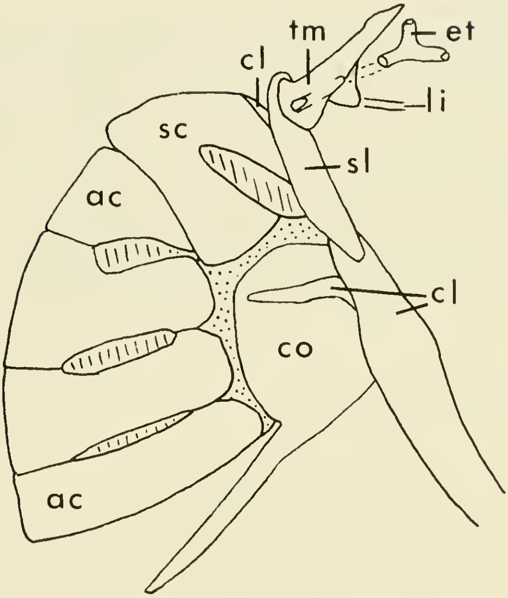

Figure 6. *Draconetta acanthopoma.* Pectoral girdle of right side, except postcleithra. Lateral line canal indicated by dashed lines. ac, Actinost; cl, cleithrum; co, coracoid; et, lateral extrascapular; li, ligament to intercalar; sc, scapula; sl, supracleithrum; and tm, posttemporal.

intercalar on the lower surface of the cranium which serves for the attachment of the ligament from the short lower wing of the posttemporal. In *Gobiesox* and *Callionymus* there is neither an intercalar nor a lower wing to the posttemporal.

The exoccipital condyles in *Draconetta, Callionymus,* and *Gobiesox* are widely separated from one another and indeed are practically or quite lateral to the basioccipital condyle. As Starks (1905, p. 293, footnote 1) has noted, this configuration of the occipital condyles is one frequently associated with a depressed body form.

Pectoral girdle. In gobiesocids the supracleithrum and posttemporal bones are both present. The cleithrum and primary pectoral girdle extend up the sides of the body. From an articulation on the top of the cleithrum, the supracleithrum extends horizontally forward, and from the front of the supracleithrum the posttemporal extends horizontally inward to an articulation with the skull. The axes of the cleithrum, supracleithrum, and posttemporal thus lie primarily in three different planes (Guitel, 1889, pl. 24, fig. 3). In *Draconetta* the supracleithrum and posttemporal are present (fig. 6) but the supracleithrum and cleithrum have the same axes. Among callionymids Briggs and Berry (1959) and Ochiai (1963) state that a supracleithrum and supratemporal are both present, though the latter author shows only one of these two bones in his figures. Starks (1923, p. 268) says that the supracleithrum is absent in Callionymidae and I can find none in *Callionymus flagris, C. decoratus,* or *Pogonymus.* Judging from the position of the supracleithrum in *Draconetta,* it would seem to have become fused with the cleithrum in the callionymids investigated by me. Perhaps its loss as a separate element is variable in callionymids.

In *Draconetta* there are 4 actinosts. The lower 3 are columnar, but the uppermost tapers to a basal point and has its entire upper edge contiguous with the scapula (fig. 6). In *Callionymus,* as in the Nototheniidae, there are only 3 actinosts, the uppermost of *Draconetta* having doubtless become fused with the scapula.

In *Gobiesox* there are not only 4, more or less hourglass shaped, actinosts, but the scapula projects around the top of the uppermost in such a way as to resemble a fifth, as was noted by Starks (1930, p. 220; see also Guitel, 1889, pl. 24, fig. 10). It is very probably a scapular projection of similar sort that provides the uppermost fifth "actinost" of the batrachoid fishes.

A further peculiarity of pectoral girdle structure unique among the Gobiesocidae is the specialization of the two postcleithra (see Starks, 1905; Guitel, 1889, pl. 24, fig. 3). Both of the postcleithra on either side are plate-like. The upper is vertically alined and has numerous fimbriae extending from its posterior surface; it appears to be only ligamentously attached to the main pectoral girdle. The lower extends inward from the side of the abdomen and, with its counterpart from the opposite side, supports the rear rim of the adhesive disc. I do not know of a similar specialization elsewhere in fishes, the postcleithra of *Cheimarrichthys,* for example, being quite normal. In *Draconetta* there is only a single, long, scimitar-like postcleithrum with the usual ligamentous attachment to the top of the cleithrum. *Callionymus* has an even longer, thinner postcleithral strut, but it is made up of 2 pieces closely bound together where they overlap.

Pelvic girdle. The pelvic girdle of the Gobiesociformes is short and broad, as in many notothenioids. The only peculiarity that I can find is in the flat, spatulate pelvic spine of *Gobiesox,* already mentioned.

Axial and caudal skeletons. In *Draconetta* there are 7 abdominal and 16 caudal vertebrae, including the urostylar centrum. In the Callionymidae, so far as is known, there are 7 + 14 vertebrae. Briggs (1955, p. 9) gives the vertebral counts of Gobiesocidae as ranging from 25–54; in *Gobiesox* the count given by Starks (1905, p. 300) is 13 + 19.

In all the Gobiesociformes the ribs start on the second vertebra. In *Draconetta* and *Callionymus* there is only 1 pair of ribs per vertebra. These, in *Draconetta,* extend out and up away from the abdominal cavity, which suggests that they are epipleurals. In *Gobiesox* the same set of ribs occurs, but from the third vertebra on there is another set of ribs extending lateroventrally from the lower surface of the main ribs about half way out along their length (Runyon, 1961, p.

136 and fig. 27). These supplementary lower ribs are, despite their configuration, probably pleural ribs (but see Starks, 1905, p. 301). In the flattened nototheniioid *Bembrops* there is only a single set of ribs, but these commence on the first, not the second vertebra (for the problem of whether a single set of ribs in acanthopterans is pleural or epipleural, see Starks, 1923, p. 290).

In the gobiesociform fishes examined there are no predorsal bones, and the first interneural extends down behind the second neural arch. In *Draconetta* the neural arch to interneural relationship is normal, but in *Callionymus* and *Pogonymus* the third and following vertebrae have V-shaped neural processes that extend out laterodorsally on either side of the interneurals.

In *Draconetta* there are 2 separate hypurals in the caudal skeleton, the lower autogenous, and the upper fused to the urostylar centrum. In *Callionymus* and *Gobiesox* these 2 hypurals are fused into a single unit basally. In *Draconetta* and *Callionymus* there are 2 epurals, in *Gobiesox* none. Unlike *Gobiesox,* the penultimate vertebra of *Callionymus* and *Draconetta* has expanded, plate-like neural and hemal arches which are fused to the centrum.

So far as the fishes examined are concerned, the characters described above may be grouped as follows. It should be noted, however, that the wider the spectrum of variation within the group the less any definition based on one or a few species, such as those given below, can be expected to hold.

Gobiesociformes.—Head and body scaleless. Circumorbital bones represented only by the lacrimal. Premaxillary with its articular process absent or merged with the ascending process (in *Draconetta*). Opercular apparatus with 1 or 2 backwardly projecting spines (except some Gobiesocidae). Metapterygoid absent. Ribs commencing on second vertebra.

Gobiesocoidei.—An abdominal adhesive disc. No spinous dorsal fin. None of the fin rays branched. Outer pelvic ray flattened and spatulate, followed by 4 segmented rays. Palatine separated by membrane from the ectopterygoid. No basibranchials. A single upper pharyngeal tooth plate on each side. Frontals separate. Mesethmoid not forming part of the orbital boundaries. Parasphenoid expanded below and between the orbits. Postcleithra expanded, platelike, the lower supporting the rear border of the adhesive disc. More than 10 abdominal vertebrae, more than 24 in all. Two sets of ribs from the third vertebra. Penultimate vertebra with its neural and hemal arches not expanded. No epurals.

Gobiesocidae.—Lateral line system limited to the head. A nasal bone on each side of head. Two nostrils on either side, which lead into a nasal sac containing a well-developed olfactory rosette. A single spine, if any, on the opercular apparatus, formed by the subopercle. Gill openings not restricted to a small hole above or behind the opercle. Mesopterygoid absent. Supratemporal commissure lacking. No median supraoccipital or frontal crest. Pleurosphenoid, basisphenoid, and intercalar absent. Posttemporal present. Four actinosts. Two postcleithra. Neural arches normal. Hypurals fused into a single plate.

Callionymoidei.—No abdominal adhesive disc. A spinous dorsal fin present, except *Draculo.* At least 1 soft ray in each fin branched or divided to the base. Outer pelvic ray spinous, followed by 5 soft rays. Palatine firmly attached to the ectopterygoid. Basibranchials present. Two upper pharyngeal tooth plates on each side. Frontals fused or mostly so. Mesethmoid forming part of the orbital boundaries. Parasphenoid forming a narrow strut below and between the orbits. Postcleithral strut narrow. Seven abdominal vertebrae, fewer than 24 in all. A single set of ribs. Penultimate vertebra with its neural and hemal arches expanded and plate-like. Two epurals.

Draconettidae.—Lateral line system limited to head. No nasal bone. Two nostrils on each side of head; no nasal rosette. Two spines on the opercular apparatus, one on the opercle and one on the subopercle. Gill openings not restricted to a small hole above or behind the opercle. Mesopterygoid present. Supratemporal commissure incomplete. A low supraoccipital crest extending forward onto the rear of the frontals. Pleurosphenoid, basisphenoid, and intercalar present. Posttemporal present. Four actinosts. One postcleithrum. Neural arches normal. Two separate hypurals.

Callionymidae.—Lateral line continued on body. A nasal bone on each side. One nostril leading into a nasal sac with a well developed olfactory rosette. Spine on the opercular apparatus single, formed by the preopercle. Gill openings restricted to a small hole above or behind the opercle. Mesopterygoid absent. Supratemporal commissure complete. No median crest on supraoccipital or frontals. Pleurosphenoid, basisphenoid, and intercalar absent. Posttemporal absent. Three actinosts. Two postcleithra. Neural arches of third and succeeding vertebrae with V-shaped flanges. Hypurals fused into a single plate.

Of the developments which characterize the Gobiesociformes as a whole, some are of a type that have repeatedly occurred in higher acanthopterans, *e.g.,* the "simplification" of skull and fin ray structure. Perhaps the absence of scales and the loss of the circumorbital bones behind the lacrimal should be placed in the same category. In my opinion the definitive peculiarities held in common by the various members of the Gobiesociformes are those of the upper jaw, gill cover, and rib configuration.

That the various members of the Gobiesociformes have diverged widely is obvious. In the first place, there is a most remarkable difference in habitat between the callionymoids, which are mostly quiet water bottom fishes, and many gobiesocids. At least some of the latter, including the close relatives of one dissected here, live among the boulders of wave-washed rocky beaches.

The way in which the gobiesocids have evolved from a proto-gobiesociform ancestor is suggested by the notothenioid *Cheimarrichthys,* which has the same

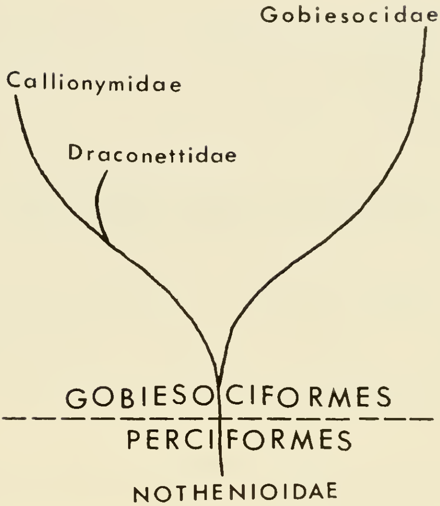

Figure 7. Suggested gobiesociform relationships.

sort of broad, flat head, small, wide-set eyes, and incipient adhesive organ on the abdomen as *Gobiesox*. However, the gobiesocids, in addition to having the premaxillary, opercular, and rib structure, etc., of all the gobiesociformes, which *Cheimarrichthys* does not have, have incorporated the postcleithra into the adhesive disc in a unique way. In short, the gobiesocids are much more highly specialized fishes than *Cheimarrichthys*.

The callionymoids would seem to have diverged from their proto-gobiesociform ancestors in two principal respects. One is that the high-set eyes have left little room for the interorbital portion of the cranium. The frontals have not only fused, but their anterior portion appears to have been pinched off and replaced in part by the mesethmoid from the preorbital region. Second, there has been a reduction in the number of vertebrae.

Between the draconettids and callionymids, the quite different opercular specializations of the two groups preclude the possibility of the one group having evolved directly from the other. In general, however, the draconettids have remained at a lower stage of specialization than the callionymids as indicated by the much lower degree of fusion in the draconettid skeleton.

In my opinion then, the relationships between the three gobiesociform groups may be diagrammed as in fig. 7.

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SCALE-EATING AMERICAN CHARACOID FISHES, WITH SPECIAL REFERENCE TO *PROBOLODUS HETEROSTOMUS*

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INTRODUCTION

Specialized scale-eaters have been discovered in three groups of American characoids. Kner (1860, p. 34) reported the stomach of a large specimen of *Catoprion* full of scales and referred to them as "Raubfische." Ladiges, observing this peculiar serrasalmid in an aquarium, saw one remove a row of scales from a specimen of *Metynnis* with one swipe of its teeth (reported by Géry, 1964, p. 460). Breder (1927, p. 127) reported substantial amounts of large scales in stomach contents of representatives of *Roeboides occidentalis* from eastern Panama and identified some of the scales as coming from *Ctenolucius,* a pike-like characoid considerably larger than the specimens of *Roeboides.* Géry (1964, pp. 459–460) reported scale-eating in *Exodon, Roeboides,* and *Roeboexodon,* of the characid subfamily Characinae. In this paper the activity is verified for *Catoprion, Exodon, Roeboexodon,* and two additional species of *Roeboides* and is reported for the first time in *Probolodus heterostomus* Eigenmann,[1] a member of the characid subfamily Tetragonopterinae.

Although Géry supposed that scale-eating occurred in *Catoprion, Exodon, Roeboexodon,* and *Roeboides* only occasionally, in these genera and in *Probolodus* scales are definitely a major item in stomach contents, and eating scales is prob-

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[1] Myers (1942, p. 91), in recording specimens from the western end of the coastal plain of Rio, commented on their almost unbelievably strange dentition. The species also occurs in the rios Doce, Paraíba (formerly spelt Parahyba), and Ribeira.

ably a significant factor in the mode of life of these fishes. *Serrasalmus elongatus* includes some scales in its diet but is primarily a fin-eater. Matthes (1961) reported that the African characoids *Phago, Belonophago,* and *Eugnathichthys* (family Ichthyboridae) are fin-eaters. There are reports in the literature on aquarium fishes that the eating of fins and scales occurs in *Phago.* Matthes (1964, pp. 65–66) reported scales in stomach contents of specimens of *Belonophago hutsebouti, Phago boulengeri,* and (1961, p. 79) *Eugnathichthys,* but these fishes are primarily fin-eaters. The only other fresh-water scale-eaters of which I am aware are certain highly specialized African cichlids (see Fryer, Greenwood, and Trewavas, 1955). I have not searched thoroughly for accounts of marine scale-eating fishes. There probably are some; Springer and Woodburn (1960, p. 22) stated that annelids and fish scales (with no other fish remains) constituted the major portion of stomach contents of sea catfish (*Galeichthys felis*) taken in Tampa Bay.

This paper was prepared at the Departamento de Zoologia of the Secretaria da Agricultura in São Paulo during a visit in April and May, 1969. All observations are based on specimens in the Departamento's collections. Measurements of fishes given in mm. refer to standard length.

OBSERVATIONS

Probolodus.

Material examined. DZSP 7903, 40 specimens, 41–97 mm., from Rio Paraíba below represa de Santa Branca (state of São Paulo), col. 10–13 February 1962 by H. A. Britski; and DZSP 7904, 92 specimens, 38–71 mm., represa de Santa Branca, Rio Paraíba, collected 10–16 September 1963 by H. A. Britski and J. Rossi.

Stomach contents. Stomach contents were examined in 30 specimens ranging from 38 to 97 mm. Twenty of these were from the February, 1962 collection, and 10 from September, 1963. The stomachs contained food in all specimens. Scales were by far the major item encountered and occurred in all but 1 specimen. They were the only item present in about 50 percent. The number of scales in a stomach varied from 3 to 40, with a mean of about a dozen. Most of the scales were 3–5 mm. in diameter, substantially larger than *Probolodus*' own scales. A white substance of loose consistency was present in large quantity in 5 specimens of the February, 1962, sample. Otherwise food items in the 2 samples were very similar. The following items were also encountered: small seeds (1 or 2), in 3 specimens; soil? (small quantities), 3 specimens; minute crustaceans (about 50), 1 specimen; insect larva (1), 1 specimen; hymenopteran (1), 1 specimen. The smallest specimens examined—38, 41, 47, and 49 mm.—have stomach contents similar to the others.

Dentition. The teeth of *Probolodus* have been described and figured by Eigenmann (1915, pp. 20–21, fig. 5). *Probolodus* has very few teeth and, as in many other characoids with highly specialized dentition, the number is constant or very nearly so. Basically there are 3 widely separated teeth on each premaxillary and 5 on each dentary. Often a tooth is missing, but this is due to loss or shedding to make way for a replacement tooth. There are usually either 3 or 4 teeth on each maxillary, but as few as 2 or as many as 5 were present on some specimens. Here, too, replacement affects the number present. All of the teeth are strictly tricuspid. The 3 cusps form a triangle with the enlarged median cusp at the anterior angle. The lateral cusps are equal in size and very small. The tooth base is moundlike and stout.

The premaxillary teeth point out of the mouth. The first 3 dentary teeth also point out. Only the fourth and fifth dentary teeth lie inside the mouth. The enlarged fourth dentary tooth is situated internally to the third and slightly posterior to it, and the reduced fifth is directly behind the fourth. (Note.— Eigenmann refers to one *or more* small teeth behind the fourth. In specimens I have examined there is only one. Perhaps the presence of additional teeth in an occasional specimen is a primitive or vestigial character.) The cusps of the anteriormost premaxilliary and dentary teeth point almost straight ahead of the fish. The third dentary tooth, and to a lesser extent the third premaxillary tooth, project laterally from the mouth. The teeth are not juxtaposed but are separated from each other by a gap about equal to the diameter of a tooth base. When the mouth is closed the teeth of the upper and lower jaws interdigitate rather than truly oppose each other. Thus the first dentary tooth occupies the gap between the first and second premaxillary teeth, the second dentary tooth that between second and third premaxillary teeth, and the third dentary tooth that between the third premaxilliary and first maxillary teeth. The fourth and fifth dentary teeth do not oppose or interdigitate with other teeth and neither do the lowermost teeth on the maxillary. One can easily imagine how scales are firmly grasped by such teeth and then dislodged by the kind of tugging movements many characids make when feeding. The number, form, and arrangement of the teeth are the same in specimens from 38 to 97 mm.

Tooth replacement. Twenty specimens from the September, 1963, collection were examined for signs of tooth replacement. In only 2 specimens were all of the premaxilliary and dentary teeth in functional position and firmly attached to the jawbones. In each of the remaining 18 from 1 to 4 teeth were in the process of replacement or had just come into functional position (teeth in the process of replacement can be detected immediately below the gum or making their way through it; teeth that have just come into functional position are recognizable as such because the cusps are unworn and very sharp, the bases are usually surrounded by soft, swollen tissue, and the attachment to the jaw is very loose). The data indicate that replacement occurs more frequently in lower jaw teeth than in upper, and that certain teeth are replaced with relatively high frequency. In all, 40 instances of tooth replacement in process and teeth newly in functional position were observed, 29 in the dentary and 11 in the premaxillary. No fewer than 9 instances involve the fourth dentary tooth. At the other extreme, the first premaxillary tooth is involved in only 1 instance. Judging from their appearance the teeth in the lower jaw receive more wear than those in the upper jaw.

SEX. Almost all specimens in the February, 1962, collection have readily identifiable gonads. The others were sexed by the presence (males) or absence of tiny serrations on the anterior anal fin rays. The reliability of this method was checked in specimens in which the sex of the gonads was obvious. Of the 40 specimens in the sample, 29 (72 percent) are females and 11 (28 percent) males. Females range from 40.5 to 97 mm. and average 68 mm., 12 mm. more than the males. Males range from 47 to 65 mm. and average 56 mm. The largest female is 32 mm. longer than the largest male. Combined biomass of females is slightly more than three times that of males. The 40.5 mm. specimen contained about 200 eggs, most .6–.7 mm. in diameter but a few somewhat smaller; a 73.5 mm. specimen contained about 2500, all about .7–.8 mm. in diameter.

Serrasalmus elongatus.

Stomach contents were examined in 7 specimens of *S. elongatus* Kner, 89–152 mm., from 3 Amazonian localities. Pieces of the rayed portion of fins and scales were present in every specimen; they were the only items encountered in 5 of the specimens. In all but 2 fin rays were by far the major item. One specimen had about 50 scales and only a few small bits of fin rays. The 152 mm. specimen (collected in Lago Jacupá, near Oriximiná, state of Pará, in February, 1967) contained 6 cichlid larvae of about 8 mm.; 13 fish? eggs of about 2 mm. in diameter; 2 large pieces of very hard, thick fin rays, perhaps from the caudal fin of a sorubim catfish; and 8 scales about 5–6 mm. in diameter. One specimen, with its stomach moderately full of fin rays and a few scales, had a small matted ball of fibrous plant material including 3 small seeds. All items encountered have been indicated; noteworthy is the absence of pieces of meat. Stomach contents of several *Pygocentrus*-type piranhas have been examined and when scales were encountered there were also bits of meat. Many piranhas feed to some extent on fins. *S. elongatus* is apparently a fin-eater which feeds to a certain extent on scales.

Catoprion.

Kner (1860, p. 34) found the stomach of a large *Catoprion* specimen full of scales. Gosline (1951, p. 54) examined the stomachs of 4 specimens and reported that "two were full of fish scales and two were empty except for a few fish scales; a small amount of unidentifiable debris was also found." Géry (1964, p. 460) found scales in stomachs of specimens from Bolivia. In examining 4 specimens, 103–109 mm., from 3 Amazonian localities I find that their stomachs are more or less full of scales about 6–15 mm. in diameter. The only other items are a few bits of leaf from a higher plant (in 2 specimens) and a small ball of fibrous plant material, probably roots (in 1 specimen). Scales are thus the only item that has been encountered in substantial amounts in stomachs of *Catoprion.* The teeth in this genus are illustrated by Müller and Troschel (1845, pl. 2, fig. 5).

Exodon.

Géry (1964, p. 459) reported scales in stomach contents of *Exodon* from the Rio Araguaia. I examined 10 specimens, 36–59.5 mm., from the Rio Araguaia at Aruanã and found from 4 to 15 scales, mostly 3–5 mm. in diameter, in every one. The only other item was small amounts of unidentifiable material in 2 specimens. Kner (1860, p. 47) found beetles in 2 specimens from the Rio Branco. The teeth of *Exodon* are figured by Müller and Troschel (1845, pl. 4, fig. la).

Roeboexodon.

This genus has hitherto been known only from a few specimens taken in French Guiana (Géry, 1959). In September, 1966 Heraldo A. Britski and P. E. Vanzolini collected 2 specimens (DZSP 4815, 41.5 and 45.5 mm.) from the Rio Araguaia near Aruanã in the Brazilian state of Goiás. The dentition of these specimens is identical with that in an alizarin preparation of a 29 mm. specimen from French Guiana (kindly sent to the Departamento de Zoologia by Géry) and they apparently represent the same species. The stomach contents of both specimens consist exclusively of scales from about 2.5 to 4 mm. in diameter. The 41.5 mm. specimen contained about 10 scales and the 45.5 mm. specimen about 20. The teeth of *Roeboexodon* are described and partially figured by Géry (1959, pp. 347–349, fig. 2).

Roeboides.

Naercio Menezes and I examined stomach contents in 9 specimens of *Roeboides guatemalensis,* 6 of *R. myersi,* and 25 of *R. prognathus.* In all 6 specimens of *R. myersi* (117–160 mm.) and in the 11 largest of *R. prognathus* (70–90 mm.) the stomachs are more or less filled with scales, to the exclusion of all else, those of *R. myersi* with from 15–35 scales mainly 6–9 mm. in diameter and those of *R. prognathus* with 40–150 scales 3–6 mm. in diameter. In 14 smaller examples of *R. prognathus* (41–68 mm.) scales predominate, but insects—Diptera, Hemiptera (Notonectidae?), and a few Coleoptera—occur with high frequency. A 64 mm. specimen contained a fish larva. Our specimens of *R. guatemalensis* (72.5–101 mm., from Gatun Lake, Panama Canal Zone, collected in November, 1965) have viscera heavily infested with nematodes and may not have been feeding normally. The stomachs are empty in 4 of them and the other five contain but little food, as follows: a few scales (in 4); shrimp (in 2); insect (in 1); and an unidentified, flocculent, white material (in 1).

In very small specimens of *Roeboides* (20–30 mm.) the teeth can be recognized as belonging to *Roeboides* because of their slightly hypertrophied bases, but they are all normal in position. Examination of stomach contents in a few specimens (unidentified to species) indicates that at these sizes they feed primarily on insects. Only at about 30–60 mm., depending on the species, is the transition made to the adult condition in which teeth with greatly hypertrophied bases project from the front of the jaws.

DISCUSSION

Stomach contents of fishes belonging to *Catoprion, Probolodus, Exodon, Roeboides,* and *Roeboexodon* indicate that their diet consists mainly of scales. The teeth are so highly specialized in some of these fishes as to suggest that they could not survive in nature on the food that their non-scale-eating ancestors fed upon. The remarkable "twin spot" color pattern of *Exodon* and relatively small scales of *Probolodus* may have evolved after the scale-eating behavior to reduce intraspecific scale-eating. Breder (1927, p. 127) speculated that the small, thin, and very adherent nature of the scales of *Roeboides occidentalis* reduces autopredation. Whereas *Catoprion, Exodon, Roeboexodon,* and *Probolodus* are monotypic, *Roeboides* has speciated extensively.

The relationships of the five genera, although not yet well understood, show that they represent at least three independent lines of evolution: 1. *Catoprion* is definitely a serrasalmid, and probably descended from *Serrasalmus. Serrasalmus elongatus* includes scales in its diet but is primarily a fin-eater and does not appear to be closely related to *Catoprion.* 2. Eigenmann (1911; 1915) stated that *Probolodus* is very similar in general appearance to *Astyanax fasciatus* but placed it in his polyphyletic subfamily Aphyocharacinae (= Cheirodontinae). In my opinion *Probolodus* belongs in the Tetragonopterinae; it probably descended from *Astyanax.* It is certainly not related to either *Cheirodon* or *Aphyocharax.* 3. *Roeboides* is closely related to *Charax* and *Eucynopotamus.* Géry (1959, pp. 404–405) suggested that *Exodon* was derived from *Holobrycon* and *Roeboexodon* from *Exodon,* and placed *Roeboides* and *Charax* in a different line. Naercio Menezes and I intend to study the osteology of these Characinae in an effort to clarify their relationships. We suspect that *Eucynopotamus,* apparently intermediate between *Charax* and *Roeboides,* is actually based on the young of *Roeboides,* and note that *Roeboexodon* bears a strong superficial resemblance to *Roeboides prognathus* Boulenger.

Perhaps the strange gymnotoid eel *Oedemognathus exodon* Myers is a scale-eater. According to Myers (1936, p. 115), in this apteronotid "the dentigerous portion of the premaxillaries is greatly expanded and bulbous, most of it not opposable to the lower jaw, and the upper part of it rising above the profile of the snout. The whole of this bulbous area is studded with many strong, slightly curved, conical teeth, placed irregularly and not very closely together. Most of the upper teeth therefore project forward, outward or upward, and are entirely outside the mouth. The lower teeth are similar to the upper ones in shape, and are numerous and arranged irregularly, but none is outside the mouth and all point in normal direction." *Oedemognathus* is known only from the holotype, 202 mm. in total length, USNM 102040, and a 92 mm. specimen reported on and figured by Eigenmann and Allen (1942, pp. 325–326, pl. 15, figs. 2–3), CAS (IUM) 15421, both from the Peruvian Amazon.

ACKNOWLEDGMENTS

I wish to thank Daniel M. Cohen of the U. S. Fish and Wildlife Service and Stanley H. Weitzman of the U. S. National Museum for critical comments on the manuscript.

ADDENDUM

Mr. William A. Bussing of the Departamento de Biologia, Universidad de Costa Rica, informs me that Sr. Carlos Leon, Administrador of the Parque Bolivar in San José, Costa Rica, observing 2 fish in an aquarium, saw one (*Roeboides guatemalensis*) butt the other (*Astyanax* sp.) with its snout and then catch the dislodged scales as they sank. Bussing has examined the viscera of about 100 representatives of *R. guatemalensis* during fieldwork on the Atlantic and Pacific slopes of Costa Rica and found almost every specimen had scales and virtually nothing else in the stomach. A few contained small insect larvae and one a small fish.

At the John G. Shedd Aquarium in Chicago, Mr. Emanuel Ledecky-Janecek, Curator of Exhibits, kindly responded to my request and placed a specimen of *Leporinus* (perhaps *L. friderici*) about 9 or 10 inches long in with a small tankful of fish belonging to *Exodon paradoxus*. Within a few moments we saw the latter agitatedly gang up to one side of the *Leporinus* victim and take turns making extremely rapid circular stabbing motions against its side, always striking towards the free margin of the scales, and removing a single scale at about every other strike. The scales were swallowed directly. On only one occasion did a scale fall to the bottom of the tank and a moment later it too was devoured. In about 5 or 10 minutes 20 or 30 scales had been eaten.

At the Steinhart Aquarium of the California Academy of Sciences I watched several fish belonging to *Leporinus fasciatus* determinedly nipping at fungus-infected sores on a specimen of *Astronotus ocellatus*. I am unsure, but think that the cichlid lost a few scales, although the *Leporinus* specimens seemed to confine their nipping to the sores.

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SCALE-EATING AMERICAN CHARACOID FISHES, WITH SPECIAL REFERENCE TO *PROBOLODUS HETEROSTOMUS*

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INTRODUCTION

Specialized scale-eaters have been discovered in three groups of American characoids. Kner (1860, p. 34) reported the stomach of a large specimen of *Catoprion* full of scales and referred to them as "Raubfische." Ladiges, observing this peculiar serrasalmid in an aquarium, saw one remove a row of scales from a specimen of *Metynnis* with one swipe of its teeth (reported by Géry, 1964, p. 460). Breder (1927, p. 127) reported substantial amounts of large scales in stomach contents of representatives of *Roeboides occidentalis* from eastern Panama and identified some of the scales as coming from *Ctenolucius*, a pike-like characoid considerably larger than the specimens of *Roeboides*. Géry (1964, pp. 459–460) reported scale-eating in *Exodon, Roeboides,* and *Roeboexodon,* of the characid subfamily Characinae. In this paper the activity is verified for *Catoprion, Exodon, Roeboexodon,* and two additional species of *Roeboides* and is reported for the first time in *Probolodus heterostomus* Eigenmann,[1] a member of the characid subfamily Tetragonopterinae.

Although Géry supposed that scale-eating occurred in *Catoprion, Exodon, Roeboexodon,* and *Roeboides* only occasionally, in these genera and in *Probolodus* scales are definitely a major item in stomach contents, and eating scales is prob-

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[1] Myers (1942, p. 91), in recording specimens from the western end of the coastal plain of Rio, commented on their almost unbelievably strange dentition. The species also occurs in the rios Doce, Paraiba (formerly spelt Parahyba), and Ribeira.

anal spine has been overlooked in *Naso*, a genus thought to be alone among the acanthurids in having only two anal spines rather than the normal three.

Naso, like *Prionurus* (including *Xesurus*), has fixed plates on the caudal peduncle rather than the folding spines typical of all other acanthurids. *Naso* and *Paracanthurus* are the only genera with 3 soft rays in the pelvic fin rather than 5. On the basis of *Naso* and *Prionurus* having fixed peduncular plates, Smith (1955: 169) recognized these 2 groups (with *Naso* divided into 5 genera on the basis of the number of peduncular plates and the snout horn development) as the family Nasidae distinct from the Acanthuridae. Randall (1955: 365–366), in a brief addendum to his revision of the surgeon fish genera, gave excellent reasons for not accepting this splitting of the family and of the genus *Naso*. Smith (1966: 635) subsequently recognized *Naso* (this time divided into 3 genera) as the subfamily Nasinae on the basis of its having 2 anal spines and 3 pelvic rays, in contrast to the 3 anal spines and 5 pelvic rays of the other acanthurids which he divided into 2 subfamilies on the basis of whether the caudal peduncle has folding spines (Acanthurinae) or fixed plates (Prionurinae). Such a system neglects *Paracanthurus,* which, in addition to 3 anal spines, has folding peduncular spines and only 3 pelvic rays. In Smith's system, *Paracanthurus* would have to be recognized as an additional subfamily. By most contemporary standards this system would seem to be far too finely split at the subfamilial and generic levels on the basis of somewhat superficial characters, even if all these characters were valid.

The fact that *Naso* has 3 anal spines like the other acanthurids is additional evidence that this genus should not be considered as a subfamily distinct from the other acanthurids. The anal spine that is supposedly absent in *Naso* is the first spine. This spine is substantially similar to the first spine in other acanthurids, except that its distal portion which would protrude through the skin is lost, leaving only the basal portion which acts as a complex locking device in basically the same manner as in other acanthurids.

An initial survey of acanthurid osteology, which cannot be dealt with here, based on representatives of all of the genera recognized by Randall (1955), shows no features that warrant the recognition of subfamilies within the group.

LOCKING MECHANISM OF THE DORSAL AND ANAL SPINES

The locking mechanism in *Acanthurus triostegus* is osteologically representative of all of the acanthurids except *Naso,* and the descriptions and illustrations of the bony parts given here based on *A. triostegus* should apply well except in fine detail to the various species of *Acanthurus, Ctenochaetus, Paracanthurus, Prionurus,* and *Zebrasoma.* The musculature of the locking mechanism is described for *A. triostegus,* and although this has not been compared with the situation in the other genera that have 3 obvious anal spines, I suspect that, based on the shapes of the bony parts, it is similar in all of them. The bony parts of the locking mechanism as described for *Naso literatus* are typical of that genus, and the few comments given here on the musculature probably will apply to all species of *Naso*.

The dorsal and anal spines and their pterygial supports are more generalized in *Acanthurus* than in *Naso*, and are described first below.

Acanthurus triostegus (Linnaeus).

Specimens examined. ANSP 109491, 7 specimens, 40.6–68.9 mm. standard length, Caroline Islands, cleared and stained. ANSP 109490, 1, 69.0 mm., no locality, cleared and stained. ANSP 108288, 4 (out of 12), 83.6–97.0 mm., Seychelles Islands, alcohol.

Dorsal spines and pterygiophores. The first two are borne on the first basal pterygiophore, and the subsequent seven spines on their own individual basal pterygiophores as well as distal pterygiophores. The first two spines articulate medially with the large flattened medial flange at the distal end of the basal pterygiophore, which projects above the level of the distal ends of the subsequent pterygiophores, as well as ventrolaterally by their divergent bases with lateral flanges on the sides of the pterygiophore. The third and subsequent spines articulate at their less divergent bases with the regions of suturing between the distal pterygiophores anteroventral to their bases and the basal pterygiophores ventrally and posteroventrally. The first basal pterygiophore is held basally between the exoccipitals and the dorsal half of the neural spine of the first vertebra. Each of the subsequent basal pterygiophores of the spiny dorsal fin is held between the neural spines of adjacent vertebrae, except that there is no pterygiophore between the third and fourth neural spines (fig. 1). This is true of all acanthurids, regardless of the number of dorsal spines, and is also true of zanclids. In the closely related siganids there is one basal pterygiophore of the spiny dorsal fin between adjacent neural spines, except that there is no pterygiophore between the fifth and sixth neural spines. In siganids the first dorsal spine is normal, not modified into an acanthurid-like locking mechanism. However, the distal ends of the pterygiophores are laterally expanded into plates in much the same manner as explained below for acanthurids, especially *Naso*.

The basal region of the first spine is deeply concave, while that of the second spine has a complete foramen anteroposteriorly through which the medial flange of the first basal pterygiophore passes, the flange in this region having a hole to accommodate the extreme ventral end of the second spine, which is solid and without a medial suture (figs. 2–3). The third spine also has a complete anteroposterior foramen in its base through which passes the medial bridge formed by the posterodorsal process of the first distal pterygiophore and the anterodorsal process of the second basal pterygiophore. The fourth and subsequent dorsal spines usually have a complete foramen ventrally, although the ventromedial region may have a sutural mark medially. The bridges formed by the processes

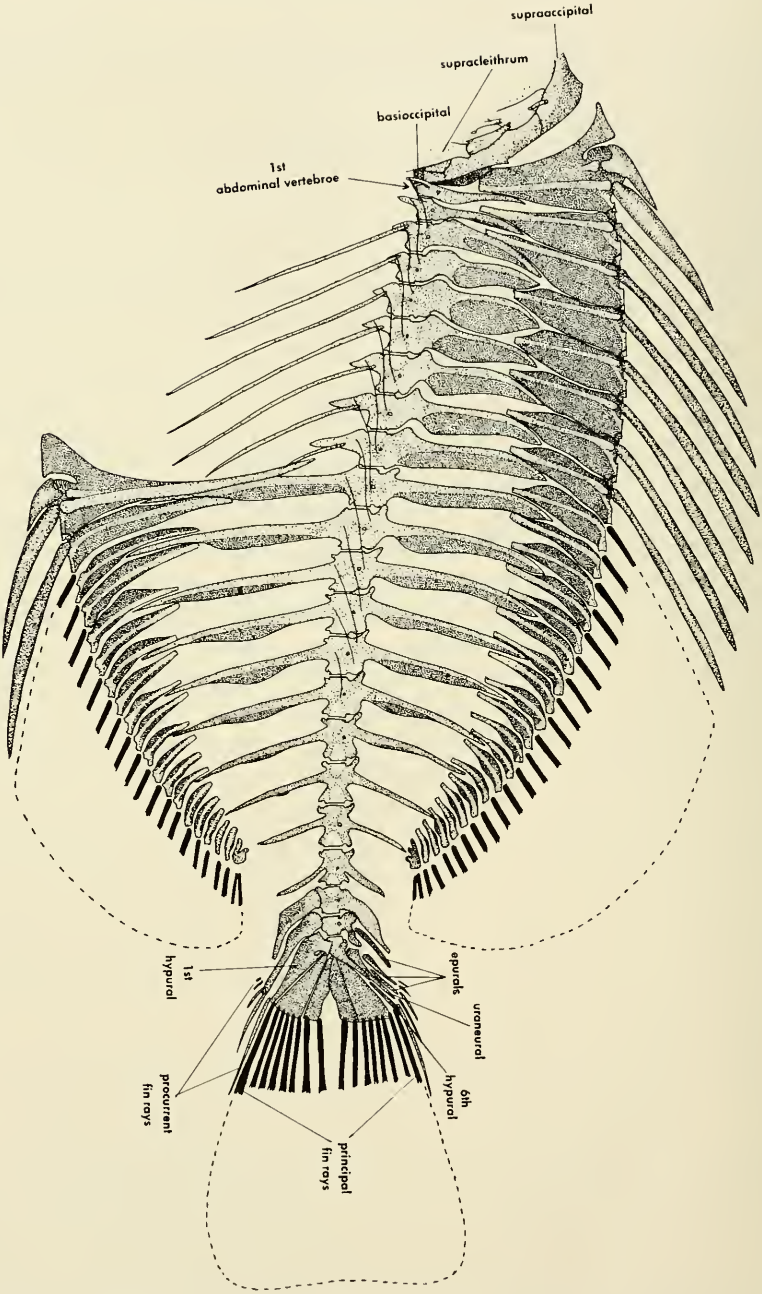

Figure 1. Lateral view of vertebral column and fin supports in *Acanthurus triostegus*, ANSP 109491, 46.2 mm. standard length. Bases of fin rays indicated in black; distal pterygiophores of fin rays not shown.

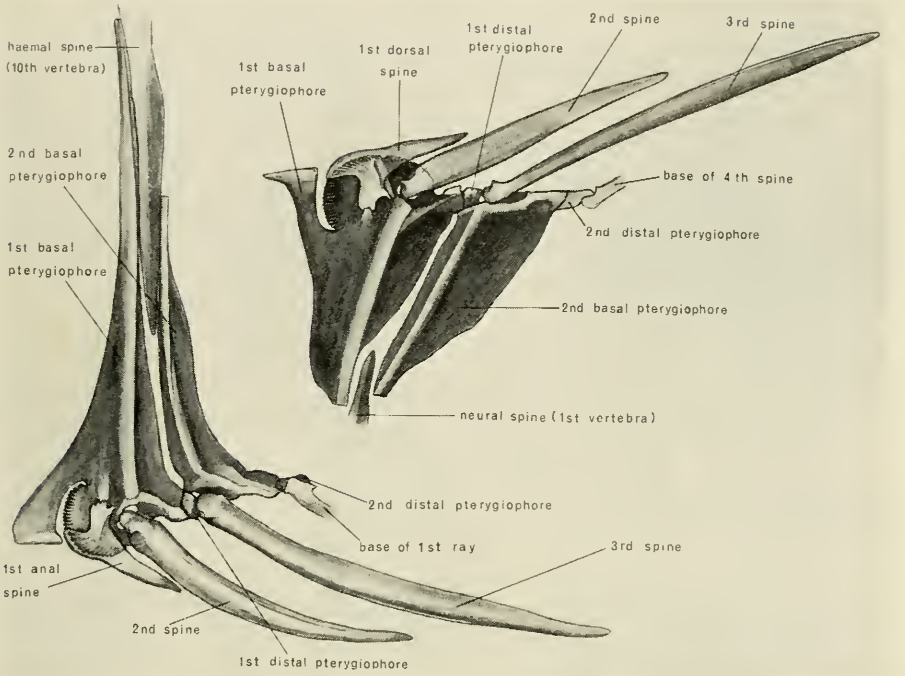

Figure 2. Lateral views of first three dorsal and anal spines and their supports in *Acanthurus triostegus,* the spines only partially erected; composite drawings based on specimens from ANSP 109491.

of the distal and basal pterygiophores, around which the foramina of the spines articulate, are slightly less well developed posteriorly in the series than anteriorly, the anterodorsal process of the basal pterygiophore especially tending to be of lesser length so that it does not quite contact the process of the distal pterygiophore in front of it and thus fails to form a complete bridge.

Distally the pterygiophores are expanded laterally to form a plate composed anteriorly of the expanded posterior half of the distal end of the basal pterygiophore and posteriorly by the expanded anterior portion of the distal pterygiophore. The tendinous insertions of the erector muscles of the spines (except for those of the first 2 spines) are accommodated by gaps between the composite plates, the gaps being between the posterior edges of the expanded portions of the distal pterygiophores and the anterior edges of the expanded portions of the basal pterygiophores (fig. 4). The depressor muscles are accommodated by similar gaps in the anterior third of the laterally expanded plates of each of the basal pterygiophores. The anterolateral edges of the basal pterygiophore plates tend to be prolonged anteriorly, partially enclosing the lateral surfaces of the insertion ends of the depressor muscles. The amount of bridging in these regions

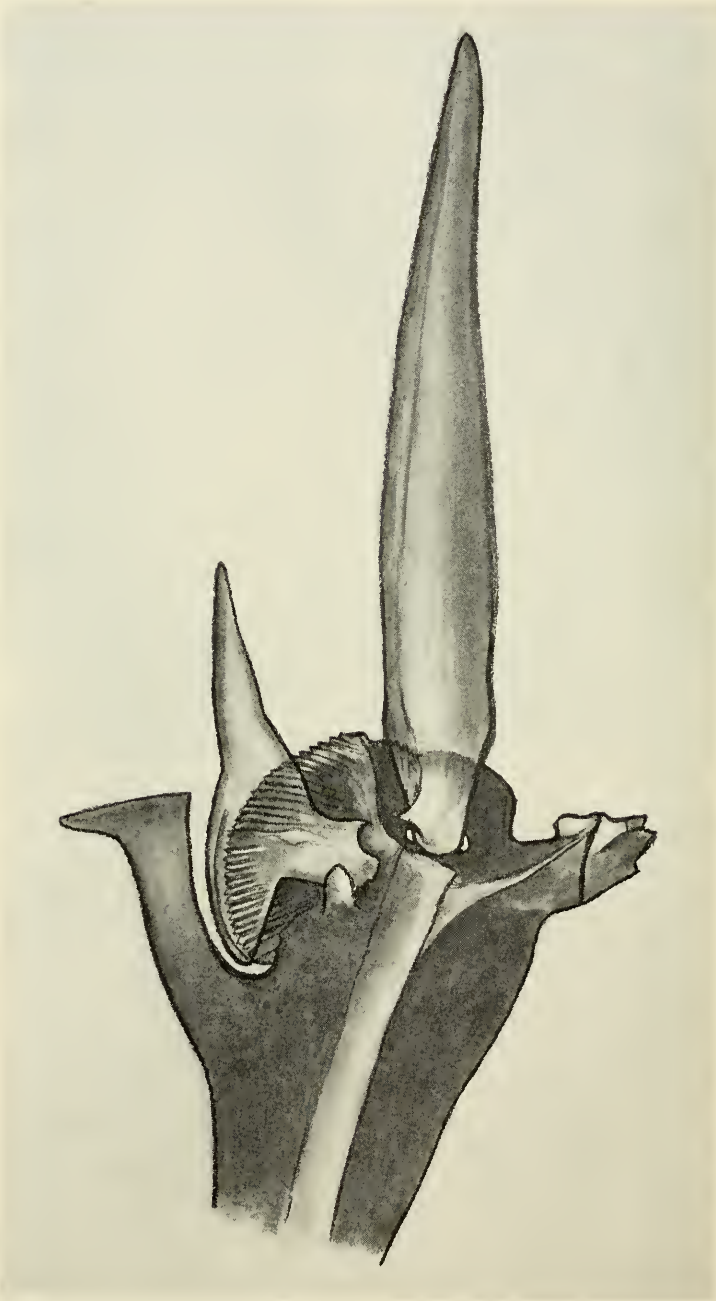

Figure 3. Lateral view of first two dorsal spines in *Acanthurus triostegus*, the spines almost fully erected; composite drawing based on specimens from ANSP 109491.

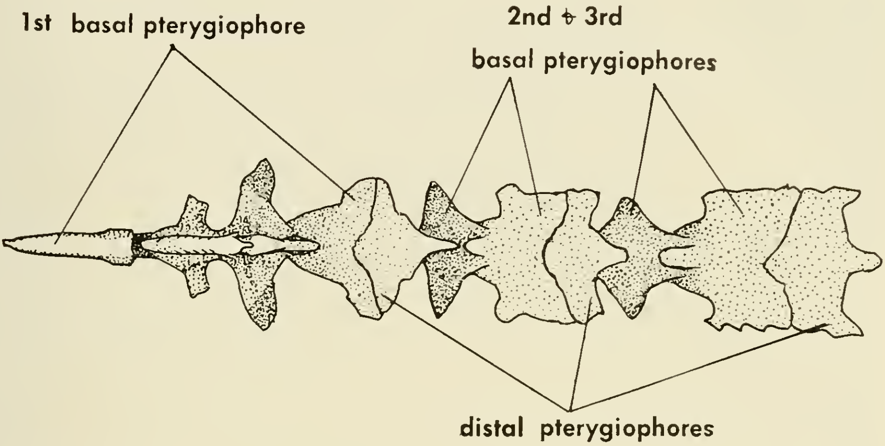

Figure 4. Dorsal view of first three basal and distal pterygiophores of dorsal fin of *Acanthurus triostegus*, after removal of the spines, ANSP 109491, 46.2 mm. standard length.

may increase with increasing specimen size, but it probably never reaches the complete bridging found in *Naso,* as discussed later.

As one of the major characteristics of the acanthurids, Gill stated (1884: 276; this statement often followed by others): "Interneurals with expanded buckler-like subcutaneous plates, which intervene between the spines and limit their erection forwards." The plates he refers to obviously are the laterally expanded distal ends of the basal and distal pterygiophores, but these plates in no way interfere with the full erection of the spines, as explained below. Connective tissue in dried skeletal preparations or unnaturally inelastic membranes and ligaments in alcohol preserved specimens must have misled him.

All of these spines can be erected at right angles to their pterygiophores. The first and second spines are bound together by a compact ligament, while the second and subsequent spines are bound together by more diffuse ligamentous connections spread out over most of the lengths of the spines. The erection or depression of one spine thus is in concert with the others. When the spines are fully erected at right angles to their pterygiophores, they tend to stay erected because of the frictional resistance of their ventral edges against the dorsal surfaces of their pterygiophores caused by the down pull of the erector muscles, but the whole series of spines can be firmly locked in an erected position varying from full to any degree of partial erection by a catching action of the small first spine against grooved surfaces on the dorsomedial flange of the first basal pterygiophore.

The locking mechanism probably develops very early in the larval stages, for the figures of 3 to 5 mm. long specimens of *A. monroviae* given by Aboussouan (1965: figs. 2–3) clearly indicate the grooved medial flange of the first basal pterygiophore, although the small first spine is not shown.

The dorsomedial flange of the first basal pterygiophore is generally circular in outline as seen laterally, with the exception of the region just behind the middle of the flange discussed below. The flange bears grooves running from its distal edge approximately towards the center. The deeply concave ventral surface of the first spine is relatively smooth and rides over the grooved peripheral surface of the medial flange of the first basal pterygiophore. The ventral arms, or extreme basal flanges, of the first spine rotate around a small flange projecting laterally from the lateral surface of the pterygiophore at the level of the horizontal base of the medial flange. The dorsal surface of this pterygiophore flange and the ventral edge of the ventral arm of the first spine which it supports are both knurled, the amount of knurling being highly variable in the specimens studied. As the first spine rotates in erection forward and downward it slides easily over the variously anteriorly to dorsally oriented grooves on the medial flange of the basal pterygiophore. When a downward and/or backward pressure is exerted on the first spine, it catches firmly on the grooves of the medial flange. Since the first and subsequent spines are ligamentously connected, the whole spiny dorsal fin is firmly held erect. Because the grooves on the medial flange are continuous from the region underlying the concave ventral surface of the first spine in its unerected position to its fully erected position at right angles to the pterygiophore, the first spine can be locked in any of the innumerable positions between the two extremes. The first spine is unlocked from its erected position by relaxation of the pressure of the muscles (as discussed below) pulling it into intimate contact with the grooves on the medial flange of the basal pterygiophore, allowing it to slide upward and posteriorly without undue frictional resistance. The rotational course of the first spine is blocked anteriorly when it reaches its fully erected position at about a right angle to the pterygiophore by its anterior edge hitting against two bony obstacles on a prong-like portion of the pterygiophore anterior to the medial flange and separated from it by a deep vertical canal into which the head of the first spine rotates in erection. The extreme anterior end of the first spine hits the bottom of the canal at the same time that a slight indentation on the mid-dorsal (as seen when unerected) edge of the spine hits against the posterodorsal edge of the prong-like portion of the pterygiophore.

The second spine rotates over the posterior half of the medial flange of the basal pterygiophore. The peripheral surface of the flange over which it slides is also grooved, although not so deeply or regularly as that portion over which the first spine slides. Nevertheless, downward pressure on the second spine serves to help lock the spiny dorsal fin in an erected position. The ventral arms (which are fully fused in the region of the foramen in the medial flange) of the second spine rotate around the oblique dorsal surface of a large flange running vertically along most of the lateral surface of the first basal pterygiophore. The rotational course of the second spine is blocked anteriorly when it reaches a fully erected position at about a right angle (or a little more) to the pterygiophore by its anterior edge just at the dorsal end of the anteroposterior hole through its base hitting against an indented and thickened region on the medial flange. The medial flange is thicker beneath the position of the base of the unerected first dorsal spine than more posteriorly, and the lateral ridge so formed corresponds to an indented region on the flange just posterior to the ridge. The anterior edge of the second spine in full erection hits against this ridge and indentation, stopping any further rotational movement forward.

The third and subsequent spines, by comparison, rotate simply over their articulations with the bridges formed by the posterodorsal processes of the distal pterygiophores and the anterodorsal processes of the basal pterygiophores, without any special mechanisms for locking them in an erected position, other than their ligamentous connections with the first 2 spines.

Musculature. When the skin is removed from the upper part of the trunk below the dorsal spines, 3 main muscle groups are seen (fig. 5, top): the general epaxial muscle mass; the inclinators which originate on the undersurface of the skin and course posterodorsally to insert variously on the expanded plates of the pterygiophores and on the ventrolateral surfaces of the bases of the spines; and the supracarinales anterior, a band of longitudinal muscle running from the supraoccipital to the lateral surfaces of the anterodorsal prong-like portion of the first basal pterygiophore and of the base of the first spine. The epaxial muscle mass has nothing to do with the erection mechanism and is not further discussed. The inclinators of the first 2 spines are poorly developed in comparison to those of the subsequent spines and of the soft rays, and they probably have little bearing on the locking mechanism. The band of muscle from the supraoccipital divides posteriorly into a deep segment attaching to the prong of the basal pterygiophore and a superficial segment attaching to the basal region of the first spine. The segment attached to the pterygiophore prong apparently is not associated with the locking mechanism, but the segment attached to the spine may help to unlock the spine prior to depression of the fin. When the first spine has been pulled firmly against the grooved surface of the pterygiophore flange it is locked in place, and a forward and/or upward directed pressure is necessary to disengage it from the grooves before it can slide without undue frictional resistance over the flange. Contraction of the longitudinal band of muscle between the supraoccipital and the first spine probably helps to disengage the spine by pulling it forward. However, the first anal spine has the same type of locking mechanism as the first dorsal spine, yet the anal spine does not have a band of muscle running forward from its base which, when contracted, would tend to disengage the spine from its locked position, nor is such a muscle present on the first dorsal and anal spines of *Naso*. I assume that the natural elasticity

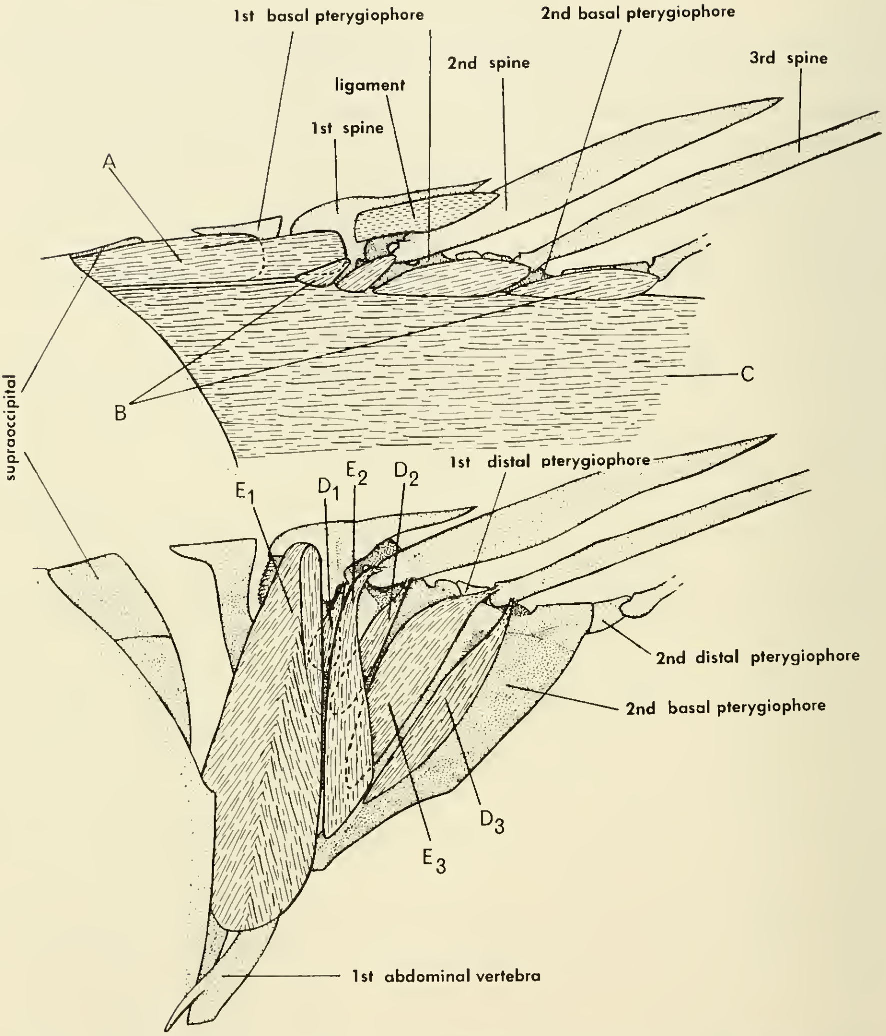

Figure 5. Lateral views of musculature of first three dorsal spines in *Acanthurus triostegus*; above, superficial musculature after removal of skin; below, erector and depressor muscles as seen after removal of superficial muscles: composite drawings based on specimens from ANSP 108288; the representational fiber structures are diagrammatic. Legend: A, supracarinales anterior; B, inclinators; C, epaxial muscle mass; D, depressors; E, erectors.

and resiliency of the various connective tissues between the first spine and the pterygiophore are strong enough to push or pull the spine the slight distance necessary to relieve the pressure on its concave ventral surface from the grooves on the medial flange of the pterygiophore. The relative smoothness of the ventral surface of the spine perhaps facilitates the unlocking of the mechanism, for certainly if it were deeply grooved like the medial flange a complex mechanism for unlocking the adpressed grooved surfaces would have to be present.

The erector muscle of the first spine is the largest in the series (fig. 5, bottom). It originates over the middle of the posterior wall of the skull and over the lateral surfaces of the first vertebral neural spine and first pterygiophore. It inserts on the forward half of the lateral face of the base of the spine. In the upper third of its length, the muscle is partially divided into a forward and rear segment. Contraction of the muscle pulls the spine forward and downward over the medial flange. When the spine is erected it is probably the contraction of the rear segment of the upper third of the muscle that pulls the spine into close contact with the grooves of the medial flange. The muscle overlies much of the length of the large lateral flange running vertically on the pterygiophore, the head of this flange being the point around which the second spine pivots. The depressor muscle of the first spine originates under the upper regions of the erectors of the first and second spines. It is much smaller than any of the other depressor muscles in the series. It inserts through a band of connective tissue on a posteriorly directed process from the posterior edge of the basal flange of the first spine. The contraction of the depressor muscle simply rotates the first spine backward over the medial flange to its unerected position.

The erector and depressor muscles of the second and subsequent spines require no special comment.

Anal spines and pterygiophores. The 3 anal spines and the distal portions of the pterygiophores to which they articulate have much the same shapes and relationships as the first 3 dorsal spines do to their pterygiophores, as described briefly above. The ventral surface of the basal half of the first spine is deeply concave, fitting over a grooved medial flange of the first basal pterygiophore; the second and third spines have complete anteroposterior foramina through their bases, that of the second spine fitting through the bridging of a hole in the posterior half of the medial flange of the first pterygiophore and that of the third spine through the bridge formed by the posteroventral process of the first distal pterygiophore and the anteroventral process of the second basal pterygiophore. The third anal spine is stouter than the third dorsal spine, and the distal ends of the pterygiophores are not expanded into large plate-like structures such as are found on the pterygiophores of the spiny dorsal fin. The locking mechanism of the first anal spine is like that of the first dorsal spine, and the rotational course of the first 2 spines is blocked when the spines are about at a right angle to the pterygiophore in the same manner as described for the spiny dorsal fin.

The long shaft-like proximal portion of the first basal pterygiophore is firmly held by connective tissue against the anterior edge of the haemal spine of the tenth vertebra, the first of the caudal series. The proximal portion of the second

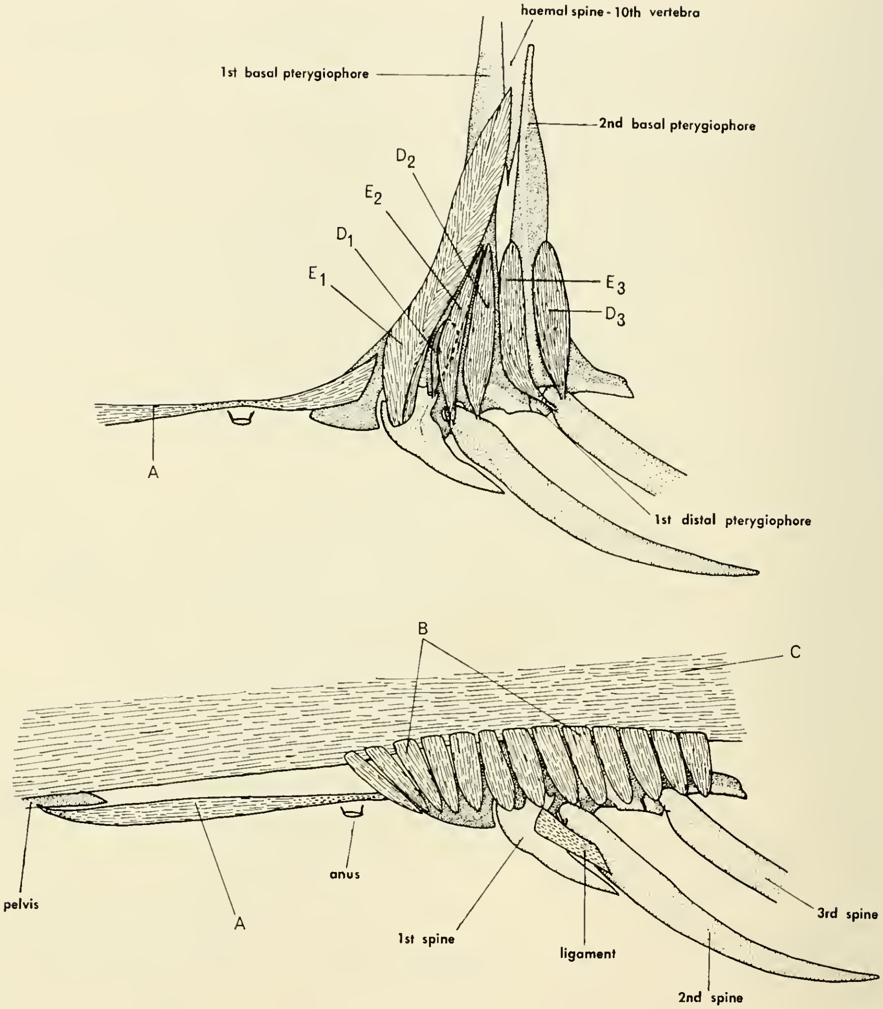

Figure 6. Lateral views of musculature of anal spines in *Acanthurus triostegus*; below, superficial musculature after removal of skin; above, erector and depressor muscles as seen after removal of epaxial muscles and inclinators; composite drawings based on specimens from ANSP 108288; the representational fiber structures are diagrammatic. Legend: A, infracarinales medialis; B, inclinators; C, hypaxial muscle mass; D, depressors; E, erectors.

basal pterygiophore is held against the posterior edge of this haemal spine, while the first and second basal pterygiophores of the soft anal fin are held respectively to the anterior and posterior edges of the haemal spine of the second caudal vertebra.

Musculature. Three main muscle groups are apparent when the skin is removed from the trunk above the anal spines (fig. 6, bottom): the general hypaxial muscle mass; the inclinators; and a band of longitudinal muscle running from the lateral surface of the pelvis just behind the level of the fin rays to the lateral surface of the anteroventrally directed medial prong-like portion of the first basal pterygiophore. The inclinators apparently are increased in number relative to those of the dorsal spines and are not associated with the anal spines on a one-to-one basis as they are with the dorsal spines. They originate on the undersurface of the skin and insert variously on the distal regions of the pterygiophores and on the lateral surfaces of the bases of the spines. The inclinators, like the hypaxial muscles, have no bearing on the locking mechanism. The band of muscle (infracarinales medialis) between the pelvis and first basal pterygiophore becomes tendinous as it passes around the anus. This muscle in some ways corresponds to the one in the spiny dorsal fin which runs from the supraoccipital to the prong of the first basal pterygiophore and base of the first spine. However, in the anal fin this muscle inserts only on the anteroventral prong of the first basal pterygiophore and does not have a superficial segment making contact with the first spine. It apparently has nothing to do with the locking mechanism.

The erector and depressor muscles are shown at the top of figure 6. As with the first dorsal spine, the erector muscle of the first anal spine is the largest in the series, and its depressor is the smallest. The erectors and depressors of the subsequent spines are of about equal size. They rotate the spines in the same manner as described for the spiny dorsal fin.

Naso literatus (Bloch and Schneider).

SPECIMENS EXAMINED. ANSP 109497, 2, 111.2–208.5 mm., tropical western Pacific, cleared and stained. ANSP 109496, 1, 191.4 mm., no locality, cleared and stained. ANSP 108416, 1, 107.3 mm., Seychelles Islands, cleared and stained. ANSP 108272, 1, 168.3 mm., Seychelles Islands, alcohol; species undetermined, but not *N. literatus,* used for muscle examination.

DORSAL SPINES AND PTERYGIOPHORES. There are 7 dorsal spines, the first of which is so distally aborted that it does not show externally, and the dorsal spine counts given in the literature are nearly always one less than in actuality (fig. 7). The second and subsequent dorsal spines are similar in their articulations to those described above for *Acanthurus triostegus,* except that the spines of *Naso* are stouter (and more heterocanth) and the distal pterygiophores to which the third and subsequent spines articulate are smaller, the latter difference being described below. The first dorsal spine of *Naso* differs from that of *Acanthurus* and the other genera of acanthurids only in having lost its distal portion that would ordinarily protrude through the skin (fig. 8). The basal region of the spine (all that remains of it) is similar to that described above for *A. triostegus,* including a deeply concave smooth ventral surface, ventral arms articu-

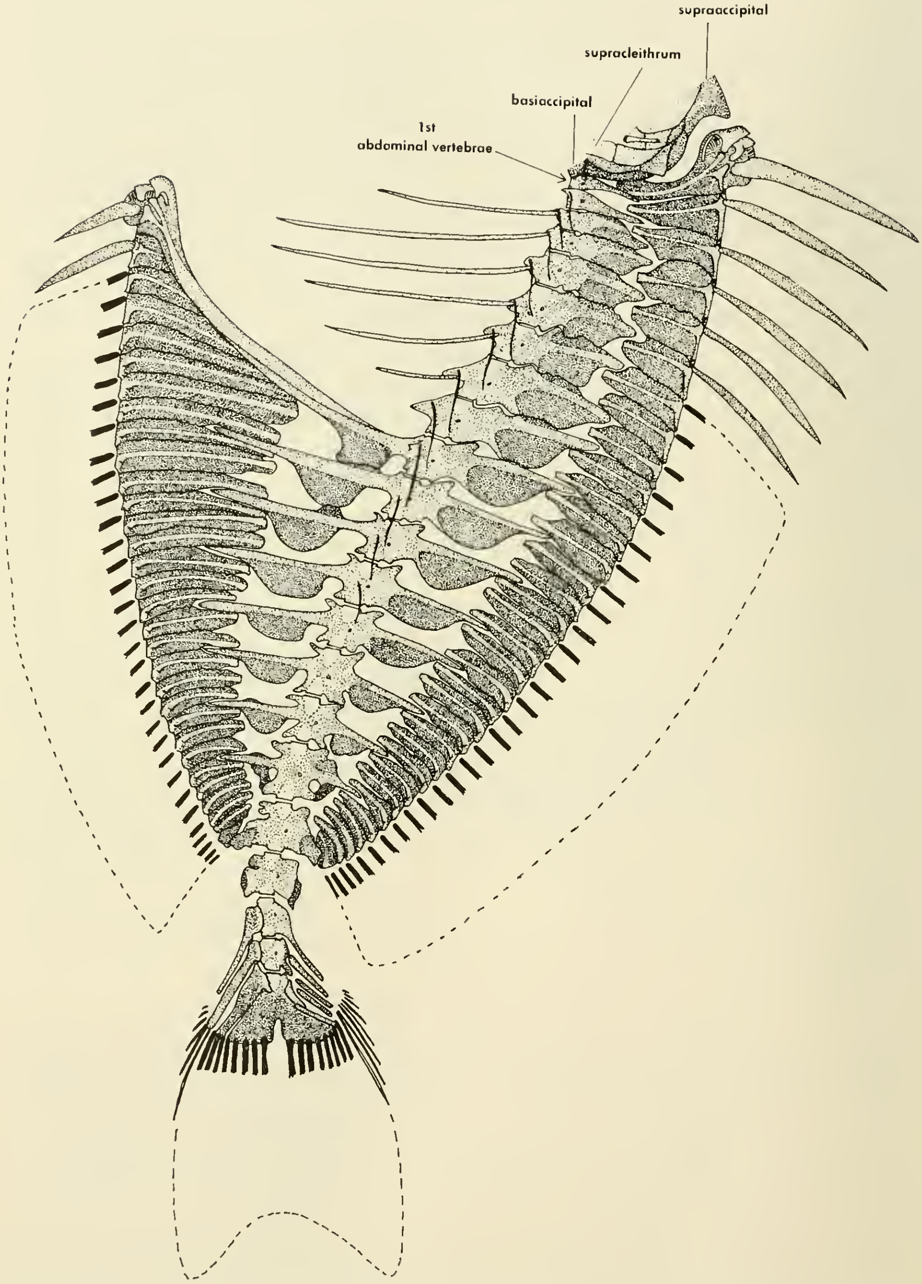

Figure 7. Lateral view of vertebral column and fin supports in *Naso literatus,* ANSP 109497, 111.2 mm. standard length. Bases of fin rays indicated in black; distal pterygiophores of fin rays not shown.

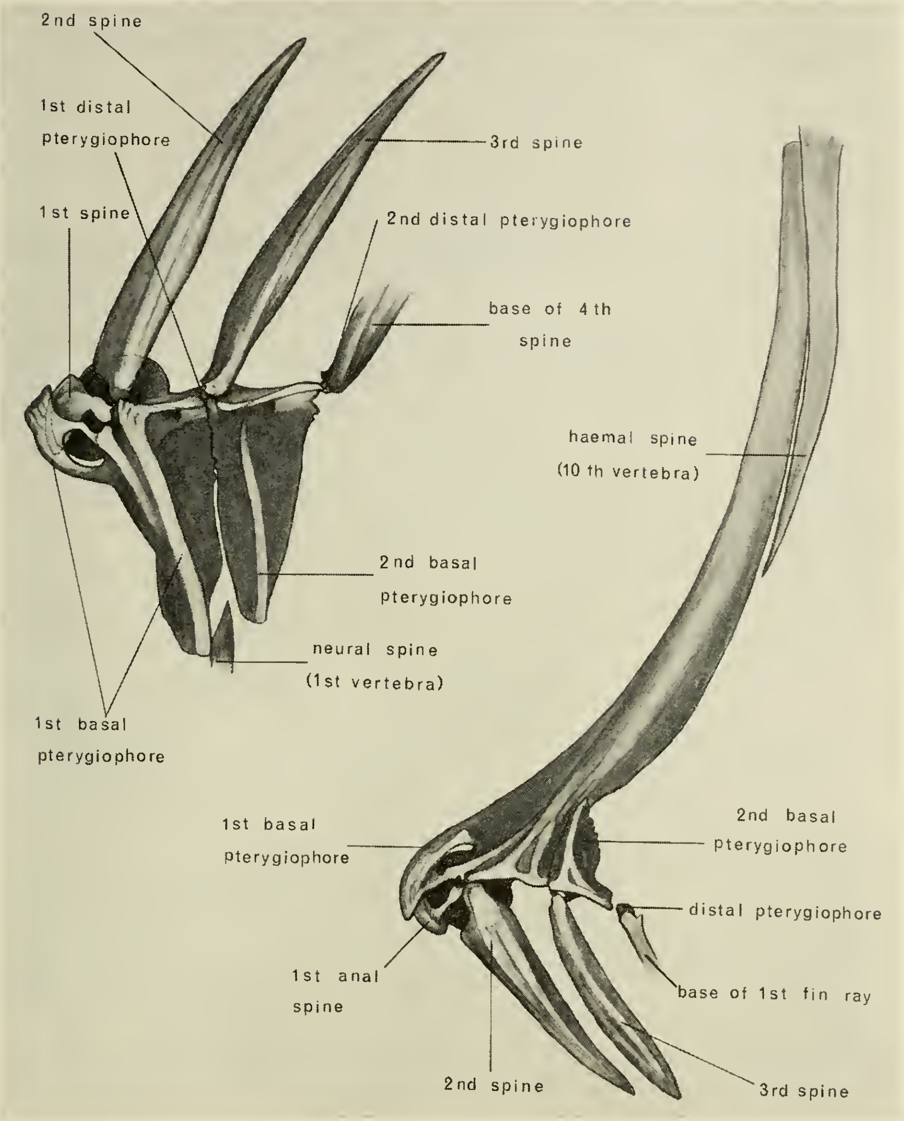

Figure 8. Lateral views of first three dorsal and anal spines and their supports in *Naso literatus,* the spines only partially erected; composite drawings based on all of the cleared and stained materials listed.

lating with lateral flanges on the first basal pterygiophore, and a posteriorly directed process from the posterior edge of the ventral arm to receive the insertion of the depressor muscle. A compact ligament connects the first spine at a groove along its dorsolateral surface to the anterolateral surface of the basal region of the second spine, and the second and subsequent spines are connected by more diffuse ligamentous connections, just as described for *A. triostegus.*

The major differences between *A. triostegus* (and the other acanthurids with an externally visible first dorsal spine) and *N. literatus* (and the other species of *Naso*), other than the smaller size of the first dorsal spine and the somewhat stouter size and heterocanth arrangement of the other spines, are in the shapes of the pterygiophores supporting them. The medial flange of the first basal pterygiophore is much less deeply grooved in *Naso* than in other acanthurids, and the anterodorsal prong of the pterygiophore, which in other acanthurids is relatively laterally compressed, in *Naso* is expanded posterolaterally into a bridge which meets and fuses or sutures with the lateral flange on the pterygiophore around which the ventral arms of the first spine rotate. The canal between the prong and the rest of the pterygiophore remains, and into this canal the first spine rotates when erected, just as described for *A. triostegus.* The rotational course of the first 2 spines is halted at about a right angle to the pterygiophore when the anterior edge of the base of second spine hits the indented region on the medial flange of the pterygiophore, and when, at the same time, the first spine can travel no farther in the canal between the anterodorsal prong and the medial flange. The second spine has a complete foramen anteroposteriorly through its base, the ventral bridge of the foramen being accommodated in a hole through the medial flange, as in *A. triostegus.* The third and subsequent spines also have complete foramina, these articulating around the bridges formed by the posterodorsal processes of the distal pterygiophores and the anterodorsal processes of the basal pterygiophores.

The basal pterygiophores of the spiny dorsal fin in *Naso* otherwise differ from those described in *A. triostegus* mainly by the greater development of the expanded plates at their distal ends, and of the lesser involvement in this structure of the distal versus basal pterygiophores (fig. 8). In *A. triostegus* the distal pterygiophores have expanded anterolateral wings which contribute substantially to the plates, but in *N. literatus* the plates are formed only by the basal pterygiophores, the distal pterygiophores remaining relatively small and medially placed in comparison to the width of the plates. Large foramina are present on each side of each expanded basal pterygiophore plate; these accommodate the depressor muscles of the second and subsequent spines, the erector muscles being accommodated in the gaps between the basal pterygiophore plates bordered medially by the small distal pterygiophores (fig. 9).

The locking mechanism in *Naso* works just as described for *A. triostegus,* and, despite the less deep grooving on the medial flange in *Naso,* the apparatus seems to lock equally firmly.

Musculature. The muscles of *Naso* have been examined only cursorily, and in a species other than *N. literatus.* But the major features of the bony struc-

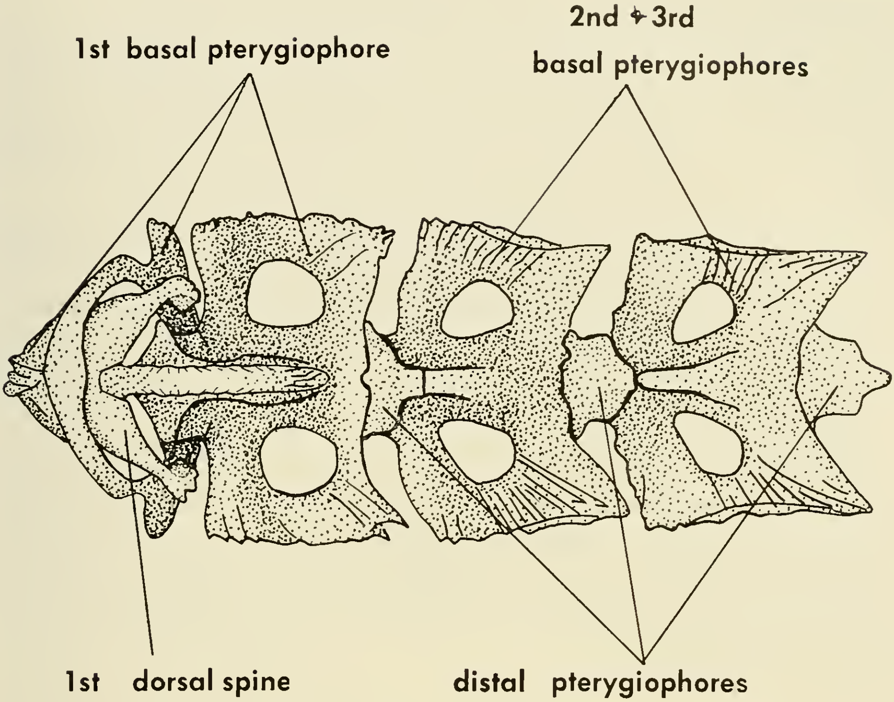

Figure 9. Dorsal view of first three basal and distal pterygiophores of anal fin of *Naso literatus*, with the first spine in place at a position about halfway to full erection and the second and third spines removed, ANSP 108416, 107.3 mm. standard length.

tures in the appropriate regions are similar in all species of *Naso*, and the musculature probably follows suit.

The longitudinal band of muscle (supracarinales anterior) between the supraoccipital and the anterodorsal prong of the first basal pterygiophore does not contact the first dorsal spine, its path being blocked by the posterolaterally expanded portion of the prong which forms a bridge to the lateral flange supporting the ventral arm of the first spine. The erector and depressor muscles of the spines do not seem out of the ordinary, although the depressor muscles are even more deeply buried beneath the erectors than the condition described and shown above for *A. triostegus*.

Anal spines and pterygiophores. The 3 anal spines and associated regions of the pterygiophores are similar in their relationships to that described for the first 3 dorsal spines, except that there is no separate distal pterygiophore between the first and second basal pterygiophores, although each of the following soft rays has separate distal pterygiophores.

The large proximal shaft-like portion of the first basal pterygiophore is firmly held along the anterior edge of the haemal spine of the tenth vertebra, the first of the caudal series, and is curved much farther anteroventrally than in *A. triostegus*. The second basal pterygiophore is aborted proximally and squeezed in between the posteroventral region of the first basal pterygiophore of the spiny anal fin and the anterior edge of the slightly larger first basal pterygiophore of the soft anal fin. The second to sixth basal pterygiophores of the soft anal fin follow in series between the haemal spines of the first 2 caudal vertebrae.

Musculature. As in *A. triostegus,* the muscle (infracarinales medialis) between the pelvis and the first basal pterygiophore does not contact the first spine and become tendinous as it passes around the anus. The shapes and sizes of the erector and depressor muscles of the anal spines are not clear to me in the single specimen examined, but the depressor muscles seem even more deeply buried below the erectors than in the dorsal fin.

Miscellaneous notes on the axial skeleton. As indicated in figures 1 and 7, acanthurids have 3 epurals, the first in close association with the neural arch of the penultimate vertebra, and a well-developed paired uroneural. The hypurals (including the parhypural) number six in most acanthurids, as shown for *A. triostegus,* but in the several species of *Naso* investigated, the middle 4 elements are fused to each other and to the centrum, leaving only 2 separate elements. The haemal spines of the penultimate and antipenultimate vertebrae are autogenous in acanthurids.

ACKNOWLEDGMENTS

Mr. Richard Winterbottom, Queen's University, Kingston, Ontario, Canada, generously advised on the musculature of the acanthurid locking mechanism, and Dr. Daniel M. Cohen, U.S. Fish and Wildlife Service, Washington, D.C., gave useful comments on the manuscript. The halftone illustrations are by the extremely competent Mrs. Mary H. Fuges.

More generally, I am in the debt of Professor Myers for much good counsel and encouragement in the study of plectognath fishes and their relatives. This short paper in his honor is only an infinitesimal token of my deepest gratitude for his innumerable hours devoted to my education.

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AMPUTATION AND REPLACEMENT OF MARGINAL SPINES IN CTENOID PERCOID SCALES

By

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In the ctenoid scales of most primitive percoid fishes the spines are found only on the free edge of the scale where it is not covered by another scale. Typically each spine with its base is a separate bone (a scalelet) fixed to the fiber layer of the scale. The fiber layer forms a flexible joint between adjacent scalelets. Cycloid scales in some genera, for example *Rypticus* and *Grammistes,* have homologous scalelets that lack spines; in other genera, for example *Siniperca*, the posterior fields lack scalelets that are homologous with the spines of ctenoid scales.

Posterior growth in the scales that have spines is by increments of single scalelets. Except for rare and inconsistent specimens or species, new scalelets do not form radially to another unless at least the tip of the spine has been lost or amputated. When two spines outgrow, the one between them (the shorter and older spine) tends to lie flatter than it did and the tip is amputated by osteoclasis. Nearly always, solution pits can be seen on the end of the stump. Then a new scalelet will be laid down distal to the stump. Eventually the new one will grow until it extends beyond its neighbors and they in turn will be amputated and replaced.

The fully grown scalelets with their spines stand erect or nearly so and hold up the connecting fiber layer and the overlying soft tissues of the epidermis and scale pocket. This forms a ridge usually in the arc of a circle that projects from the side of the fish. Except at the free edge, the posterior fields of such scales are covered with the amputated stumps of scalelets that once bore the spines that made the scale ctenoid.

The figure shows all the steps in the life cycle of one of these marginal spines except for some intermediate sizes in the growth of the scalelet. It shows part of the free margin of the posterior field of a scale, 2.79 mm. long, from the flank of a pike-perch, *Stizostedion canadense* (Smith), SU–5673. It is unusual in that it shows the amputated tip of a scalelet still in position. Usually such a tip is lost soon after it is cut off. Most of the scales from this fish show 1 or 2 scalelets in this condition. It is the only fish I have yet encountered that showed any tips of amputated spines and the beginning of the new scalelets beneath them.

The scalelet that has just been amputated is the marginal one that does not reach as far back as the others. The original length of this scalelet was 0.165 mm. The tip is 0.059 mm. long. The gap from which the bone was removed is 0.013 mm. wide. The primary ossification of the forming scalelet is wider than the old tip and lies beneath it. The new ossification measures 0.027 mm. in the anteroposterior diameter and is 0.045 mm. wide. Eventually the new scalelet will extend beyond the two beside it and they in their turn will be amputated and replaced.

The specimen was cleaned of as much adhering soft tissue as possible, stained with Alizarin Red S., and mounted in air under a cover slip secured with a few drops of polyvinl chloride glue. The mount is so made that it dries under pressure and the free edge of the scale is held down. The gaps between the scalelets shrink on drying and are now narrower than they were in life. In spite of the cleaning, a layer or two of cells lies over the bony tissues in most of the figure.

Williamson (1851) was the first to notice that the posterior field of perch, *Perca,* scales were made up of the bases of spines that were broken off. Baudelot (1873) saw that the perfect spines were only at the margins and that all spines not marginal were broken (brisée). He concluded, as had Williamson, that the spines were formed at the free edge. Neither one is able to explain how the scalelets became broken and Bauelot says that more observations are needed. Hase (1911) studied perch, young of the year, and reached the mistaken conclusion that the posterior scalelets were formed near the nucleus and pushed out toward the margin. At the margin they then grew their spines. There was no clear explanation of what happened until I completed my doctoral research (McCully, 1961).

From my examination of this and material from the Serranidae I conclude:

1. That the small size of the amputation gap means that only a few cells can be excreting the osteoclastic material.

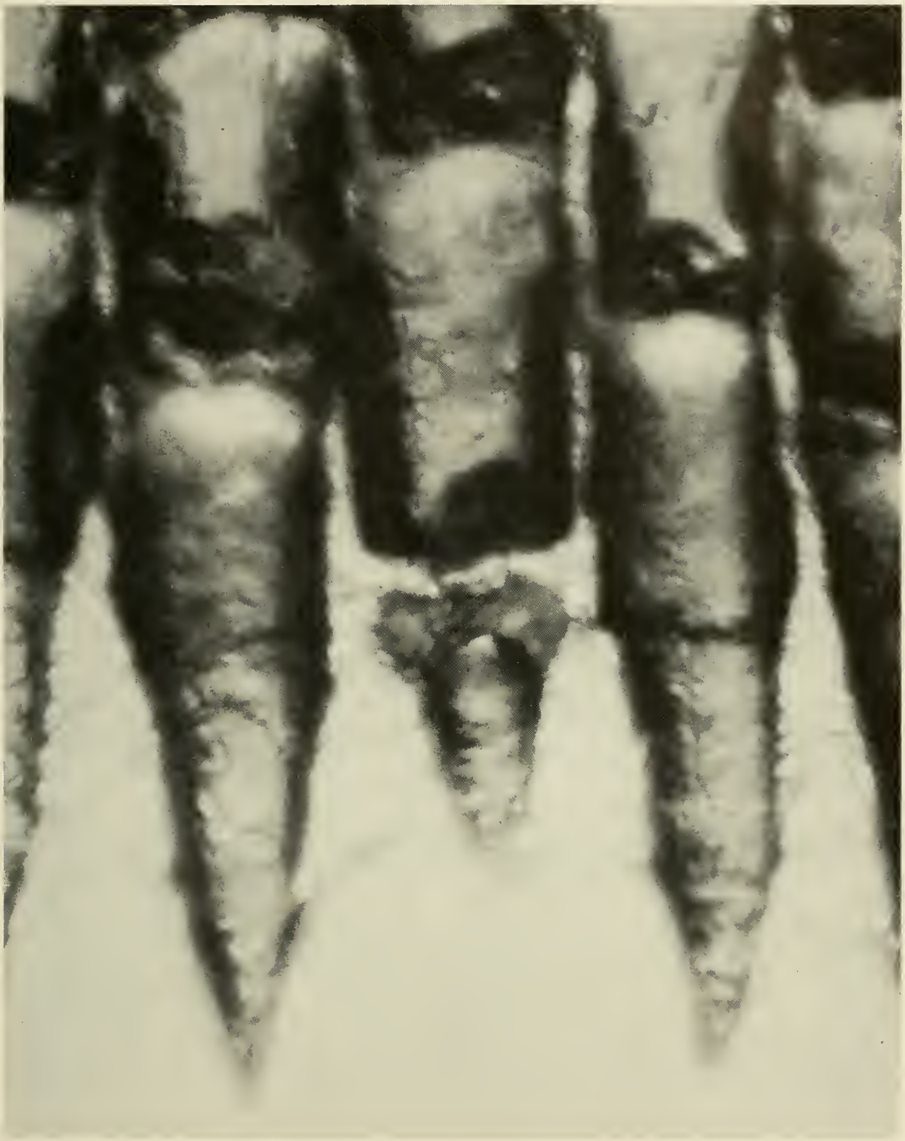

Figure 1. Posterior margin of scale from the flank of a pike-perch, *Stizostedion canadense.* (See text for explanation.)

2. Nearby cells must be protecting the bone that is not attacked.
3. The material removed from the bone may be redeposited nearby.
4. There is a regulating mechanism that can differentiate the excretory activities of a few selected cells from their neighbors. Another regulatory

change stops the unusual secretion and returns the cells, presumably, to their former state.

5. It is possible that migratory cells are the source of osteoclastic excretion.

6. There is, in a very small area, exposed to external observation and manipulation the whole of the sequence of bone growth and absorption. This type of scale offers a convenient way to test the action of drugs in an intact animal on any aspect of the physiological processes of bone growth and absorption except for those peculiar to the replacement of cartilage.

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SIZE AND DISTRIBUTION OF PROTEINS IN ELASMOBRANCH PLASMA

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As part of a project sponsored by the Office of Naval Research (N0014-67-C-0343) some members of the staff at Steinhart Aquarium embarked on an electrophoretic investigation of the classification value of elasmobranch plasma proteins. Samples from 11 of the 27 species available were sent to the Naval Biomedical Research Laboratory for ultracentrifuge analysis. The results show species and perhaps family differences not suspected from cellulose acetate and acrylimide gel electrophoresis.

Similarities in blood constituents have been used by many investigators to show relationship between various animals. Genetic changes and natural selection are believed to affect serum or plasma constituents less than the gross anatomy or other such features. Thus, similarities in composition of blood or serum would indicate a relationship; certainly if they differed significantly it would indicate that the individuals are not closely related. Such classification of elasmobranchs has been the subject of immunologic or electrophoretic analyses (Clem

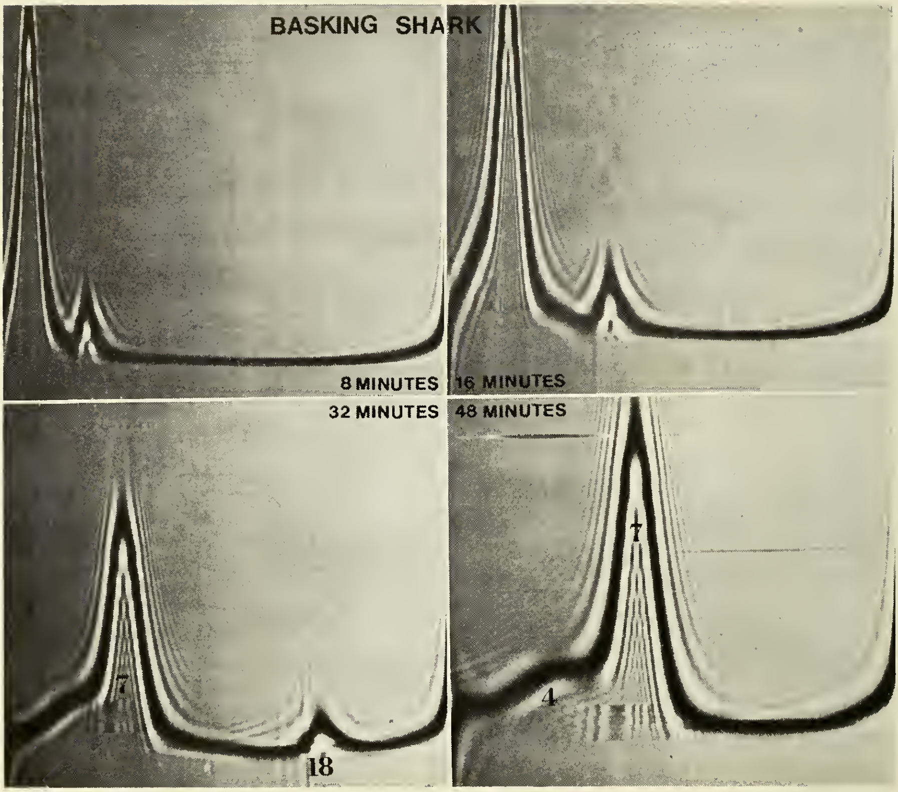

Figure 1. Schlieren patterns obtained from plasma sample of 696 cm. adult male basking shark (*Cetorhinus maximus*). Photographs were taken at indicated times after rotor attained full speed (59,780 rpm). Numbers below major peaks in last two frames refer to observed sedimentation coefficients.

and Small, 1967; Irisawa and Irisawa, 1954; Rasmussen and Rasmussen, 1967; Shuster and Goodman, 1968) but no comparative study of molecular size of serum proteins has been made. This report describes the results of some ultracentrifugal analyses of blood plasma from several selected species.

MATERIALS AND METHODS

Blood was usually obtained by caudal puncture using Sequester-Sol (a dipotassiumethylenediaminetetracetate supplied by Cambridge Chemical Products, Inc., Detroit) and for most samples, immediately centrifuged; the plasma was then removed and stored at 2° C. Analyses were made with a Spinco Model E Analytical ultracentrifuge fitted with schlieren optics using 12 mm. cells. The plasma were analyzed at the highest practical concentrations, either 1:2 or 1:4,

Table 1. *Sedimentation coefficients of the principal plasma proteins.*

Common Name	Scientific Name	Sex	CM Total Length	Total Protein	Component S Values			
Pacific lamprey,	*Lampetra tridentata*	F	49.5	3.1	3.4	8	13	—
Sevengill,	*Notorynchus maculatus*	F	64.7	1.9	3	7	—	17
Horn shark,	*Heterodontus francisci*	M	75.7	5.3	4	7	—	17
Basking shark,	*Cetorhinus maximus*	M	696.0	—	4	7	—	18
Swell shark,	*Cephaloscyllium ventriosum*	F	94.0	3.4	4.5	7	—	17
Leopard shark,	*Triakis semifasciata*	F	119.3	2.75	4.3	7	14	17
Dogfish,	*Squalus acanthias suckleyi*	F	—	—	4	7	—	17
Shovelnose guitarfish,	*Rhinobatos productus*	F	89.0	5.9	5.6	8	12	17
Thornback ray,	*Platyrhinoidis triseriata*	F	57.2	0.64	4	8	—	17
Pacific electric ray,	*Torpedo californica*	M	78.6	—	5	8	12	17
Big skate,	*Raja binoculata* (A)	M	76.2	—	5	11	14	—
Big skate,	*Raja binoculata* (B)	M	90.2	—	5	11	14	—

so that minor constituents would be detected. In all instances the centrifuge was operated at 59,780 rpm.

RESULTS

Figure 1 shows a series of photographs taken during the sedimentation of serum from a basking shark. The first three frames clearly show the separation and sedimentation of the 18 S component. However, even after 48 minutes the 4 S component had not been completely resolved from the 7 S proteins. Since the area under the curve is proportional to the concentration of that component it is clear that the major protein in this serum had a high molecular weight. If the 7 S material is a globular protein, its molecular weight is probably in excess of 160,000.

The results of ultracentrifuge analyses of plasma from a number of animals are summarized in figures 2 and 3 and the observed sedimentation coefficients are listed in table 1. The relative concentrations of the various components in each plasma can be estimated from the schlieren patterns.

Except for the sevengill shark and thornback ray, the relative concentration of macroglobulin (17 S component) in shark plasma is higher than in mammalian serum. As is evident in figure 2, the 7 S globulins in human serum have not been resolved from the albumin, but of course, continued centrifugation did separate the 7 S proteins from the albumin. Similarly, low molecular weight proteins were resolved from the 6 to 8 S components in the other plasma on prolonged centrifugation indicating that there is at least a small amount of albumin-sized material in all of the elasmobranch plasma, even though this is not evident in the 32-minute frames shown in figures 2 and 3.

In addition to indicating relative concentration, the schlieren patterns provide a measure of homogeneity of the protein components in that if all mol-

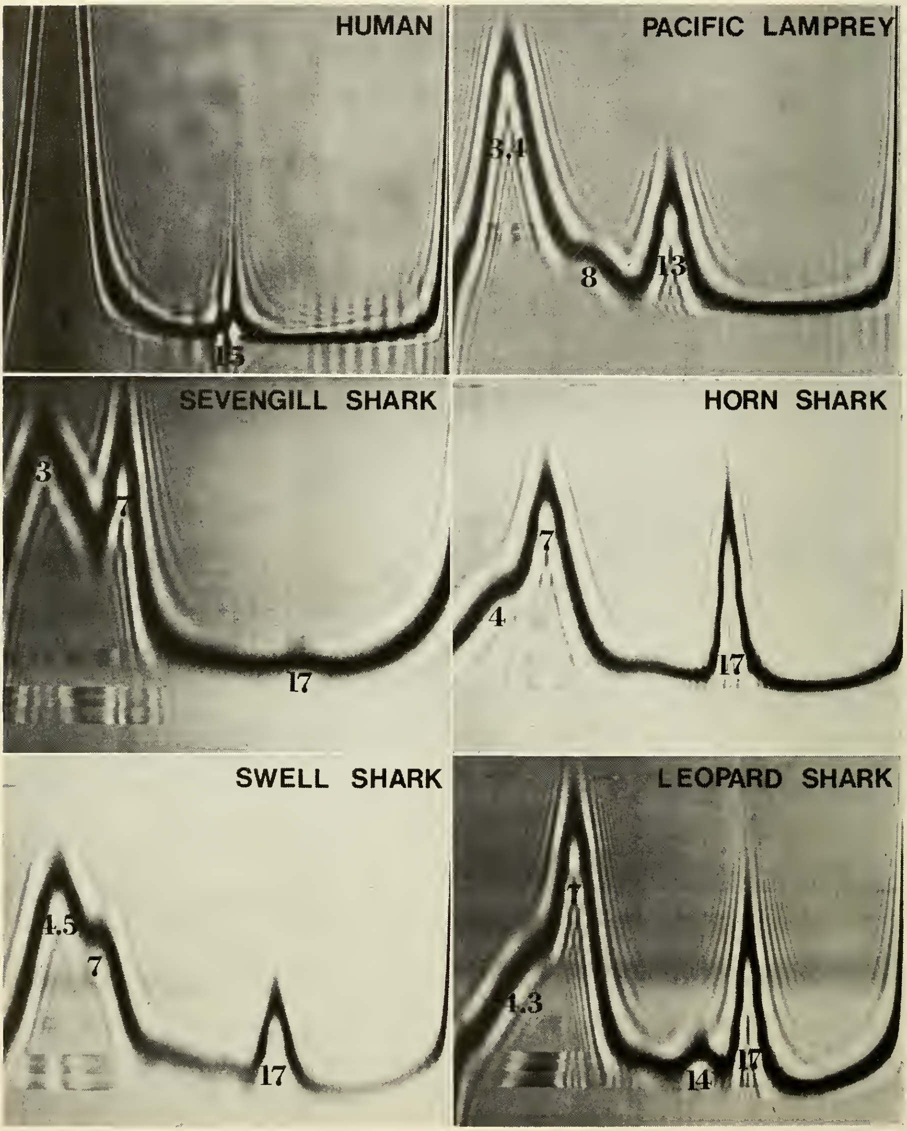

Figure 2. Schlieren patterns obtained with various plasma 32 minutes after rotor attained full speed, 59,780 rpm. Numbers given below patterns indicate approximate sedimentation coefficients of components represented by peaks.

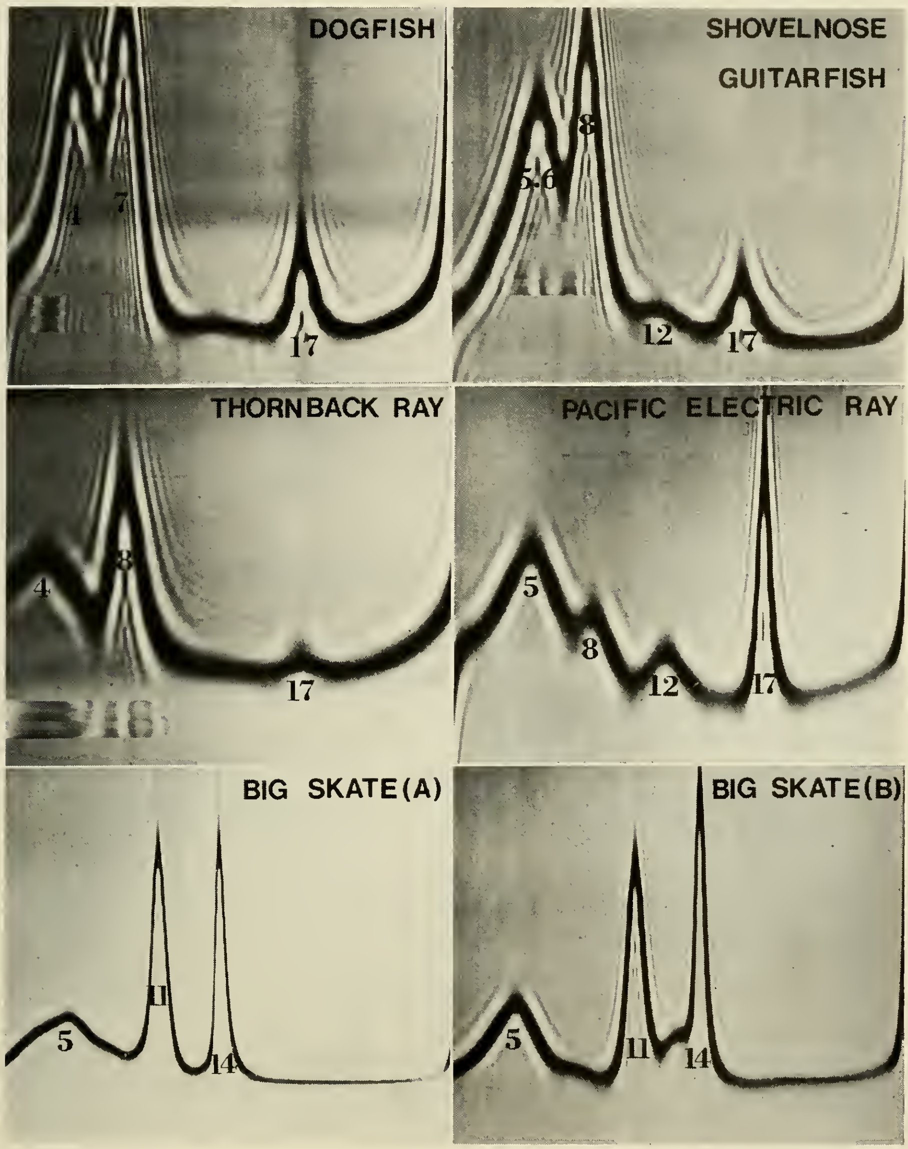

Figure 3. Schlieren patterns obtained with various plasma 32 minutes after rotor attained full speed, 59,780 rpm. Numbers given below patterns indicate approximate sedimentation coefficients of components represented by peaks.

ecules are the same size the schlieren peak will be sharp, such as is demonstrated by the patterns for the skate and ray. A broad peak indicates either heterogeneity of the component with respect to sedimentation velocity or a high diffusion coefficient. For instance, albumin, even though it is homogenous, would result in a rather broad peak after 32 minutes.

The lamprey is unusual in that it appears to have a higher relative concentration of albumin (the 3.4 S component) than the elasmobranchs, and in this respect it is more like mammalian serum because, as is well known, albumin is the principal constituent in normal mammalian serum. In contrast, as is shown in figure 1, the principal protein in the basking shark was of the 7 S variety.

Skates appear to lack 17 S protein in their plasma but they have high concentrations of both the 10 and 14 S proteins. Although the patterns from different skates do not yield identical patterns the variations that have been observed are shown in the last two photographs of figure 2. Since the presence or absence of a component is perhaps more significant than small differences in concentration, it is of interest that neither the lamprey nor the big skate have 17 S proteins and that they both have proteins in the 8 to 14 S range.

Also of interest are the differences in the component S values between the guitarfish and the thornback. These two species were formerly placed in separate families now combined in a single family (Rhinobatidae). It would seem logical that all family members would have similar sedimentation coefficients, yet in this case the shovelnose has a 12 S component which is strangely lacking in the thornback. Further study will be needed to evaluate this difference.

As is shown in figures 2 and 3 and in table 1, the leopard shark, shovelnose, guitarfish, and electric ray have four distinct S components in their plasma, whereas all the other eight species studied have only three major components. With the exception of the guitarfish and thornback all species are representatives of individual families not closely related.

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INDEX TO VOLUME XXXVIII

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New names and principal reference in **boldface** type