THE

BASHFORD DEAN MEMORIAL VOLUME

ARCHAIC FISHES

Edited By
EUGENE WILLIS GUDGER

PART I

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AND
ARTICLES I, II, III, IV, V

THE
AMERICAN
MUSEUM
OF
NATURAL
HISTORY
SCIENCE
EDUCATION

NEW YORK
PUBLISHED BY ORDER OF THE TRUSTEES
1930–1933

PART I

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INTRODUCTION

INTRODUCTION

The value to science of the Bashford Dean Memorial Volume will be apparent chiefly to those who will build further upon it as a foundation; but it is also of historical interest as a document both of science and of civilization as they were during the latter half of the nineteenth century and during the first decade or two of the twentieth century. In that period descriptive embryology held a high place in the interest of zoologists and though many of its problems still call for more complete answers, it helped to lead the way for studies on cell lineage and on the mechanism of cell division and eventually led to the recognition of the significance of chromosomes. But Bashford Dean, following closely in the footsteps of Balfour, Dohrn, and von Kupfer, collected and studied his fossil and recent fishes and amassed his material illustrating the embryology of fishes, primarily because he was interested in evolution in general and especially in the origin, rise and branching of the major groups of fishes. And since the known species of fishes number far too many thousands to be investigated by one man, he diligently sought out and concentrated his efforts on the oldest known fossil fishes and on the most archaic and primitive fishes of the present day. These included the lampreys and hagfishes (cyclostomes), the frilled shark, the cestraciont or heterodont sharks, the chimaeroids and the survivors of the ancient lungfishes and ganoids, especially *Acipenser*, *Polyodon*, *Polypterus*, *Lepidosteus*, and *Amia*.

In search of material, Dean made voyages to various parts of the world but, as it was manifestly impossible for him to collect continuously, he availed himself freely of the then active international cooperation of Japanese, American, German, and English scientists in the collection and exchange of material. He also assigned many special problems to his students—N. R. Harrington, L. Hussakof, W. E. Kellicott, R. C. Osburn, C. R. Stockard, W. K. Gregory and B. G. Smith.

In the period between 1891 and 1912, Dean published his memoirs and papers on the oldest fossil sharks, on the fin-fold origin of the paired fins, on the embryology of the hagfishes, on chimaeroid fishes and their development and on the embryology of the Ganoids—*Acipenser*, *Amia* and *Lepidosteus*. Meanwhile, as traced in Article I of this volume, Dean's abiding interest in the collection and the history of arms and armor culminated in his career as Curator of Arms and Armor in the Metropolitan Museum of Art. These duties, together with his responsibility for bringing the Bibliography of Fishes to publication, conspired to delay the completion of his later zoological projects. After his retirement from the curatorship in the Metropolitan Museum in November, 1927, Dean planned to take up and finish his long-delayed work on certain archaic fishes for which material had been collected in Japan years before. This plan was broken off by his untimely death on December 6, 1928.

After Dr. Dean's death, examination of his scientific relicta brought to light a large amount of zoological materials, consisting of notes, photographs, drawings done in the best Japanese technique (of which he himself was a master), and specimens of certain archaic sharks and of their eggs and embryos. It was soon seen that these would be lost to science unless a well-planned, well-supported and continued effort should be made to organize, classify, record, study, interpret, reproduce and publish the results of these studies in a series of papers based on these materials.

Some measure of the deep and abiding impress of Dean's character and achievements is afforded by the record of activities undertaken in his honor and memory by his colleagues and former students during the fourteen years since his decease.

First, the Bashford Dean Memorial Committee was organized on January 18, 1929. The first formal meeting of the committee was attended by President Henry Fairfield Osborn, Director George H. Sherwood, Dr. William K. Gregory (Curator of the Department of Fishes), Mr. John T. Nichols, Dr. E. W. Gudger, Dr. Bertram G. Smith, Miss Francesca La Monte, and Mr. Alexander McMillan Welch representing Doctor Dean's family. Dr. Gregory was elected permanent chairman and the following subcommittees were appointed:

Subcommittee on Memorial Exhibit: Doctor Gregory, Miss La Monte, Doctor Sherwood.

Subcommittee on Memorial Tablet: President Osborn, Mr. Nichols, Mr. Welch, Miss La Monte.

Subcommittee on Memorial Publications: Dr. Gudger (*Editor*), Drs. Gregory, Smith, and Leroy Conel, and *ex officio*, Mr. Hawthorne Daniel (Curator of Publications).

Subcommittee on Finances: Cleveland E. Dodge, Evelina B. Perkins, Alexander M. Welch, Francesca La Monte (*Treasurer*).

Next, the Bashford Dean Memorial Exhibit of Fossil Fishes in the American Museum of Natural History was planned, installed and dedicated to his memory on June 10, 1929. This exhibit sets forth many of the choicest fossil fishes which had been collected by Dean himself and by his teacher and predecessor, Professor John Strong Newberry of Columbia University, whose famous collection Dean had secured for the Museum. Portrait plaques of both Dean and Newberry were installed on either side of the entrance to the exhibit, together with their field notebooks and sketches. President Osborn, Dean's colleague both at Columbia University and in the American Museum, welcomed the guests and spoke on Dean's life work. Dr. Gudger reported on the plans for the publication of a Memorial to Dr. Dean.

About the same time the Bashford Dean Research Room in the Museum was set apart for research in ichthyology and for the reception and care of his ichthyological library, which he had left to the Museum together with a fund for its maintenance.

In response to letters sent out by the Subcommittee on Finance, contributions came in from Dr. Dean's colleagues, friends and former students in America and Europe. After paying the sculptor, the companies which cast the plaques, and all accessory expenses, a considerable sum of money was left. This, it was determined, should be applied to the publication of a Bashford Dean Memorial.

At first it was planned merely to issue an Atlas of Dean's collection of colored drawings of embryological and kindred material with appropriate legends. But it was soon realized that it would serve better to advance the science in which Dean had labored so productively if his materials should be used as the prime basis for a series of original articles by competent authorities to make a Bashford Dean Memorial Volume: Archaic Fishes. The realization of this ambitious project was made possible by continuing co-operation from many sides. First, came the unfailing generosity of Mrs. Bashford Dean and of Dr. Dean's sister, Miss Harriet Martine Dean; secondly, there was the steady support of the Museum, which agreed to publish the memoirs except for the cost of making and printing the lithographed plates; thirdly, came the enthusiastic labors of the editor, Dr. E. W. Gudger, and of his collaborators, especially Dr. Bertram G. Smith, a former student of Dr. Dean at Columbia University.

The work of preparing the majority of the Articles composing the Memorial fell to the lot of Dr. Smith and Dr. Gudger. Dr. Smith was a professor of anatomy in the New York University College of Medicine, and Dr. Gudger was not only editor of the Dean Volume, but also bibliographer and associate curator of fishes in the American Museum. Hence, since each man had heavy work of his own, the preparation of papers for the Dean Volume necessarily went forward slowly. This will make clear why twelve years elapsed between the publication of Articles I and VIII. However, the results of the labors of all the collaborators speak for themselves.

In the making of the Bashford Dean Memorial Volume, the technical knowledge and skill of many persons has been utilized. And it is our pleasure to make grateful acknowledgment of their devoted services.

The illustrations in the Volume came from many and various sources. The hundreds of text-figures were made from Dr. Dean's photographs and drawings, and from figures in scores of books and journals wherever they could be found to illustrate our authors' texts. The illustrations from these latter sources were copied in our photographic studio, mainly by Charles H. Coles and Thane Bierwert. Then they were turned over to W. H. Southwick, who, at the very beginning of the work on Article I was chosen as artist of the Dean Memorial Volume. Working with the editor, he prepared all the figures for reproduction. His judgment and skill are reflected in the high quality of the illustrations as reproduced herein.

All half-tone cuts and plates were made by the Sterling Engraving Company of New York City, whose representative, Mr. Harry Duysters, freely gave the editor the benefit of his experience and judgment.

Certain woodcuts used in the text are of historical interest. The first investigator to study the Japanese frilled shark was Samuel Garman of the Museum of Comparative Zoology, Cambridge, Massachusetts. The illustrations for his researches on the anatomy (1885), antedating the day of line-cuts and half-tones, were made from woodcuts. When Dr. Thomas Barbour, Director of the Cambridge Museum, learned of our work here, with great courtesy he had all these woodcuts collected and sent to us. Even after fifty years a number of these blocks were in such good shape that they were used in illustrating Articles VI and VII of this Volume.

Most of the illustrations for the article on the Structure of *Dinichthys* were prepared by the author, Dr. Anatol Heintz, Curator of the Paleontological Museum, Oslo, Norway. Dr. Heintz came to the United States in 1930 to study the Arthrodire material in various museums here. He worked at the American Museum for several months, chiefly with the fossil remains of *Dinichthys intermedius* Newberry, assembled by Newberry, Dean and others. The publication of Dr. Heintz's Article as no. IV in the Dean Volume is very fitting since this enigmatic fish and its numerous fossil relatives had engaged Dr. Dean's attention and study during many years.

The scores of drawings for the plate figures of Articles II, III, VII and VIII were made in part by Dr. Dean and in part by Japanese artists working in Japan and in New York under his personal direction. Prepared in a technique suitable only for reproduction by lithography, the majority are in pencil (gray) but many others are beautifully done in the natural colors of the eggs and embryos. However, there was little uniformity in their arrangement and in other essential features, and the final preparation of these plates presented many difficulties to the editor and his assistants. It was not until each figure had been photographed and the prints had been trimmed and arranged in dummy plates that satisfactory plates for reproduction by lithography could be produced.

The lithographed plates of Articles Nos. II, III, VII and VIII were made by the well-known firm of A. Hoen and Company of Baltimore, Maryland. The head of the firm, Mr. A. B. Hoen, took personal charge of our work. Being in New York frequently, he came to the Museum, advised as to the order and arrangement of figures on the plates, and later with authors and editor he studied the proofs of the plates and advised as to corrections. The finished printed plates reveal the integrity with which the superb originals have been reproduced.

The printing of this Volume has been done in the Museum's Print Shop, at first under Stephen Klassen, later under Edward Burns whose skill is reflected in the fine typography and layout of the Volume. To printers Bailey Lewis, Dominick Caggana, and Albion Haddon grateful appreciation is tendered for their excellent work.

The very full Analytical Subject Index was prepared by Miss Jannette M. Lucas with great care and skill.

In short, it has been the aim of all concerned in the production of this Memorial Volume to bring out a work worthy of dedication to the imperishable memory of Bashford Dean.

William K. Gregory,
Chairman Dean Memorial Committee

THE
BASHFORD DEAN MEMORIAL VOLUME
ARCHAIC FISHES

Edited By
EUGENE WILLIS GUDGER

Article I

MEMORIAL OF BASHFORD DEAN

BY WILLIAM K. GREGORY
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American Museum of Natural History

NEW YORK
PUBLISHED BY ORDER OF THE TRUSTEES

Issued December 15, 1930

MEMORIAL OF BASHFORD DEAN

1867–1928

By William K. Gregory

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Article I, Plate I

Bashford Dean

MEMORIAL OF BASHFORD DEAN

1867–1928

By William K. Gregory

GENERAL IMPRESSIONS

On a certain bright California day in the summer of 1899, I looked out of the window from my table at the Hopkins Marine Laboratory at Pacific Grove and saw Dr. Bashford Dean swinging rapidly up the path leading to the laboratory. A few steps in front of him was a dumpy little Chinese woman, the wife of Ah Tak the fisherman, and from Dean's square shoulder to hers stretched a stout bamboo pole. Between them was slung a large tin can full of water and evidently containing some zoological treasure brought in from the waters of the bay by Ah Tak.

I rushed out to meet them and assisted in turning the can gently over so that its contents poured slowly into a large wooden trough containing fresh sea water. Then out came a living Silver Shark (*Chimaera colliei*) glistening in silver and black, waving its gossamer wing-like pectorals and staring vacantly with great round eyes. At that moment I caught for the first time a spark from Dean's ardor, which had already sent him into many parts of the world in pursuit of chimaeroid fishes and their development. Nor shall I ever forget his eagerness when the next day I innocently asked him if he had put a fresh Chimaera egg into the same trough with the living Chimaera. He almost leaped down stairs to find the spindle-shaped, dark brown egg which our noble captive had so obligingly laid. And with what joy did he open the egg and find therein a pulsating embryo! The color drawing that he made upon that occasion, and which now lies before me as I write, immortalizes this priceless embryo and shows us its swelling brain, its red blood vessels, the root-like nutritive outgrowths from its gills, and its gracefully tapering flanks, with all the delicacy and insight for which Dean's drawings were famous.

The embryology of the cyclostomes, sharks, ganoids and other piscine relics of earlier geologic ages was indeed one of the central themes of Dean's zoölogical career, but these interests were closely connected with his work on the fossil sharks and armored fishes of the Devonian period. His admirable text-book on "Fishes, Living and Fossil" (1895) illustrates how completely he synthesized the viewpoints of embryology, palaeontology and comparative anatomy, which up to that time had too often been cultivated by separate schools or under opposing leaders.

As instructor, and later as professor of vertebrate zoology at Columbia University, he left behind him a generation of his old students eager to carry on his work. As curator of recent and fossil fishes at the American Museum of Natural History, he founded and guided successfully an active department of ichthyology, published an important series of memoirs and papers on the sharks and arthrodires of Devonian times and brought to completion a great three volume "Bibliography of Fishes," dealing with living and fossil fishes in their manifold aspects. Upon this *magnum opus* he and his loyal staff labored for many years.

His early studies on the methods of oyster culture practised in various countries, together with his quest for archaic fishes and their development, carried him into Alaska, California, Japan, and many countries in Europe, where he picked up an amazing store of sketches of the people and their surroundings, together with much knowledge of their language, customs and history.

His career in zoology and palaeontology, however, constituted only a part of his training for his peculiar and unique achievements in the field of European arms and armor, for he brought to his historical study of cultural evolution his wide and authentic knowledge of the ways of organic evolution. Thus he was able to reveal a surprisingly close general parallelism between the evolution of helmets and pole arms on the one hand, and the evolution of organisms on the other. Meanwhile his tireless wanderings in pursuit of elusive embryonic and fossil fishes in many parts of the world trained him to follow the still more tangled trails of valuable pieces of armor.

Although the full results of his forty odd years intensive study of European and Japanese arms and armor remain to be published, even the casual visitor to his uniquely arranged exhibit of arms and armor in the Metropolitan Museum of Art in New York grasps the splendor of the collection if he does not realize the vast labors that went into its upbuilding.

As to Dr. Dean's personal characteristics, young students were apt at first to be a little in awe of this short, square-shouldered man with his prominent chin, quick darting eyes, and unpredictable sallies of wit and irony. But his enthusiasm was easily communicable to receptive minds. Moreover, he could "suffer fools gladly" or at least with commendable good grace, and, all things considered, was surprisingly slow to wrath. The psychologists might class him as an "extravert," but his friends would say that the term "gentleman" would be more descriptive. At any rate, his untiring interest in other people, places, and things was joined with remarkable tact and courtesy, with unassumed friendliness and with a modest spirit of "noblesse oblige."

BIRTH, CHILDHOOD AND YOUTH

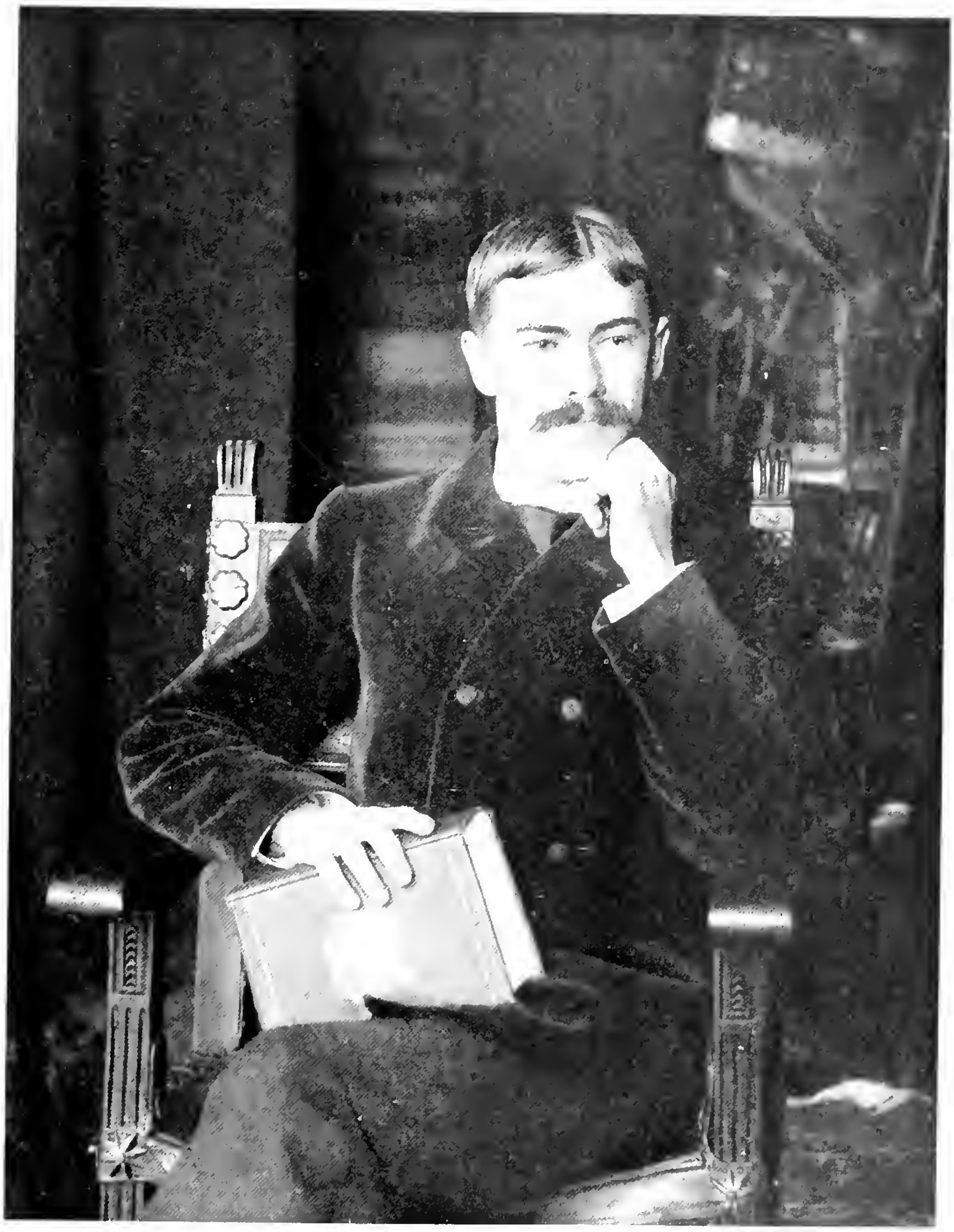
1867-1887

With this preliminary impression before us of what manner of man Dean was, it may now be well to take up in order some of the many threads of his life. From his sister, Miss Harriet Martine Dean, to whom I am under obligations for many illuminating details, I learn that the Dean family was of English and Holland Dutch stock, located around Tarrytown, New York. Bashford Dean's paternal great-great-grandfather, John Dean, was a captain in the American Revolutionary Army who took part in the capture of Major André. His father, William Dean, a Columbia graduate, was a lawyer who commenced professional work with one of the large life insurance companies of New York. At the time of Bashford Dean's birth (October 28, 1867), the family resided on Lexington

PLATE II

PLATE II.

Bashford Dean at the age of twenty four, an instructor in geology at Columbia University and a student of the Devonian Placoderms. 1891.



Avenue in the Murray Hill section of New York City. His mother, Emma Frances Bashford, who was of English and Huguenot French stock, gave her family name to her third and youngest child. Fortunately his widow, Mrs. Mary Alice Dyckman Dean, and his sister possess a remarkable series of documents, including many drawings, letters, and similar memorabilia of Dean's childhood, together with his own notebooks of his early travels in Europe, to which they have kindly given me access.

At the age of possibly seven or eight years the young Bashford was already drawing spirited pictures of knights in combat. Later with several of his schoolmates he issued miniature "newspapers," his own being very neatly lettered by hand, on little folded sheets not more than two by three inches. The name of his paper was "The Comet," while, as he records it, the names of some of the other "papers" were "The World," "The Sun," "The Meteor," etc. Each issue was filled with interesting notes and subjects, including brief descriptions of native birds, their nests and eggs. Thus at an early age we have manifested or at least foreshadowed his interest in knights in armor, his knowledge of birds and their habits, his fondness for minute writing and drawing, his gift of precise statement and accurate observation. How did he acquire these traits?

According to Miss Dean's interpretation, he derived his early interest in natural history largely from association with his father, who himself was an enthusiastic collector and cataloguer of fossil invertebrates and a student of birds in the field. According to Bashford Dean's memories of his childhood, as well as those of his sister, his first interest in armor was manifested when, as a very young child he saw a beautiful European helmet at the residence of Carlton Gates in Yonkers, when he was calling there with his mother. He was so much attracted by this object that he asked and received permission to hold it in his hands. Early in this period also belongs a large picture book of King Arthur and his Round Table, showing knights in combat, which evidently inspired some of his first drawings already mentioned. Thus his parentage, earliest training, and surroundings were essentially Victorian, in the best sense. His continental culture came later.

About this time Professor Edward S. Morse, of Salem, Massachusetts, a friend of his father, used to be a guest of the family whenever he came down to give popular lectures on science at Cooper Union. On these visits Professor Morse often amused the Dean children by making sketches of pterodactyls and other strange animals including the "gyascutus." Several of these quaint drawings are still extant. Miss Dean states that it was Professor Morse who taught Bashford, who was left handed, to draw with both hands simultaneously and with two crayons in each hand. This habit later enabled him to draw, with astonishing speed and skill, black-board diagrams of cross-sections of vertebrate embryos showing the three germ layers in all their windings. These sketches were at once the envy and the despair of his admiring students.

Before he was fourteen years old he was ready to enter the College of the City of New York, but because of his extreme youth it required the special intervention of General Alexander Webb, the president of the college and a friend of his father's, to secure his admission. A batch of his college themes on many subjects show that during his college course his handwriting approached the minute, rapidly cursive style that later on became so well known to his friends and students.

EARLY SCIENTIFIC WORK

Beginning 1887

During his summer vacations in the region of the old family home in Tarrytown, he spent much time fishing with his father, thus acquiring some of the first-hand knowledge of fresh water fishes and other forms of life which is revealed in his earliest papers. An excellent wash drawing of a catfish, noted as having been taken at Philipse Manor Mill Pond, near Sleepy Hollow, Tarrytown, N. Y., dates from his seventeenth year. At the City College he studied biology under Professor William Stratford, who had a profound influence upon his subsequent career. He graduated with high honors in the class of 1886 and was then appointed to the teaching staff of the College in the Department of Natural History, where he served until 1891. During this period he doubtless acquired the broad foundations of his life work.

Early in this period (1885, 1886) Eugene Blackford, another friend of his father's, who was in charge of an investigation and survey of the oyster territories of the state of New York, began to interest young Dean in this subject, which was to engage part of his time for many years to come. His first scientific paper, entitled "The Food of the Oyster; its Conditions and Variations," was published in connection with Blackford's investigation, in 1887, the year after his graduation from college when he was about twenty years old. It is illustrated with three excellent plates drawn by himself. In the same year (1887) he made his first trip to Europe, filling his notebook with quick sketches of the interesting buildings and inhabitants of Portugal, Spain, and France, and beginning his studies of foreign methods of oyster culture for the United States Commission of Fish and Fisheries. His subsequent reports on this subject embody his observations on the oysters and oyster beds of New York (1887), South Carolina (1892), France (1892), other European countries (1893, 1895) and Japan (1900, 1901).

His acquaintance with the genial Major Mather, a fish culturist, aided him in the field study of the biology of fresh water fishes. He collaborated with Mather in a report on the plants and animals of the Long Island lakes at Ronkonkoma and Riverhead, published in 1889. During this formative period he was a keen student and collector of plants, insects, diatoms, fresh water invertebrates, geological specimens, fossil fishes, and armor. The fish-eating plant (*Utricularia*) was the subject of a careful report (1889). The timber-boring insects were described in a special chapter in a book by Ivin Sickels on wood working (1890). A little later (1890) Dean was appointed the first director of the summer school of biology held at Cold Spring Harbor, Long Island, in the New York State fish hatchery. His magnetic enthusiasm aroused the support of John D. Jones, who gave a building and lands to this laboratory, which from that time on played an important part in the development of biology in the United States. Meanwhile, through his contact with Dr. John Draper, he studied physiological chemistry and later

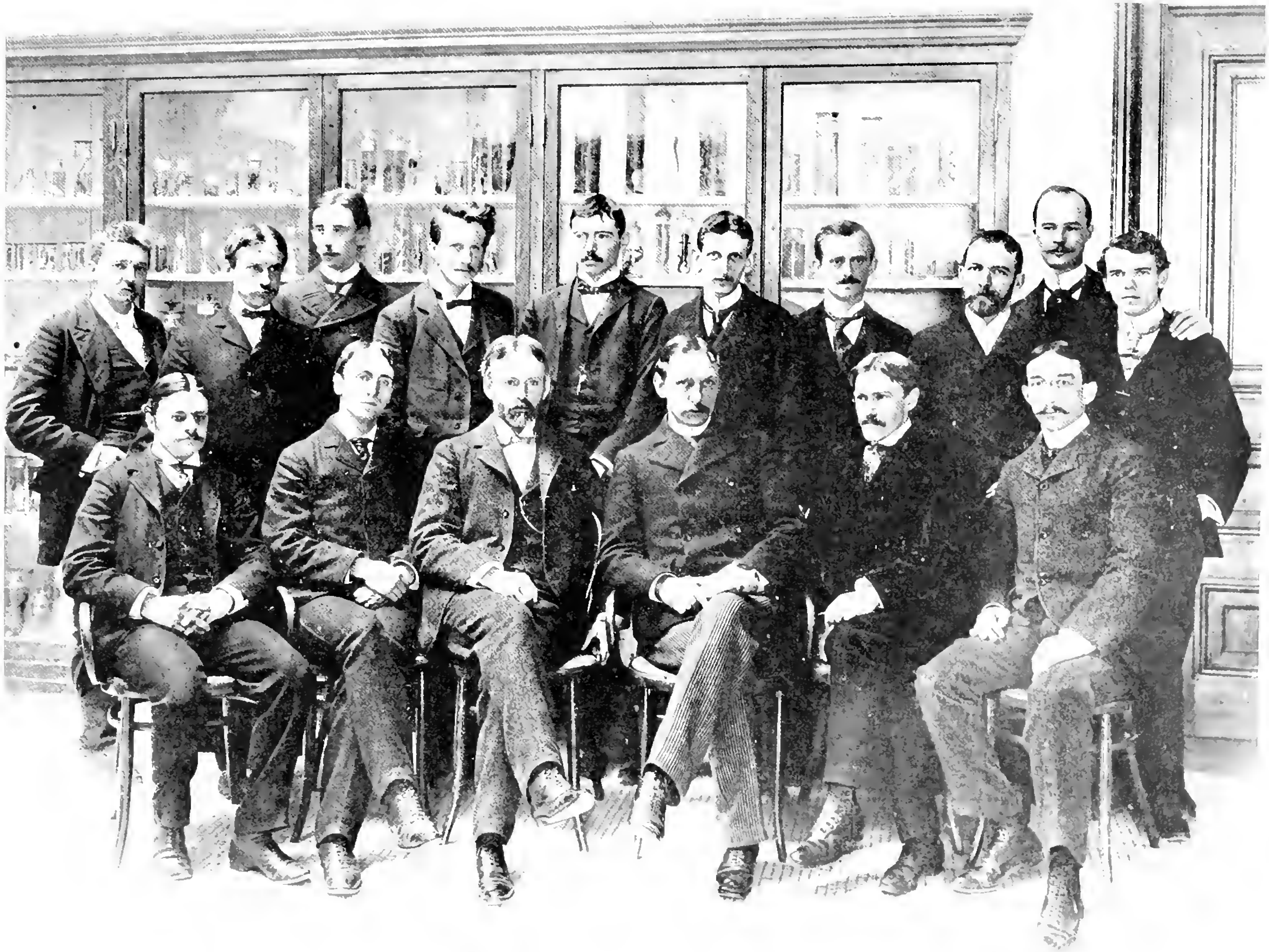
PLATE III

PLATE III.

Dr. Dean with colleagues and graduate students in the Department of Zoology at Columbia University. April, 1898.

Seated from left to right: Oliver S. Strong, Gary N. Calkins, Edmund B. Wilson, Henry Fairfield Osborn, Bashford Dean, Henry E. Crampton.

Standing from left to right: Arnold Graf, Nathan R. Harrington, Frederick C. Paulmier, Albert P. Mathews, Francis B. Sumner, Robert W. Shearman, George B. German, Marshall A. Howe, Tracy H. Holmes, James H. McGregor.



taught this subject at Bellevue Medical College and it is known that many years later he still took a lively interest in it.

RESEARCHES AT COLUMBIA UNIVERSITY

1890 1912

We do not know under what circumstances this eager brilliant youth came under the influence of the famous geologist, Professor John Strong Newberry. But it is a matter of record that after entering Columbia University as a graduate student in geology and biology, he became at first instructor in geology and was soon associated with Professor Newberry in the latter's studies on the fossil fishes of the Devonian of Ohio.

STUDIES ON THE DEVONIAN PLACODERMS

1890–1909

His doctor's dissertation, "Pineal Fontanelle of Placoderm and Catfish" (1891), was richly illustrated with his own drawings; in it the histology and anatomy of the pineal organ in recent vertebrates were thoroughly explored, and much new light was shed upon the probable function of the so-called pineal funnel in the top of the skull of *Dinichthys* and other armored fishes of the Devonian period. The long prevalent but erroneous view that the catfishes were somehow an extraordinarily ancient offshoot from near the base of the true fishes was accepted in this paper for what seemed to be at the time good and sufficient reasons.

His subsequent papers on the structure and classification of these enigmatical placoderms and their allies numbered a dozen or more and ranged from 1893 to 1909. They contributed greatly to the necessary facts of the case and led him to the interesting view that the arthrodires and their allies were neither peculiarly specialized dipnoans as held by Eastman and others, nor modified crossopterygians as suggested by Tate Regan, but that they were a wholly independent class of chordates that merely paralleled the other fishes without being nearly related to them. On the other hand, both Dean and his assistant Dr. L. Hussakof believed that the arthrodires might be an offshoot from the base of the stem leading to *Pterichthys*. While studies by Stensiö, on the distribution of the vascular and neural canals and on brain casts of early arthrodires, indicate a somewhat nearer relationship to the elasmobranch stock than Dean suspected, the other connection, with the stem of *Pterichthys* still appears highly probable.

STUDIES ON DEVONIAN SHARKS AND THE ORIGIN OF PAIRED FINS

1893–1909

Dean's studies on the Devonian sharks, also beginning while he was an assistant to Professor Newberry, led to a far reaching contribution to the problem of the origin and evolution of the paired appendages of vertebrates. In 1893 when 26 years of age he contributed his first "Note on the Mode of Origin of the Paired Fins"; he dealt also with various phases of this topic in many subsequent papers. His Devonian Cladodont shark, *Cladoselache newberryi* which he first described in 1893, showed that the paired fins were essentially like the median fins and brought weighty evidence in support of the Thacher-Balfour fin-fold theory of the origin of the paired limbs, in opposition to Gegenbaur's view that the paired fins had arisen from feather-like "archipterygia," like those of the existing lung-fishes.

Subsequent papers and memoirs of his on *Cladoselache* and on sharks as ancestral fishes appeared at intervals up till 1902. He also inspired his student, Raymond C. Osburn, to prepare a detailed critique of the opposing "fin-fold" and "archipterygial" theories and supplied him with the material which demonstrated that during the course of ontogeny the skeleton of the paired fins has a similar origin to that of the median fins and a radically different origin from that of the branchial arches.

The *Cladoselache* material described by Dean (1902, 1909) was also remarkable for containing well fossilized muscle segments and even red muscle fibres, as well as the glomeruli of the kidneys. Under the general heading of "Studies on Devonian Sharks" we may also note the fact that after Professor Newberry's death Dean edited one of the latter's memoirs on American Palaeozoic fishes, containing descriptions of various forms of dental plates and fin spines of elasmobranchs (1897). Dean's 1907 paper on Acanthodian sharks was in the nature of a general morphological review of conspicuous members of that group and contained many valuable sketches made in European museums.

STUDIES ON THE EMBRYOLOGY OF SHARKS AND GANOIDS

1893–1909

Dean's interest in the Palaeozoic sharks led him into his world-wide search for the embryonic stages of the Port Jackson Shark (*Cestracion* or *Heterodontus*), the Japanese Frilled Shark (*Chlamydoselachus*), and other archaic survivors of the class, in order to compare the findings of embryology with those of palaeontology. This division of his researches resulted also in the accumulation through the years of a great series of beautifully executed plates on the development of these forms, but most of these plates remained unpublished at the time of his death. Nevertheless he published various brief papers dealing with the eggs and cleavage stages of the sharks as follows: "Reminiscence of Holoblastic Cleavage in the Egg of the Shark, *Heterodontus* (*Cestracion*) *japonicus* Macleay." (1901), "The Early Development of Sharks from a Comparative Standpoint" (1901), "A Preliminary Account of Studies on the Japanese Frilled shark, *Chlamydoselachus*" (1903).

From the time of his early association with the fish-culturists, he lost no chance of securing embryological material among the fresh-water Ganoids. Beginning in 1893, several papers deal with the spawning habits and early developmental stages of the sturgeon (*Acipenser*, 1895), garpike (*Lepidosteus*, 1895) and bowfin (*Amia*, 1895, 1896). These studies in turn led to some comparative observations on the gastrulation of teleosts (1895) and finally (1909) to a comparative study of "The Plan of Development in Series of Forms of Known Descent and its Bearing upon the Doctrine of Preformation." His general conclusion in this brief but important paper was that apparent preformation in the embryo arises from the acceleration of the process of epigenesis.

HIS TEXT BOOK "FISHES, LIVING AND FOSSIL"

1895

By 1895, at the age of 28 and after scarcely more than five years of active work in ichthyology, he had already accumulated enough illustrative material along all the lines previously mentioned to publish his notable text-book, "Fishes Living and Fossil: An Outline of their Forms and Probable Relationships" in the Columbia University Biological Series. This text-book, like everything else Dean wrote, was marked by its extreme compactness and clarity; but it has also been especially prized for the large number of carefully drawn comparative figures and highly useful tables. On the other hand, the book was very sketchy in its treatment of the teleosts, containing ideas as to the relationships of the catfishes and other teleosts which have not been supported by later investigations. The fact is that Dean was interested primarily in the archaic fishes of all groups and that, this being a field wide enough even for his amazing activities, he refrained from wandering far among the swarming tribes of the modernized teleosts. Somewhat later he delegated the preparation of a general review of the phylogeny and classification of the teleosts to one of his students, the present writer.

PALAEOSPONDYLUS AND THE DEVELOPMENT OF THE CYCLOSTOMES

1896–1904

The year 1896 brought his first paper on *Palaeospondylus*, which was a puzzling little Devonian chordate supposed by Traquair to be related to the cyclostomes. "Is Palaeospondylus a Cyclostome?" he queried, and in several papers, culminating in his memoir on the subject in 1900, he stoutly supported the opinion that it was not. This last paper contains some of his most beautifully executed lithographic plates, showing the finer details of this enigmatical fossil. However, according to Stensiö's recent researches and in the light of much fuller knowledge of the Ostracoderms, *Palaeospondylus* may after all be more nearly related to the cyclostomes than Dean was willing to admit.

Meanwhile the subjects previously noted kept crowding each other in his bibliography of subsequent years. However, it should be noted that both because Dean spent considerable part of his time in the field as well as because he was extremely concise and pithy in his writings, his bibliography rarely runs to more than ten short papers in a year. Perhaps Dean's interest in the fossil *Palaeospondylus* roused him to special exertions to secure the embryology of certain of the existing cyclostomes. At any rate during the next few years (1895 to 1899) he combed the waters of Alaska, California, and Japan for eggs of the hagfishes which sometimes came up on the fisherman's lines, entangled in the slime exuded from the hagfishes themselves. As these priceless relics were worked over, Dean issued a series of papers on the development of *Bdellostoma* and related forms beginning in 1897 and running at intervals till 1904. His most important contribution in this field was his memoir on the embryology of *Bdellostoma stouti* (1899) in which he was able to muster an imposing and closely knit developmental series of this most rare and significant material. He was able to show, among other things, that the hagfish development stood in wide contrast all along the line to the development of the lampreys. Thus the hagfish eggs were so packed with yolk that the cleavage planes were confined to one end of the egg as in the sharks, in contrast with the total or holoblastic cleavage of the lamprey egg. He also showed that the development of the hags is direct, so that the newly hatched larval hags are far more like their elders than is the case with the larval lampreys, which differ radically from the adults.

From the fact that in these and other features of their development the hags differed from the lampreys almost as much as the amphibians do from the sharks, Dean concluded that the hags and lampreys must belong to two stocks which have been separated from each other for long geologic periods, an opinion which in the light of Stensiö's recent studies becomes all the more probable. His papers on this subject abound in critical and constructive comments on such classic problems as the behavior of the cells during the differentiation of the primary germ layers, the relations between the branchiomeres and the cephalic segments, and the supposed parallelism between individual development and phyletic history. As to this last topic, if, under the influence of von Kupffer, in whose laboratory he had worked, he had ever taken the doctrine of Recapitulation too literally, his observations on the development of the hagfishes, as well as his other embryologic studies tended rather to emphasize the physiologic necessities of the developing organism under the stress of a new environment; too close an adherence on the part of the embryo to the theory of Recapitulation might well be a costly luxury, while on the other hand the more pressing physiological needs of the embryo acted as premiums or rewards for short cuts, accelerations, and new larval adaptations, so that the recapitulative background became badly obscured.

Dean's *Bdellostoma* material was also studied by one of his students (C. H. Stockard) who published a paper in which he defended the thesis that the so-called tongue of the cyclostomes was not homologous with the true tongue of higher fishes but represented the fused mandibular arches of the gnathostome chordates. But by far the greater part of the organogeny of the hagfish, as revealed in Dean's *Bdellostoma* embryos remains to be described. It is therefore gratifying to state that several years ago Dr. Dean handed over much of this material to Dr. J. Leroy Conel, of the Boston University School of Medicine, who is studying in it the development of the brain.

STUDIES ON THE BEHAVIOR OF LARVAL AND ADULT FISHES

1896–1912

Dean never lost an opportunity to observe at first hand either the spawning and nesting habits of lampreys, garpikes, Amia, and other fishes, or the behavior of the newly hatched larvæ in reference to food reactions, mode of locomotion, etc. Observations on such topics were incorporated in all his larger papers on development, but in a number of cases were set forth in brief articles. Thus, in 1896 he published a brief abstract of notes on the behavior and food-taking of newly hatched *Amia* and the feeding habits of larval *Necturus;* in 1898 appeared a paper (with Francis B. Sumner) on the spawning habits of the brook lamprey; in 1901 a longer paper on the habits and breeding of *Amia*; in 1903 an "Obituary Notice of a Lung-fish"; in 1912 a paper on the behavior of larval eels during their transformation stages. An important paper in this series was his "Notes on the Living Specimens of the Australian Lung-fish, *Ceratodus forsteri* in the Zoological Society's Collection" (1906). This contained many excellent sketches showing the movements of the fish, the paired fins in various postures, etc.

CHIMAEROID FISHES AND THEIR DEVELOPMENT

1903-1906

Undoubtedly the most comprehensive single monograph Dean ever published was his Carnegie Institution memoir "Chimaeroid Fishes and their Development" (1906), the subject having been dealt with in a number of preliminary and advance papers beginning in 1899. The embryological material for this memoir he had sought for and collected: first in Naples and in Portugal in 1891; in Puget Sound and Alaska, in 1896; at Pacific Grove, California in 1896 and 1899; finally at Misaki and Tokyo, Japan in 1900, 1901. Meanwhile he had searched the Museums of Paris, London, Berlin, Bergen, Tromsoe, and Tokyo for comparative material among fossil and recent chimaeroids. The most important conclusion was that the chimaeroids, in spite of the opinions of many authors, are clearly nothing but highly specialized offshoots from some lowly branch of the true sharks, because they are almost wholly shark-like in their entire plan of development. The memoir will long stand as a model for its many-sided marshalling of evidence from embryology, comparative anatomy, and palaeontology.

PAPERS ON ZOOLOGICAL LABORATORIES, BIOGRAPHIC MEMOIRS, REVIEWS OF BOOKS, ETC.

1891-1910

In 1891 he began a series of papers in which he described the numerous laboratories wherein he had worked at various times, including Cold Spring Harbor (Long Island) and the laboratories of France, England, Holland, Italy, Austria, Germany, Norway, Russia, California, and Japan. These brief papers scattered in various publications contain much that will be of interest to the historian of zoology in the nineteenth century, and the same may be said of his biographical notices of many zoologists and others with whom he had been associated. Under this last heading we may list his address on "Dr. Ryder's Work with the United States Fish Commission" (1895); his memorial notices of his junior colleagues and students, Bradley G. Griffin (1897) and Nathan Russell Harrington (1899); of his friend Major Frederick Mather (1900) the fish culturist; of Eugene G. Blackford (1905) the oyster-culturist; of his old teacher in biology Dr. William Stratford (1908); of Karl von Kupffer (1900) his preceptor in the embryology of fishes; of the Japanese artist T. Nishikawa (1909) and of his old friend the Japanese zoologist Professor Kakichi Mitsukuri (1909). The writing of these memorial notices of his friends and colleagues in the midst of all his other activities, is a manifestation of his generous loyalty and unselfishness. He was also the author of an important series of critical reviews of zoological works, including A. S. Woodward's "Catalogue of Fossil Fishes in the British Museum" (1896), Garman's memoir on "The Cyprinodonts" (1895),Baskett's "Story of the Fishes" (1899), Max Weber's "Siboga Expedition to the Malay Archipelago" (1902), O. P. Hay's "Bibliography and Catalogue of the Fossil Vertebrata of North America" (1902), Traquair's "The Lower Devonian Fishes of Gemünden," T. H. Morgan's "Evolution and Adaptation," C. R. Eastman's papers on the kinship of the arthrodires (1907), Vernon L. Kellogg's "Darwinism Today" (1908), Gaskell's "The Origin of the Vertebrates" (1909). For his efforts towards advancing the memorial to Lamarck (1744-1829), the renowned naturalist of France, he was awarded the Lamarck Medal and was made a Chevalier of the Legion of Honor in 1910.

PAPERS ON THE BROADER PROBLEMS OF EVOLUTION

Beginning in 1902

These reviews above mentioned, besides containing many penetrating observations on the immediate subject, also include passages that summarize Dean's views on the broader problems of evolution. While ever cautious and conservative about rising too rapidly to higher philosophy, Dean was rarely content with mere descriptive labors and as the years passed he began to formulate and express his general views on evolution. But it is not until 1902 that we find him issuing brief notices dealing especially with these broader aspects.

Here may be listed the following titles, which indicate sufficiently the general trend of his thoughts: "A Case of Mimicry Outmimicked?" (1902); "Albinism, Partial Albinism, and Polychromism in Hagfishes" (1903); Review of T. H. Morgan's "Evolution and Adaptation" (1904); "Evolution in a Determinate Line as Illustrated by the Egg-cases of Chimaeroid Fishes" (1904); "When Do Variations Attain Selective Value" (1908); "Accidental Resemblances among Animals. A Chapter in Unnatural History." The latter paper cited a number of quite surprisingly close but accidental resemblances between widely different parts of organic forms, such as the "Samurai's face" on the back of a certain species of Japanese crab. If, argued Dean, such resemblances may come into being without having any value in terms of Natural Selection, should we not be cautious in invoking Natural Selection to account for similar resemblances, as of butterflies to leaves, which may conceivably be equally fortuitous and valueless? Later papers of this series include "A New Example of Determinate Evolution" (1909), and "The Plan of Development in Series of Forms of Known Descent in its Bearing upon the Doctrine of Preformation," (1909).

In general it may be said that in Dean evolution found an historian of judicial temper whose prime motive was the establishment of the facts of the case, and to whom simple general explanations were regarded with some misgivings. As the greater part of his zoological research was accomplished before 1905, he was scarcely vexed with the complexities of the mechanism of heredity revealed by contemporary genetics. Even so his knowledge of the ways of embryologic development in its relation to phylogeny was notably broad and well founded.

PLATE IV

PLATE IV.

Dr. and Mrs. Dean in Japanese costume. Misaki, 1900.

SERVICES TO THE AMERICAN MUSEUM OF NATURAL HISTORY

1903-1928

We have already given a preliminary outline of Dean's activities at the Museum. In 1903, his friend Professor Henry Fairfield Osborn, who was also his colleague in the Department of Zoölogy at Columbia and who was now President of the American Museum of Natural History, arranged for him to come to the Museum and take charge of the fossil fishes in the department of vertebrate palaeontology. At first the embryonic division of fishes was not considered large enough to be a department by itself and Dean served as curator of the "Department of Reptiles and Fishes," collaborating in the former field with Miss Mary C. Dickerson. Meanwhile, by arrangement with Columbia, the great J. S. Newberry collection of fossil fishes was transferred to the Museum. This included Newberry's valuable collection of Devonian placoderms (arthrodires) and sharks. The extensive collections of fossil fishes made by the late Professor E. D. Cope were presented through the generosity of Morris K. Jessup, the late President of the Museum. Also the Reverend D. Stuart Dodge presented a large collection of Cretaceous fishes from Mt. Lebanon, Syria.

Dean, as already noted, thereafter published in the Museum memoirs some of his important papers on various arthrodires and other Devonian fishes. Through the generosity of Mr. Cleveland H. Dodge he was able to extend and amplify the collections of fossil fishes. With the assistance of one of his old students, Dr. Louis Hussakof, who was later appointed Curator of the Department of Fishes, the collections of fossil fishes were duly catalogued and installed, field expeditions were conducted in search of exhibition and study materials of the spoonbill sturgeon, the gar-pike, *Amia*, the brook lamprey, etc. A nearly complete skull and shoulder plates of the giant *Dinichthys terrelli* were assembled, mounted, and placed on exhibition. Life-like restorations of the principal types of antiarchs (*Pterichthys*), placoderms (*Coccosteus*), ganoids, lung-fishes, and acanthodian sharks, which were found as fossils in the Lower Old Red Sandstone of Great Britain were prepared and assembled in a "Devonian Aquarium." A synoptic collection of the principal orders of fossil fishes was also placed on exhibition. He also induced the President and Trustees of the Museum to set aside a large exhibition hall for the collections of recent fishes in the projected new east wing of the Museum, and laid the basic plans for the hall, the completion of which he entrusted to another of his old students (the present writer).

THE BIBLIOGRAPHY OF FISHES

1916, 1917, 1923

When Dean became a graduate student under Professor J. S. Newberry, he began to accumulate a bibliography of fishes, including titles on embryology, fossil and recent fishes; it is a remarkable example of his patience, persistence, and astonishing energy that he managed to keep steadily enlarging this bibliography, in spite of all his prolonged excursions in the field through all the years of his active professorship at Columbia, until, when he was appointed Curator of the Department of Reptiles and Fishes at the American Museum of Natural History, the bibliography included some 20,000 titles. At this time the Museum engaged an assistant for him to carry on this work which finally saw the light in three volumes, in 1916, 1917, and 1923, after Charles R. Eastman, E. W. Gudger and Arthur W. Henn had spent several years at work on various sides of it under Dean's personal direction. It would be difficult to overemphasize the importance and usefulness of this great work which makes readily accessible to all future students of the many phases of ichthyology the treasury of knowledge gleaned by hundreds of workers in the past. Together with his textbook on "Fishes, Living and Fossil," the "Bibliography" exemplified Dean's high ideals of service to other seekers after knowledge. In recognition of the great value of this work, the National Academy of Sciences awarded him the Daniel Giraud Elliot medal in 1923.

CONNECTION WITH THE METROPOLITAN MUSEUM OF ART

1903–1928

We have noted above that even as a small child Dean manifested a strong interest in European armor. The incident of the helmet seen in the residence of a friend of the family later led to the boy's unsuccessful effort to purchase this helmet at the executor's sale of Mr. Gates' estate. We learn however that he purchased two beautiful daggers from this collection and that this was the beginning of his collection of arms and armor which was always his principal avocation and which finally became the ruling interest of his life.

Probably his early journeys in Europe, while he was studying the methods of oyster culture practised in various countries, afforded him the opportunity to visit museums where armor was exhibited and perhaps to attend occasional auction sales of these highly prized objects. At any rate, by 1899 he was already in possession of a growing collection of European armor and weapons. During his journeys in Japan in 1900, 1901, and 1905, he accumulated an imposing series of Japanese armor and side arms, together with much documentary evidence as to the history of each piece. A photograph which I received from him in 1901 shows him arrayed in the panoply of a Japanese samurai. When he returned from Japan, laden also with zoological treasures, his house was crowded with suits of Japanese armor of many generations. He soon loaned these to the Metropolitan Museum of Art and some of them were later purchased by the Museum for the gallery of Japanese armor which he consented to arrange. The remainder of his collection, 459 pieces, he presented to the Museum in 1914.

In 1903 appeared the first of his many papers on this subject, the "Catalogue of the Loan Collection of Japanese Armor" in the Museum series of Handbooks. In 1905 this was followed by the "Catalogue of European Arms and Armor," a handbook containing a most illuminating historical review of the development of armor in Europe. He was appointed Honorary Curator of Arms and Armor in 1906 and from

PLATE V

PLATE V.

"He was a verray parfit gentil knight."

this time onward the pursuit and study of armor occupied by far the greater part of his time. With the consent of President Butler and the Trustees of Columbia University, he retired from active duties there in order to devote practically his entire time to the arduous task of building up the collections of armor in the Metropolitan Museum of Art. Almost every year he made long journeys in Europe ransacking every available corner for these treasures. As a result of Dr. Dean's unceasing efforts, Mr. William H. Riggs in 1913 presented his great collection of armor to the Museum. This gift together with his own personal gifts and loans to the collection, finally brought the collection of arms and armor in the Metropolitan Museum to rank among the great ones of the world.[1]

The history and authenticity of each piece were of course of the greatest importance, and in connection with this side of the subject, Dean brought together an unrivalled assemblage of documents, books, and other collateral evidence. His handbooks and brief papers on arms and armor from 1903 to 1928 number about 137. Nearly all were sublimations and digests from the vast material that he had accumulated and which lies unpublished even today.

Even a hasty perusal of these titles suggests the multitude of technical lines in which Dean was expert. For to be successful both in preserving the purity of one's collection and in purging it from dross and counterfeits one must for example learn to look for all the little detailed earmarks of authenticated specimens as they vary in different countries at different periods. One must further know or quickly ascertain who the grand seigneur was for whom the armor was designed; thus in the long run one will find it convenient to be a sort of living "Almanach de Gotha" for both Europe and Japan. One must next learn to recognize or be able to identify the initials of the armorer, the small differences which distinguished his work from that of others. One must have at least some first hand experience as to the steps in the manufacture of the completed object, so one will find it convenient to maintain a laboratory for the repair and reconstruction of the thousand and one pieces that went into the whole equipment. Obviously no true student of armor and arms would be content with inadequate notions of the ways in which each piece was used in combat.

A growing knowledge of the chronological sequence of types finally results in a general concept of the evolution of arms and armor as it was even after the invention of gunpowder drove them into new and strange reincarnations and vestigial remnants. Here Dean's authentic knowledge of the ways of organic evolution gave him an immense advantage over the mere historian. For example, his drawings of the evolution of various lines of helmets and pole arms in Europe strongly recall the phylogenetic tree of certain groups of fossil cephalopods, for in both cases a certain very primitive and ancient pattern gives rise to gradually diverging series which toward the end take on the "phylogerontic" extremes that precede sudden extinction, through failure to meet new changes in the environment. Some zoologists have objected to the stretching of the word "evolution"

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[1] Cf, "The Catalogue of Arms and Armor, including the William H. Riggs Donation. 1921."

to cover such an historical process, but, as Dean showed, the evolution of arms and armor is only a sort of biological evolution once removed, the conservatism of armorers and purchasers taking the place of heredity in tending toward continuity, and the stress of environment evoking mutational changes in type.

WORK ON THE DYCKMAN HOUSE MUSEUM AND PARK

1915-1916

The Dyckman House Museum and Park is a restored Dutch farm house, originally built about 1783 and set in the midst of a pleasant garden. It is located on a low hill just above 204th Street and Broadway, New York City. The interior is beautifully arranged, and each room is restored with furniture and equipment appropriate to the days when the old Dyckman family lived in it. Mrs. Bashford Dean (Mary Alice Dyckman) and her sister, Mrs. Alexander McMillan Welch (Fannie Fredericka Dyckman) in 1916 presented this house and park to the City of New York in memory of their parents Mr. and Mrs. Isaac Michael Dyckman. On this occasion Dr. Bashford Dean and his brother-in-law Mr. Alexander McMillan Welch were the "honorary curators," but they were also extraordinarily active curators, for to them the city is indebted for intensive work in restoring the old house to its pristine plan and in assembling and installing the hundreds of quaint and well authenticated relics that bring back the old days of the Dyckman family so vividly to the eye of the visitor. Dr. Dean's brochure (1916) on the history of the house is a masterpiece of antiquarian and historical research everywhere illuminated by his kindly humor and insight.

SERVICES IN THE WORLD WAR

1917-1918

When this country entered the war it was natural both that the government should look to Dr. Dean for advice as to the designing of helmets and other armor for trench warfare, and that he should volunteer for this service, serving as Chairman of the Protective Body Armor Committee of the National Research Council, and later as Major in the Ordnance Department. After a personal inspection of field conditions of trench warfare, he set about designing and testing various types of helmets and body armor. His light body armor (weight nine pounds) stopped automatic pistol fire at muzzle velocity; but his heavier armor, which withstood gunfire at fifty yards, was the more successful and was adopted by army aviators. In this connection he was the author of "Helmets and Body Armor in Modern Warfare" (1920).

THE CROWNING DECADE

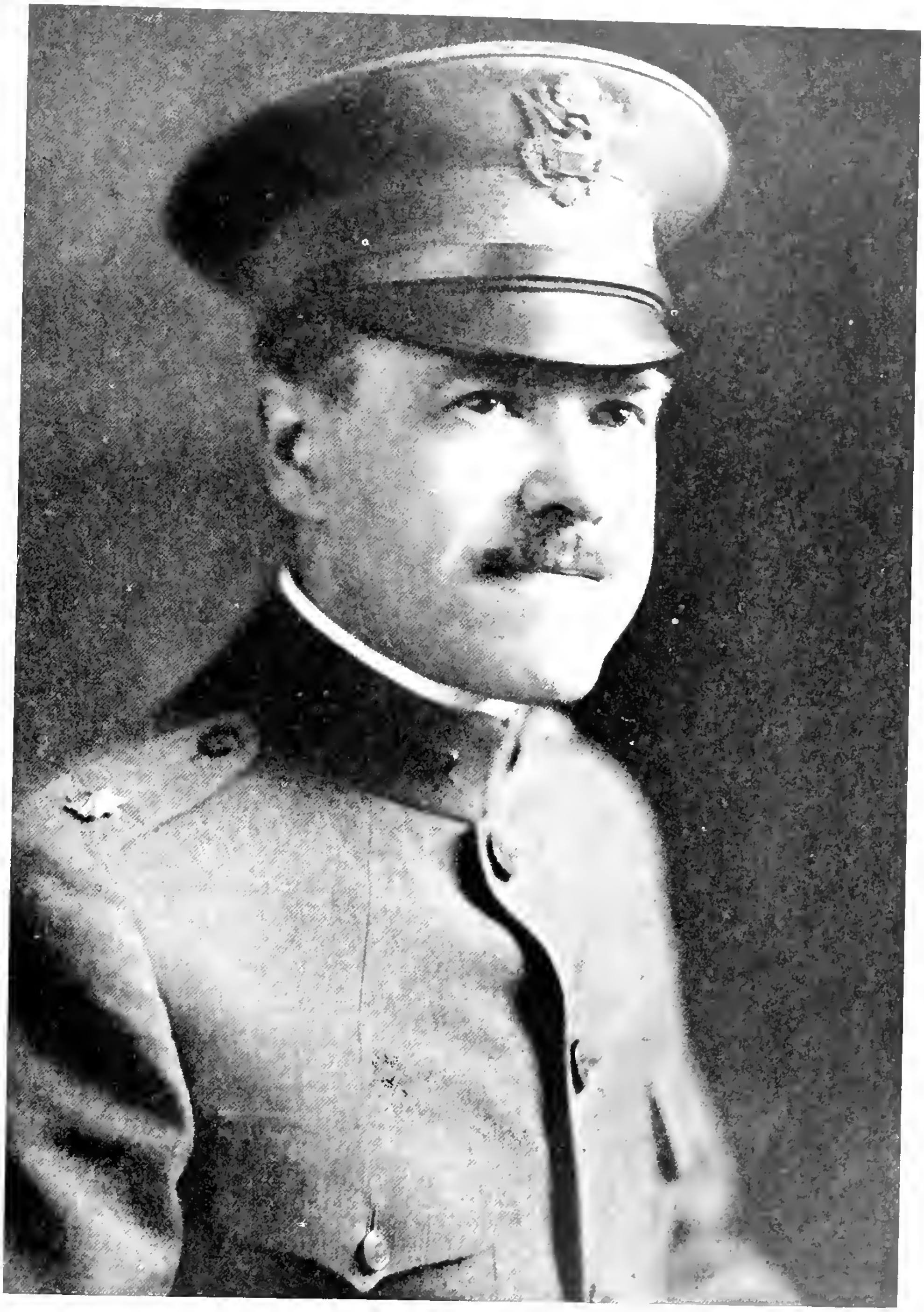
1918-1928

In spite of frequent ill health and enforced rests, the closing decade of Bashford Dean's life yielded an abundant harvest. Among the brightest gems of this time is the

PLATE VI

PLATE VI.

Major Bashford Dean, U. S. Ordnance Service, 1917-1918.



series of twelve descriptive labels or small charts published by the Metropolitan Museum of Art, showing development (or evolution) of arms and armor. Into these labels or charts he put the finest products of his researches on the historical development of helmets, breastplates, gauntlets, shields, pole arms, swords, crossbows, guns and spurs. From this period of comparative quiet after the great war also date numerous small papers on arms and armor and the manuscripts of his catalogues of European daggers, court swords and hunting swords published since his death. The "Bibliography of Arms and Armor" (in collaboration with S. V. Grancsay), is still in course of preparation (1930).

The last grand act of his life was the building of a noble Gothic hall adjoining his residence at Riverdale-on-Hudson. In this he intended to place the finest pieces of his own collection of armor. But the cord of life was snapped shortly before the great day when all would have been ready for the opening. Nevertheless his devoted family and his colleagues from the Metropolitan Museum of Art have arranged in this hall numerous pieces from his collection of armor. There his friends may stand reverently before the austere beauty of mediaeval armor revealed by this incomparable man.

SUMMARY

The foregoing pages give us the outline of Bashford Dean's life and works without enabling us ever to answer why under a given set of circumstances he reacted precisely as he did. Other men of "Old American" stock and of Victorian culture have early manifested a keen interest both in nature and in their fellow men; have followed various branches of natural science, archaeology or history; have left behind them perhaps equally great evidences of their unceasing labors for science or art. But it is the individual patterns of their lives that baffle explanation, except that once having been started in certain directions, they themselves wrought these patterns through intelligent use of the opportunities that circumstances chanced to open before them. And so it was with Bashford Dean. From his father's friend Professor Edward S. Morse he is said to have learned a certain trick in drawing with two crayons in each hand, but it was he who developed this talent to the advantage of his students who received with delight his beautiful blackboard diagrams of the germ layers of vertebrate embryos. It was apparently from Eugene Blackford that he derived his interest in the problems of oyster culture; and this opened the way for his early visits to various countries in Europe, where he acquired the continental culture which was so essential in all his later work.

The wide fame of Tennyson's poetic version of the Arthurian legend was probably responsible for the existence of the picture book from which as a child Bashford Dean loved to copy pictures of knights in combat. The incident of the helmet which excited his eager curiosity and interest while he was still a very young child seems to bring us near to the origin of his lifelong hobby, the study of arms and armor. But it was he who chose to follow this hobby, at first almost apologetically as a relaxation from more serious pursuits.

Whatever may have been the circumstances of his meeting with Professor J. S. Newberry, the influence of this man upon Bashford's Dean's life was decisive, for it was Newberry who introduced him to the grand problems of the origin and evolution of the fishes and thus the eager young student of fish culture was started both upon the study of the fossil fishes of the Palaeozoic Era, and upon the pursuit of the embryologic history of their present day relatives, the archaic cyclostomes, sharks and ganoids. And here again his frequent journeys in Europe and Japan on these quests gave him many opportunities for the ferreting of old armor from out of the way places. And so well were these opportunities followed up that long before his first professional paper on the subject appeared (1903) his private collection of European and Japanese armor was already worthy of the noble setting that it eventually obtained.

It was through his presence at Columbia College, as a graduate student and instructor in geology and zoology, that he became associated with Professor Henry Fairfield Osborn in the founding of the department of zoology and in the planning of the laboratories and lecture rooms. Here Dean's wide experience in the biological laboratories of Europe was joined with Professor Osborn's sagacious foresight of the needs of research workers for private rooms and of students for spacious well equipped laboratories, the results being eminently satisfactory to the many generations of students of the past thirty years who have worked there. Here also Dean's passion for collecting early led to the building up of excellent teaching collections especially the systematic collection of types of fishes and the beautiful anatomical preparations illustrating the courses in general zoology, ichthyology and embryology. He was also highly successful as a "fisher of men." With incomparable art he set forth to his enthusiastic students the beauties of his favorite subjects, the study of the Devonian placoderms and the embryology of their surviving remote relatives, the cyclostomes, sharks and ganoids. One of his men (N. R. Harrington) secured much valuable material of *Polypterus* in Africa (although at the cost of his own life, a loss that Dean never ceased to regret); another (W. E. Kellicott) followed through the development of the vascular system of *Ceratodus;* a third, (Raymond C. Osburn) produced evidence that was fatal to Gegenbaur's "archipterygial theory" of the origin of the paired limbs of vertebrates; a fourth (L. Hussakof) contributed worthily to the knowledge of the Devonian placoderms; others carried the influence of Dean's unique personality into many other fields of natural science. It was also through his friendship for Professor Osborn that Dean finally became a curator at the American Museum of Natural History. Here he founded an active department of recent and fossil ichthyology, and prepared for publication many of his papers on the Devonian placoderms; his great three volume "Bibliography of Fishes," which had grown out of his early attempts to compile a bibliography for his own use, was with the aid of several collaborators also published by the Museum during this period.

The circumstances which led him to shift the main stream of his tireless activities from zoology to the science and art of arms and armor are complex and somewhat obscure. For various reasons, both the demand and the opportunities for further studies on the palaeontology and embryology of fishes were unfortunately rather restricted, while the demand and the means for the development of the collection of arms and armor at the Metropolitan Museum of Art were growing rapidly, and that too, largely because of the brilliance of his own success in this field. At any rate his extensive collection of Japanese armor, chiefly made in 1900 to 1901, was loaned and later presented in large part to the Metropolitan Museum of Art, and he was soon persuaded to prepare a "Catalogue of the Loan Collection of Japanese Armor" which was issued in 1903. By 1905, he had completed and published the "Catalogue of European Arms and Armor" in the Metropolitan Museum including the great collection of the Duc de Dino. Later it began to appear that the greatest private collection of armor in existence, namely that of William H. Riggs of Paris, might probably find its way to the Metropolitan Museum if only Dr. Dean's time and knowledge could be enlisted in this cause. Mr. J. Pierpont Morgan, a lifelong friend of Mr. Riggs, and at that time president of the Metropolitan Museum, urged Dr. Dean to drop everything else and concentrate upon securing this superb collection for the Museum. President Butler and the Trustees of Columbia University, recognizing the urgency of the situation, granted Dr. Dean's request to be relieved of classroom duties, and he was thereafter enabled to spend a great deal of time with Mr. Riggs in Paris, going over the latter's great collection, making an inventory, and with Mr. Riggs' help establishing the provenience of its individual specimens. Mr. Riggs consulted President Morgan and Vice President Rutherfurd Stuyvesant about conditions in the Museum and in 1913 he signed the deed of gift at Dr. Dean's house in Riverdale-on-Hudson, with Messrs. Cleveland H. Dodge and George F. Perkins as witnesses. The collection in a hundred odd cases arrived at the Museum in 1914 and Dr. Dean spent the next year in accessioning, cataloguing and arranging it for exhibition. Early in 1915 the galleries containing these wonderful examples of the armorer's art were opened to the public.

Thus we enter the period of Dean's transition from zoology to the study of armor. Inspection of his bibliography shows that in the first five years of the period from 1903 to 1928 (inclusive) the number of his papers on zoological subjects as well as the number of pages therein considerably exceeded those devoted to arms and armor or closely allied subjects. In the next ten years (1908 to 1917 inclusive) there were 33 zoological papers and 58 papers on arms and armor; in the remaining years of his life (1918–1928 inclusive) he produced 178 papers, of which (apart from the third volume of the "Bibliography of Fishes," edited by his colleagues, and apart also from a few very brief notes on zoological matters) nearly all were devoted to arms and armor.

In short, during the thirty-three years from the time of publication of his first scientific paper (1887) to his death in December, 1928, Dr. Dean published 312 papers, of which about 170 dealt with matters pertaining to biology. The first twenty years (1887–1907) were devoted primarily to the science of ichthyology in its several aspects; after 1909 he published but little in zoology with the notable exception of his "Bibliography of Fishes," which had been under way for many years. The subject of arms and armor, on the other hand, was practically a lifelong interest, and from 1906 to his death in 1928 absorbed the greater part of his energies. Both his own inclinations and the force of circumstances led him to make this unique transition from zoology to the science of arms and armor, and in the opinion of the present writer even his great accomplishments in zoology were far outweighed by his contributions in the latter field. He himself felt that while his unfinished work in ichthyology could be carried on by his students and successors, the most pressing matters were first for him to build up the collections and exhibits of armor and secondly to secure and record the "vanishing data" regarding the provenience of every piece in the collection. At the time of his death several of his important works were still unpublished, namely the "Catalogue of European Daggers," the "Catalogue of European Court Swords and Hunting Swords," and the very extensive "Bibliography of Arms and Armor" in collaboration with S. V. Grancsay. All but the last of these works have since been published by the Metropolitan Museum of Art. It is also gratifying to state that, on the side of zoology, his great series of plates illustrating the embryology of the primitive sharks will be published as a Memorial Volume, by The American Museum of Natural History.

Book plate drawn by C. W. Sherborn of the British Museum (Natural History)

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265. 1921 Recent sales of armor. *Bulletin Metropolitan Museum Art*, Vol. 16, pp. 188–192, 5 figs.

266. 1921 Models of beautiful cannon. *Bulletin Metropolitan Museum Art*, Vol. 16, pp. 210–211, fig.

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APPENDIX A

OTHER BIOGRAPHICAL AND MEMORIAL SKETCHES OF BASHFORD DEAN

In addition to the foregoing, sketches of Dr. Dean's life and work have appeared as follows: W. K. Gregory, *Science*, 1928, Vol. 68, pp. 635–638; Henry Fairfield Osborn, *Natural History*, 1929, Vol. 29, pp, 102–103, portrait; A. S. Woodward, *Nature*, 1929, Vol. 123, pp. 99–100; [E. W. Gudger], *Scientific Monthly*, 1929, Vol. 28, pp. 191–192, portrait; Naohide Yatsu [Text in Japanese], *Shizen-Kagaku* (*Natural Science*), Tokyo, 1929, Vol. 4, no. 1, portrait; Erich Haenel, *Zeitschrift fur Historische Waffen- und Kostumkunde*, 1929, N.S. Vol. 3 (12), p. 48; *City College Alumnus*, New York, 1929, Vol. 25, pp. 14–15, 28, portrait; "In Remembrance of Bashford Dean" [By Various Hands], *The Riverside News*, New York, May 1929, Vol. 16, no. 5, pp. 11–17, 3 portraits, 3 illustrations: W. K. Gregory, Bulletin Geological Society America, 1930, Vol. 41, pp. 16–25, portrait; [Editorials], *The New York Genealogical and Biographical Record*, 1929, Vol. 60, p. 101, portrait; *The New York Times*, Dec. 12, 1928; *New York Herald-Tribune*, Dec. 17, 1929; *National Bulletin Published by the Military Order of the World War*, Jany. 1929.

APPENDIX B

RESOLUTIONS AND MEMORIAL MINUTES RELATING TO BASHFORD DEAN

Resolution Adopted by the Associate Alumni of the College of the City of New York

A resolution prepared, by direction of the President, by Charles A. Downer, '86, read at the annual meeting of the Associate Alumni of the College of the City of New York, and ordered spread upon the minutes, published in the *City College Alumnus*, and transmitted to the family of the late Bashford Dean.

The Associate Alumni of The College of the City of New York record with deep regret the death of Bashford Dean, '86, their Vice-President, and one of the most widely known and highly honored of the graduates of the College. He passed away in Battle Creek on the sixth of December of this year. He was a student of the Class of 1886, and was graduated with high honors. Already in his undergraduate days he had shown marked ability in the subject in which he was destined to achieve such unusual distinction, known in those days as Natural History, but he was nevertheless a well rounded student, excelling in all subjects, as later he manifested deep interest in various human activities, and became a great expert in two wholly divergent fields.

Immediately after graduation he was appointed to the teaching staff of the College, being attached to the Department of Natural History, in which his success had so amazed his fellow students. He continued the study of his specialty at Columbia University and within a few years had obtained there the degrees of Master of Arts and Doctor of Philosophy. In 1891 he gave up his position in our College to accept an appointment to the Department of Biology at Columbia University. Five years later he was made an Assistant Professor of Zoology, and in 1904 Professor of Vertebrate Zoology. Last year he was given the title of Honorary Professor of the University.

Along with this work as an educator, he carried on investigations as a member of the United States Fish Commission and was soon travelling to all parts of the world. His visit to Japan led him into a second field, which he made his own, and he presently was known as a specialist not only in Japanese armor, but as probably the greatest living authority on every sort of armor, and as one of the great collectors of armor of the world. While still a young man he held positions as curator in our two great city museums, the Museum of Natural History, and the Metropolitan Museum of Art, thus being recognized as possessing extraordinary expert knowledge in both these great divisions of human achievement, science and art. During the Great War he held the rank of Major in the Army, and by the invention of a special helmet rendered a great service to his fellow men.

Numerous distinctions came to him. He was a prophet not unhonored in his own country and almost equally honored abroad. He was a prolific writer in his two specialties, and an active member of many learned societies. When he died he was an Honorary Fellow for Life in our two Museums and a Trustee in the Metropolitan Museum of Art.

Our College may well be proud of him and our City grateful for the service he performed in helping New York to stand in a higher position than before among the cities of the world that are reckoned as great centres in art and science.

Not a large man physically, he was endowed with untiring energy and untiring enthusiasm. He had the gift of winning friends, of inspiring confidence, of exciting admiration. Like most men of really fine abilities, he was modest and unassuming. All who knew him felt the charm of markedly individual personality, felt themselves in the presence of a man very sure of himself, but by no means self-centered, and altogether free from vanity. He was singularly courteous and gentle and accomplished much in his dealings with men through the possession of these qualities. His was a remarkably successful life, for it was a useful life, and although his taking off was untimely, he had achieved his aims to a most astonishing degree.

He leaves a fragrant memory behind him, and he leaves besides a substantial, visible monument that will endure.

December 16, 1929.

RESOLUTION OF THE FACULTY OF PURE SCIENCE OF COLUMBIA UNIVERSITY

Whereas, the death of Professor Bashford Dean on December sixth, 1928, is a grievous loss to his friends and colleagues of Columbia University; and

Whereas, Professor Dean served the University with devotion and distinction from the days of his assistantship with Professor J. S. Newberry in the Department of Geology; and

Whereas, he took a prominent part in the early development of the Department of Zoology soon after its foundation under the leadership of Professor Henry Fairfield Osborn; and

Whereas, he served for many years as Professor of Vertebrate Zoology, inspiring and training many who have since become active in various branches of Zoology; and

Whereas, he contributed greatly to the advancement of science by his numerous publications, especially those on the fossil fishes of the Devonian age and on the embryology of the sharks, ganoids and other archaic fishes, and to the advancement of the Department of Zoology by many manifestations of his versatile genius in science and art; and

Whereas, whether in the classroom and laboratory or in some distant corner of the world in search of zoological or historical treasures, his untiring energy and rare charm of friendliness were always equally in evidence;

Therefore, be it resolved: That the colleagues and friends of Professor Bashford Dean in Columbia University hereby record this expression of their sorrow for his loss and of their appreciation of his life work;

And be it further resolved: That the Secretary of the Faculty of Pure Science be requested to transmit a copy of this resolution to his widow and family.

April 26, 1929.

RESOLUTION OF THE EXECUTIVE COMMITTEE OF THE LONG ISLAND BIOLOGICAL ASSOCIATION

The following resolution was adopted and sent to Mrs. Dean:

The Executive Committee of the Long Island Biological Association have learned, with deep regret, of the death of Dr. Bashford Dean. Dr. Dean was the first director of the Biological Laboratory and it was due directly to his interest that the Laboratory received a firm foundation, through the gift of John D. Jones of a building and lands. The noteworthy development of the Laboratory is largely due to the vigor of the germ that Dean planted and nourished. So long as the Laboratory persists his memory will be cherished by it.

The Executive Committee of the Long Island Biological Association desire to express to you their sympathy in your bereavement.

December 8, 1928.

A MEMORIAL MINUTE ADOPTED BY THE COUNCIL OF THE NEW YORK ACADEMY OF SCIENCES

Dr. Bashford Dean who died at Battle Creek, Michigan, on December 6, 1928, at the age of 61 years was an active member of the Academy for forty years and served it with distinction in many directions. He was elected a fellow of the Academy in 1889 while he was a student and assistant of Professor J. S. Newberry in the department of geology at Columbia College. Altho then only 22 years old he had already published several valuable papers on the food of the oyster, on the supposed fish-eating plant *Utricularia* and on the animals and the plants of the Long Island lakes. Under Prof. John S. Newberry's stimulating influence he took up the study of the American Palaeozoic fishes with great enthusiasm and ability; from 1891 to 1909 he published a long and brilliant series of papers dealing chiefly with the arthrodira or joint-necked forms, with the cladodont sharks and with other early fishes and fish-like vertebrates. Of these papers some 15 appeared in the Transactions and Memoirs of the Academy, the rest mostly in the Bulletins and Memoirs of the Museum. He was also the author of many important papers on the embryology of the living ganoids, cyclostomes, sharks, and chimaeroids. Doctor Dean was thrice elected curator of the Academy's collections. At various times he served as Librarian, Councillor, Chairman of the Section of Biology, Vice-President of the Academy, and Member of the Finance Committee. He was Professor of Zoology at Columbia College, Curator of the Department of Reptiles and Fishes at the American Museum of Natural History, and Curator of Arms and Armor at the Metropolitan Museum of Art. During the World War he served as Major in the Ordnance Department, designing helmets and other special armor for trench warfare. In search of the early developmental stages of the hagfishes and sharks he made many journeys in the field in Alaska, California, Japan, Norway, Russia, Italy, Portugal, and elsewhere. While in the pursuit of mediaeval armor he many times ranged over Europe ransacking every remote corner where armor was to be found. A few years ago he conducted archaeological investigations in Syria and recovered there much valuable data concerning the life of the Knights Templars in their wars for the recovery of the Holy Sepulchre from the Saracens. He applied to the study of arms and armor the view-point and methods of palaeontology and was thus enabled to throw a flood of light upon the historical development of helmets, pole arms, and armor. Not the least of his achievements was the publication, with the collaboration of several colleagues, of a great Bibliography of Fishes in three volumes.

In spite of his vast and multifarious activities, pursued at high tension, under the handicap of a delicate digestive system, his work never bears the traces of haste or immaturity. Even his youthful writings carry the conviction of well seasoned judgments, and an exceptionally broad outlook, and were fortified by great reserves of detailed knowledge and skill in many branches of science and art.

Members of this Academy who had the privilege of knowing him well will recall with gratitude and satisfaction Dean's ever friendly and sustained interest in *their* interests and problems. Friendliness and service with him were not pawns to win advantage with in the game of life; they were the spontaneous reactions of a generous companionable spirit. Thus the pursuit of truth and beauty in science and art Dean keenly enjoyed for himself, but he also always succeeded in recording and visualizing the results so that others could enjoy them with him. The superb exhibit of armor brought together by him and left as his legacy to the world at the Metropolitan Museum of Art is the most brilliant expression of his altogether unique life and individuality. If his life had been prolonged only a few years more he undoubtedly could have accomplished much more that he had planned to do; nevertheless we may well rejoice in the perfection and magnitude of his achievements in many fields.

February 28, 1929.

RESOLUTIONS ADOPTED BY THE AMERICAN SOCIETY OF ZOOLOGISTS

We, the officers and members of the American Society of Zoologists, wish to place on record in the form of this resolution our sorrow and deep sense of loss at the death of our colleague Dr. Bashford Dean.

As founder, Curator, and later Honorary Curator of the Department of Ichthyology of the American Museum of Natural History, Doctor Dean continued the work of Professor J. S. Newberry of Columbia University who had brought together a famous collection of armored fishes of the Devonian. He carried on a brilliant series of researches on these and others of the earliest fish-like vertebrates, installing also the American Museum exhibit in this subject as well as the series of groups illustrating the habits of the ganoids and other fishes. In the meantime he carried forward his catalogue of references to scientific books and papers dealing with all phases of fish life. This was later published by the Museum in the three great volumes of the "Bibliography of Fishes." He also laid the basic plans for the recently completed Hall of Fishes of the World.

Dr. Dean was for many years actively connected with the teaching staff of Columbia University in Zoology, and through travel and study became a leader in our knowledge of the embryology of fishes.

We record with deep friendship our conviction that science has lost one of its most distinguished figures.

Therefore be it resolved that this expression of our sorrow be incorporated in the minutes of this meeting.

Dec. 28, 1928.

RESOLUTIONS ADOPTED BY THE PRESIDENT, DIRECTOR, SCIENTIFIC AND ADMINISTRATIVE STAFFS OF THE AMERICAN MUSEUM OF NATURAL HISTORY

We, the Scientific and Administrative Staffs of the Museum, including the entire Department of Ichthyology, have assembled to record our sorrow and deep sense of loss at the death of our beloved colleague and friend Bashford Dean.

As founder, curator, and later honorary curator of the Department of Ichthyology, Doctor Dean continued the work of Professor J. S. Newberry of Columbia University, whose famous collections of armored fishes of the Devonian were, through Dr. Dean's efforts, deposited in this Museum; thereafter he carried on a brilliant series of researches on these and others of the earliest fish-like vertebrates, installing also the Museum exhibits in this subject, as well as the series of groups illustrating the habits of the ganoids and other fishes.

In the meantime he carried forward his catalogue of references to scientific books and papers dealing with all the phases of fish life, which he had begun many years before, and which with the aid of his colleagues and assistants was finally published by the Museum in the three great volumes of the Bibliography of Fishes. He also laid the fundamental plans for the recently completed Hall of Fishes.

We record with deep affection and friendship our conviction that the Museum has lost one of its most distinguished figures; ardent champion of his associates, and ever their wise counselor and friend.

Therefore be it resolved that this expression of our esteem and of our sorrow be incorporated in the minutes of the Scientific Staff of the Museum and that a transcription be sent to his wife and family with our profound sympathy.
December 10, 1928.

RESOLUTION ADOPTED BY THE BOARD OF TRUSTEES OF THE METROPOLITAN MUSEUM OF ART

At a meeting of the Board of Trustees the following memorial resolution upon the late Bashford Dean was adopted:

In the sudden death of Bashford Dean, the Metropolitan Museum of Art has suffered an irreparable loss. His loss was grievous to many other public institutions: to the American Museum of Natural History, which crowned his work there by the opening of its Hall of Fishes at which he was to be the guest of honor only the day before his death; to Columbia University, where he was professor of vertebrate zoology; to the College of the City of New York, of which he was a graduate and where he was tutor in natural history from 1886 to 1890; and in many other directions of public service. But to our Metropolitan Museum the loss is irreparable in the fullest sense of that word.

He volunteered to be honorary curator of arms and armor without salary in 1906. His offer of service was gladly accepted. Later on, in the year 1912, he was persuaded to become curator of this department on a regular salary. He continued in this position until the close of the year 1927, when he resigned. But his connection with the Museum was made even more intimate and honorable by his immediate election as one of its trustees.

He was, in fact, the founder of its now notable collection of arms and armor. True, the Museum had a small collection of this kind before he entered its service, but under his management and inspiration it has now become by far the most important collection of arms and armor in America and vies in importance with the greatest collections of Europe. It was his ambition to make it fourth among the armor collections of the world and he has gone far to realize that ambition. It was largely due to his influence that William H. Riggs and Jean Jacques Reubell gave to the Museum the important collections that bear their names. There was not a nook or corner of Europe or Asia which escaped his search for additions to his department. Farthest Japan was as familiar to him as nearer France, Germany, and England. He seems to have known the location of every potentially purchasable piece of armor in existence and he never forgot it. He was indefatigable in pursuit. He never lost the trail. After years of effort he usually succeeded in obtaining the desired object, sometimes by purchase and not infrequently by gift. His recommendations to purchase were invariably approved. If the Museum itself did not have the needed money, he would persuade some of his friends to supply it. He was a generous donor himself, far beyond the amount of his salary. The Museum's collection of armor is really his monument.

Nor was his knowledge of arms and armor of merely historical interest. It was put to use during the Great War when he was called upon by the War Department to design the protective helmet for the American army, for which service he, as well as the Museum, received the special thanks of the Secretary of War.

He was a prolific writer about subjects on which he was an authority. His contributions to our Museum Bulletin were notable. It is a satisfaction to know that one of his most important works, a bibliography of arms and armor, was practically completed before his death and is among the publications soon to be issued by the Museum. A bibliography in three volumes on books and papers dealing with fishes, which he undertook with Dr. C. R. Eastman and Dr. E. W. Gudger of the American Museum of Natural History, was published a few years ago. It was in recognition of this work that the National Academy of Science awarded to him in 1923 the Daniel Giraud Elliot Medal, for outstanding work in zoology.

He was Chevalier of the Legion of Honor and had many recognitions of service both at home and abroad. He was eminently human. He had a rare capacity for friendship. His knowledge was always at the service of every person he could aid, and these were many.

His widow and the surviving members of his family have our warmest sympathy in our common bereavement.
December 17, 1928.

Resolution of the Board of Trustees of the Museum of the City of New York

Resolved that this Board desires to record its distress at the loss of their valued associate, Professor Bashford Dean, recently deceased, whose keen interest in the Museum, valued advice and continued labors in its behalf have been most valuable.

Further resolved that the Secretary be and hereby is requested to write to Professor Dean's widow expressing the foregoing sentiments in behalf of the Board and extending to her the sympathy of each and every Trustee.
January 10, 1929.

Resolution Adopted by the Board of Trustees of the Cleveland, Ohio, Museum of Art

The trustees of the Cleveland Museum of Art wish to record their sense of great loss in the death of Bashford Dean, which removes the outstanding international authority on the subject of arms and armor.

Dr. Dean had a rare capacity for friendliness, and his great knowledge was always at the service of those he could aid. This Museum is greatly in his debt for expert advice and assistance in securing its important collection, and records its appreciation of his many kindly and invaluable services.

To Mrs. Dean, and to the Metropolitan Museum of Art, the Trustees wish to express their sorrow at the loss of a wise adviser and a charming friend, and to offer to Mrs. Dean their profound sympathy in her bereavement.
December 24, 1928.

Memorial Certificate of the Military Order of the World War

Whereas, Almighty God has, in his inscrutable wisdom, seen fit to remove from our companionship and intercourse our esteemed friend and fellow-officer

MAJOR BASHFORD DEAN

whose qualities as a man and as a soldier have endeared him to us; therefore be it

Resolved, that the heartfelt sympathy, of the New York Chapter be extended to his family and friends at this time of trial and bereavement; and be it further

Resolved, that a copy of these resolutions be sent to the family of our comrade and friend; that they be inscribed in the Minutes of the Chapter, and that they be published in the National Bulletin of the Order.
January 29, 1929.

APPENDIX C

RESEARCH AND MEMORIAL ROOMS AND EXHIBITS DEDICATED TO BASHFORD DEAN

At The American Museum of Natural History

In 1925 upon the recommendation of Dr. Dean, the Trustees of the American Museum of Natural History appointed one of his old students, Dr. William K. Gregory, to be Curator of the Department of Ichthyology. Mr. J. T. Nichols (now Curator of Recent Fishes) continued his research work as Associate

PLATE VII

PLATE VII.

Memorial portrait tablet in the American Museum of Natural History dedicated June 10, 1929.


BASHFORD DEAN
1867 — 1928
JOHN W. HOPE SC
1929
FIRST CURATOR OF THE
DEPARTMENT OF FISHES

Curator and Dr. E. W. Gudger was appointed Bibliographer and Associate. With the approval of the administration the Department of Ichthyology decided to continue the Bashford Dean Bibliography of Fishes and to bring out supplementary sections from time to time. Dr. Dean left his invaluable library of ichthyology on deposit in the department and in his will he bequeathed it to the Museum, together with a fund for its maintenance. In 1925, with the approval of the President and Trustees, Dr. Dean's former office in the Department of Ichthyology was formally designated "The Bashford Dean Research Room in Ichthyology" and his library was installed there, as well as the card catalogue of the Bibliography of Fishes. The room is also used for research work in ichthyology by visiting scientists, while various memorabilia of Bashford Dean are also preserved there.

During the years 1925 to 1928 the exhibits of recent fishes, which had been prepared under the curatorship of Dr. Dean, were made the nucleus of a new and greatly expanded exhibit which was installed in the new hall, the basic plans for which Dr. Dean had prepared. On the evening of December 5, 1928, on the occasion of the opening of this hall, the Trustees tendered a reception to Dr. and Mrs. Dean. Unfortunately they could not be present in person on account of his illness, the seriousness of which was not yet realized, but they were represented by his sister, Miss Harriet M. Dean, and by Mr. and Mrs. Alexander McMillan Welch. Here in this exhibit the Museum visitor may learn of the science of ichthyology in general and of many of its special problems in embryology, etc., to the solution of which Dean made signal contributions.

During the first half of the year 1929 the Department of Ichthyology devoted itself to the further development of the exhibit of fossil fishes, which had been installed under the direction of Drs. Dean and Hussakof. Special efforts were made to make this exhibit still more useful to graduate classes and to introduce new features of interest to the public. On June 10, 1929, this exhibit, now named "The Bashford Dean Memorial Exhibit of Fossil Fishes," was eloquently opened by President Henry Fairfield Osborn in the presence of Mrs. Dean, Miss Harriet Dean, other members of the family, and many friends. Mr. Nichols spoke of Dr. Dean's great work in bringing together and preparing for exhibition the collection of fossil fishes, and of Dr. Gregory's studies which are carrying forward this line of Dr. Dean's work. Dr. Gudger next presented the Bibliography of Fishes as one of Dr. Dean's great monuments, and told how the continuation card catalogue is keeping this going.

Miss Francesca La Monte, Assistant Curator of Fishes, then unveiled two bronze memorial bas-relief tablets. One of these is of Professor J. S. Newberry, Doctor Dean's preceptor in palaeichthyology, whose collection forms part of the exhibit. The other, of Dr. Dean, by John W. Hope, is shown in the accompanying plate.

AT THE METROPOLITAN MUSEUM OF ART

The President and Trustees of the Metropolitan Museum of Art in 1929 unanimously determined to make one of the galleries of its armor collection a memorial to Bashford Dean and to exhibit therein the most important part of his notable collection of armor. For this hall, the eminent sculptor, Daniel Chester French, designed and presented a bronze tablet commemorating Dr. Dean's services to the Museum.

The opening of the Bashford Dean Memorial Gallery took place on April 14, 1930, with a private view for the members of the family of Dr. Dean and their friends, and for the Trustees and Members of the Museum. Mr. Clarence H. Mackay, representing the Trustees made a brief but eloquent address:

> I count it a privilege to speak here today in honor of the man to whose memory this hall is dedicated—Bashford Dean. We were good friends and I came to know in him a sterling character. That character had as its cornerstone one virtue which it is especially appropriate for us to remember amid the arms and armor he collected, and that was his insistence upon the truth, upon exact knowledge, only reached after the most painstaking research. This same arduous research and exhaustive study and devotion to his subject were the result of his early scientific training in the field of biology in which, subsequently, he became an authority. As a master craftsman and

student of metallurgy he enjoyed a world-wide reputation. The subject that he made his lifelong passion is highly technical; the secrets of the old armorers, the construction of their suits and weapons, beautiful in line, contour, and ornament, vibrant and strong; the characteristics of one master or another in the various centuries— the knowledge of all these can be acquired only through constant and indefatigable study. In such study, Bashford Dean never spared himself. He knew intimately all the great collections in the world. He knew the literature of the subject, its historical and sentimental value. His watchword was 'thoroughness' and his ideals high; in his ambition to make the armor collection of the Metropolitan take its place among the greatest in the world he never flagged. Within the relatively short space of twenty-five years the Department of Arms and Armor at the Metropolitan Museum rose from practical obscurity to a position of first rank. The reason for this remarkable achievement was that the collection in this Museum was brought together by a master armorer. With his scholarship, his taste, his historical knowledge, and his fine, subtle instinct, he had a rare gift of discovery. No journey was too long for him; he roamed the world in search of objects which ultimately found a place in that institution which he loved so well and to which he gave the best years of his life—The Metropolitan Museum of Art.

As it has been my good fortune to have been closely associated during the past year with the Department of Arms and Armor in this Museum, I have marveled more and more at the stupendous task that Dean had set himself, not only as regards the seeking out and purchasing of objects but the installation of them and the administration of his department, to which he brought that extraordinary quality known as enthusiasm which overcame all obstacles. We remember him with admiration and affection; remember him as a great and devoted public servant; and it is because the Trustees hope that the public which he served will so remember him that this memorial has been established. A large part of it was bequeathed to us by Bashford Dean himself; another part was purchased by the Museum; some of the objects were graciously presented by Mrs. Bashford Dean, Miss Harriet M. Dean, Mr. and Mrs. Alexander McMillan Welch, Mrs. Helen Fahnestock Hubbard, Mr. Edward S. Harkness and Mr. and Mrs. Robert W. de Forest; everything in it passed through his hands, bears the impalpable stamp of his approval of its authenticity, its historical interest, its artistic value and craftsmanship, and its usefulness to the student. It is as though Dean spoke to us through his beloved treasures, by which we are surrounded today. Those silent figures, reminiscent of bygone ages when knighthood was in flower, live on as symbols of the genius of Bashford Dean.

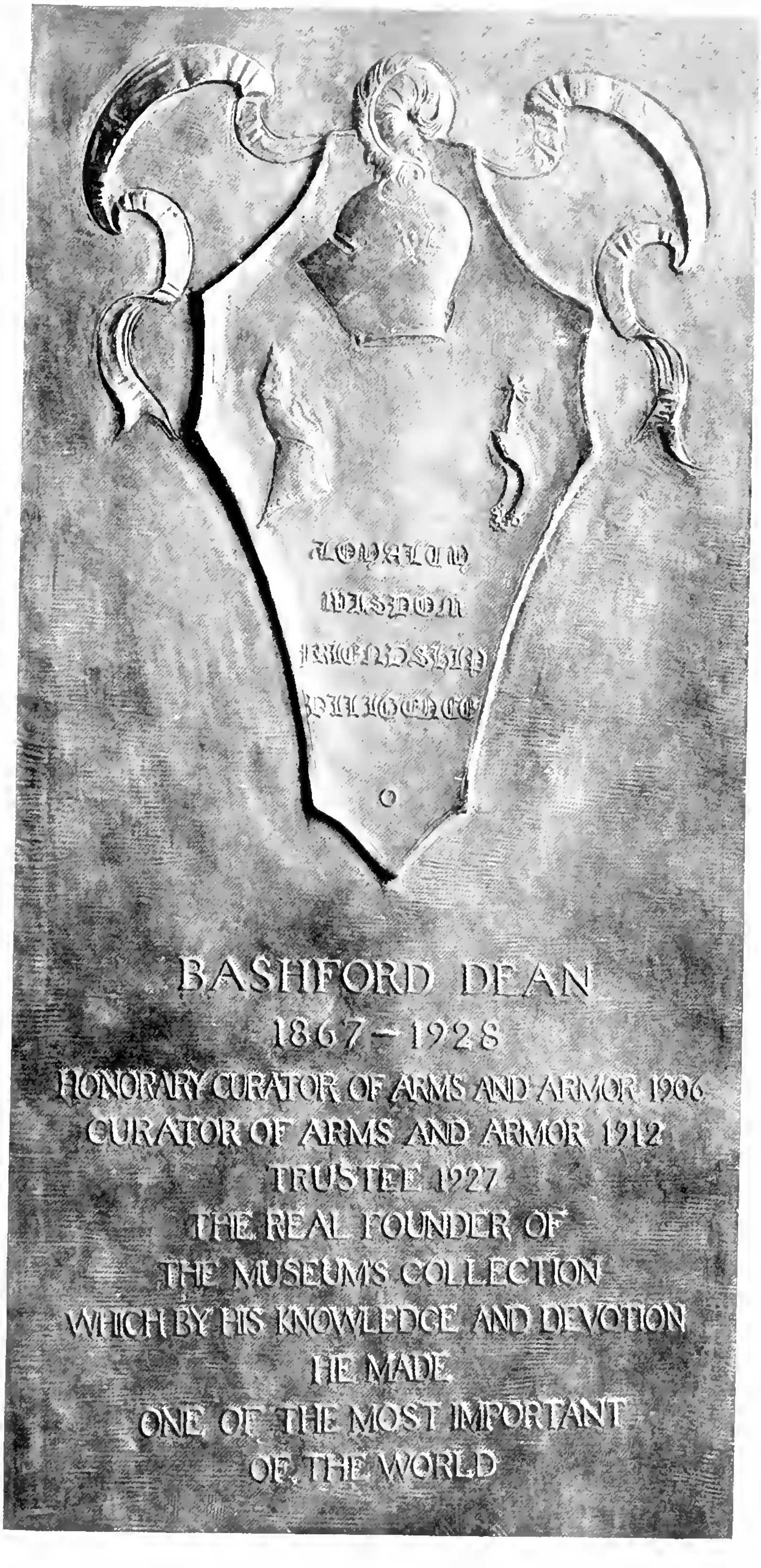
Miss Anita Reinhard, Assistant Curator of Arms and Armor, then unveiled the symbolic tablet which is shown on the adjoining plate. On this tablet are found a helmet with a crest, a gauntlet, and a spur. The symbolism of these parts of a knight's armor is as follows: the spur, with which he incites his horse to action, is the symbol of Diligence; the gauntlet is the symbol of Friendship, since in the western world in all ages, striking hands has signalized friendship; the helmet is the symbol of Wisdom, since it crowns the head, in which is housed the brain, the seat of knowledge; and lastly the helmet is surmounted by the crest which symbolized Loyalty. It has been well said that one who commands should have insignia by which he might be recognized. This was particularly true in those days when men went forth concealed in armor, and no place could have been more suitable than the top of the helmet. Hence the leader wore a plume, or a crest of some kind, so that his loyal followers might be able to rally around him.

These were the ideas that guided the sculptor of this tablet, because the qualities symbolized by these insignia and inscribed on this tablet are qualities possessed in a preeminent degree by Bashford Dean.

PLATE VIII

PLATE VIII.

Armorial tablet in the Metropolitan Museum of Art unveiled on April 14, 1930.



LOYALTY
WISDOM
FRIENDSHIP
DILIGENCE

BASHFORD DEAN
1867—1928
HONORARY CURATOR OF ARMS AND ARMOR 1906
CURATOR OF ARMS AND ARMOR 1912
TRUSTEE 1927
THE REAL FOUNDER OF
THE MUSEUM'S COLLECTION
WHICH BY HIS KNOWLEDGE AND DEVOTION
HE MADE
ONE OF THE MOST IMPORTANT
OF THE WORLD

THE
BASHFORD DEAN MEMORIAL VOLUME
ARCHAIC FISHES

Edited By
EUGENE WILLIS GUDGER

ARTICLE II

THE SEGMENTATION OF THE EGG OF THE MYXINOID, *BDELLOSTOMA STOUTI*, BASED ON THE DRAWINGS OF THE LATE BASHFORD DEAN

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NEW YORK

PUBLISHED BY ORDER OF THE TRUSTEES

Issued May 7, 1931

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CONTENTS

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INTRODUCTION

The late Bashford Dean, formerly curator of fishes in the American Museum, published in 1899 an extensive memoir[1] on the external development of this member of the family Myxinidae from material secured in Monterey Bay, California, in August and September, 1896. In this he dealt very briefly with the segmentation of the egg, this section of his paper covering two and a half pages with only five text-figures (four of which are herein reproduced as Text-figures 4, 5, 6, and 7) as illustrations. Of his material he says:—"An . . . examination . . . has afforded an almost complete series of segmentation stages which will enable a detailed consideration of the earliest developmental features. In the present paper the following preliminary account may be given—illustrated by several text-figures . . . drawn from reconstructions in wax of serial sections." This short section was plainly intended as merely preliminary to a fuller description and discussion of the subject. This is confirmed by his further statement that:—"In these [text-figures made from wax reproductions and reproduced later herein], accordingly, the marginal limits of the germinal area [of these meroblastic eggs] are not so softly shaded as they would appear from direct surface drawings of the segmenting eggs. The lines of cleavage are also somewhat sharper than in the surface drawings of the segmenting eggs which I have in part prepared for lithographic reproduction." From this it is clear that Dean from his fairly abundant material intended to write a paper based on careful and detailed study of the segmentation of the egg of *Bdellostoma* fully illustrated by figures from his own hand. It is these drawings which are now under consideration.

Doctor Dean's *Bdellostoma* materials, other than slides and alcoholic specimens, consist of a portfolio of miscellaneous drawings labelled "Bdellostoma 1896-1901," and of four notebooks labelled "Bdellostoma" but undated. In the portfolio we found four mounted plates of drawings containing thirty-four figures showing the blastoderms of eggs in process of segmentation. Of the thirty-four figures, some are duplicate drawings of the same egg or at any rate of the same stage of cleavage, and others are incomplete. From these thirty-four figures we have chosen the twenty-four which are most represen-

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[1] On the Embryology of *Bdellostoma stouti*. A General Account of Myxinoid Development from the Egg and Segmentation to Hatching. (*In* Festschrift zum siebensigsten Geburtstag von Carl von Kupffer. Jena, 1899, pp. 221-276, 12 pls., 25 text-figures.)

tative both of the typical and of the usual variational segmentations, and reproduce these as two plates. The notebooks contain various fragmentary notes made in America and Japan. Only one, however, contains any data on the cleavage stages, and this information is contained in two tables labelled "Segmentation Stages."

Since both notes and drawings of segmentation stages bear no labels other than those referred to above, our first task was to find out if these notes and drawings applied only to *Bdellostoma stouti* studied in America in 1896 and not to some other species which Dr. Dean might have studied during his visits to Japan in 1899-1900, and also 1905. Among the notes were the two tables already referred to in which the various stages were lettered to correspond with the letters (A, B, C, etc.) on the individual drawings. These figures we believe to have been made at Monterey Bay from fresh material, or later in New York from eggs fixed and preserved in alcohol. It is, however, possible that Dr. Dean took this *Bdellostoma* collection with him to Japan, whither he went in 1900 in further search of myxinoid material. At first we thought that some of these drawings might have been made in Japan, from eggs of another species of myxinoid collected there. However, we were subsequently convinced that this view is incorrect and our conclusions are based on the following evidence.

Dean did get a batch of eggs of the related form *Homea burgeri*, but he does not state that this material included embryos. However, he does state that all the other eggs of all the other myxinoids collected in Japan on this trip were taken from the body of the mother. From this and from the fact that fertilization in these fish is external it is clear that Dean obtained no myxinoid embryonic material whatever on this expedition. Therefore we feel entirely justified in declaring our belief that the drawings under consideration were made from the eggs of *Bdellostoma stouti* from Monterey Bay, and not from any other myxinoids, from Japan or elsewhere.

After Dean published the article on *Bdellostoma* noted above, his interests spread out into a number of more or less related fields—into a study of the chimaeras (collected on this same trip to Japan) and of the primitive sharks both fossil and recent. On this same expedition to Japan he obtained much priceless embryonic material from *Chlamydoselachus* and *Cestracion*. From these embryos he made many drawings which still remain unpublished. Then, too, after his return from Japan he was engaged in teaching embryology in the Department of Zoology in Columbia University and in curatorial work in the Department of Ichthyology and Herpetology in the American Museum of Natural History. Also he was laboring hard in pushing forward the foundational work which eventually produced the great three-volume "Bibliography of Fishes" (1916, 1917, 1923). Furthermore, another and heretofore secondary interest of his many-sided nature awoke—his enthusiastic love for and study of arms and armor. Indeed his interest in such received a great impetus while on this visit to Japan, and he brought back with him what is probably the finest collection of Japanese arms and armor to be found anywhere outside of the Land of the Rising Sun. Thus little by little he was lured away from fishes and more and more became immersed in the study of armor. This resulted, in 1910, in his being made curator of arms and armor in the Metropolitan Museum of Art. However, the American Museum was not ready to lose him entirely and he was made honorary curator of fishes—a post which he held until his death. Under the circumstances set forth he never found time to take up the projected further work on the segmentation of the egg of *Bdellostoma*.

The publication of Doctor Dean's exquisite drawings of the segmentation of the egg of *Bdellostoma stouti* has been undertaken by us, one his former pupil and both his longtime friends, that they may not be lost to science and that their publication may be a memorial to their maker. These figures, in storage for 30 years, had undergone some deterioration, in particular the board on which they were drawn had become stained and yellow with age. Their preparation for the lithographer was entrusted to Mr. W. H. Southwick, who has skilfully cut out the figures and has mounted them without any retouching in such a way as to bring out their artistic as well as their scientific value.

Since we could find no *Bdellostoma* eggs in cleavage stages that had not been sectioned, we at first thought that we could not do more than write a running text consisting of expanded captions for the various figures. But as we have studied the drawings and the few notes left by Dean, we have been able in a certain degree to describe the segmentation as if we had before us if not the living eggs at least preserved material. The results of our studies will now be set forth.

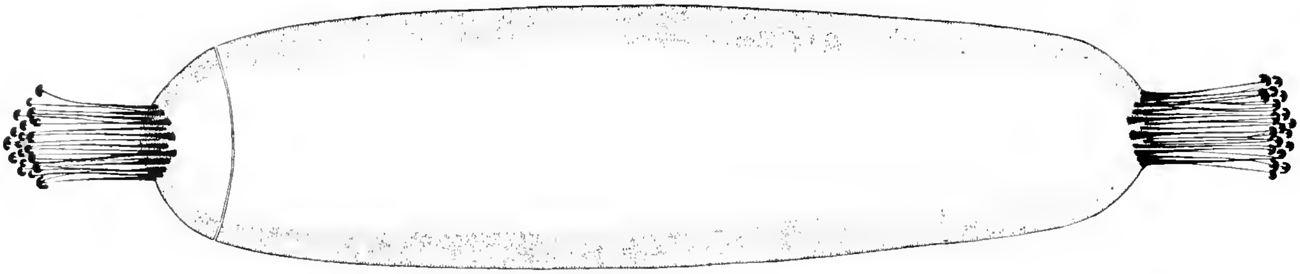
THE EGG

The structure of the unsegmented egg and of its membranes has been adequately described by Dean in his memoir cited in the introduction, and our information on this subject has been gained from his paper as well as from an examination of entire eggs and a few serial sections of eggs found in Dean's collection. In his 1899 memoir he says:—

> "The egg of *Bdellostoma* . . . is bean- or sausage-shaped, measuring about 22 mm. in length and about 8 mm. in width. Its color is Indian-yellow. It is encased in a horn-like shell, which is thinnest at the midcircumference of the egg and thickest at the ends, a membrane as transparent as common tracing paper. One end of the egg is slightly larger than the other, is pierced by a single polar micropyle and is circumscribed by an opercular groove, which enables the terminal portion of the shell to be thrown off like a cap at the time of hatching. . . . The eggs taken on a spawning ground are in nearly every instance fastened together in clusters or bunches [by the anchor filaments shown in our text-figures 1, 2, and 3 herein].

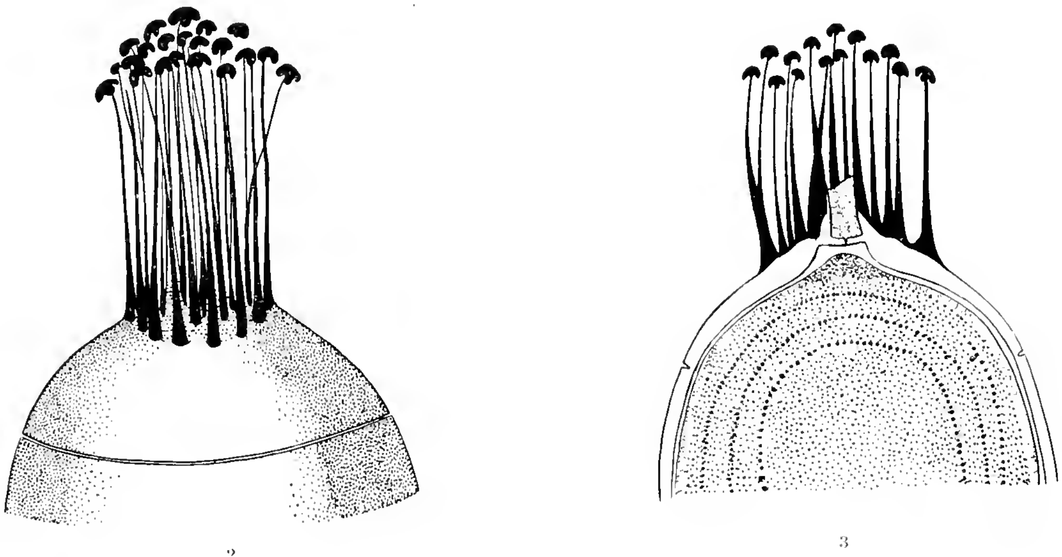
Specifically Dean notes a considerable variation in the size of the egg: "The egg-length varies . . . between 14.3 and 29 mm. The average of 70 eggs was 22.8, of which number 50 measured between 21 and 24 mm."

The egg of *Bdellostoma* possesses a definite polarity, which has already been indicated by the shape of the egg as a whole, by the presence of the opercular cap, and by the micropyle in the center of the cluster of anchor filaments at the animal pole. The outer egg membrane or shell, it is interesting to note, is produced by the ovarian follicle and not by an oviduct as in the case of many other vertebrates. The recess just above the micropyle,



Text-figure 1. Entire egg of *Bdellostoma stouti* including the capsule and anchor filaments. The operculum is delimited by a circular groove situated a short distance below the animal pole.

After Dean, 1899.



Text-figure 2. This drawing of a portion of an egg of *Bdellostoma stouti* illustrates in greater detail the structure of the anchor filaments and the opercular groove shown in text-figure 1.

After Dean, 1899.

Text-figure 3. Median longitudinal section through the animal pole of an egg of *Bdellostoma stouti*. The opercular cap, a part of the egg-shell, is limited by the opercular groove. At the centre of the group of filaments is the minute micropylar canal having above it a plug of mucus and below it the germinal hillock. This latter is continuous with the protoplasmic mantle enveloping the yolk which is arranged in concentric layers.

After Dean, 1899.

in the center of this group of filaments, is occupied by a plug of material which Dean says "may represent the granulosa, although I believe that there are grounds for regarding this mass of tissue in eggs long deposited, as in part or even entirely derived from the mucous elements in which the eggs have been embedded." All these structures are made clear in Text-figures 1, 2, and 3. One of the sections examined by us shows the micropyle very clearly, and is probably the identical section from which Text-figure 3 was drawn.

The egg proper is composed mainly of its great mass of yolk, but at the surface there is a practically yolkless layer of germinal substance thickened at the operculate end (the animal pole) and traceable in sections to the vegetal pole. In eggs recently deposited, the germinative protoplasm is collected into a definite hillock lying immediately below the micropylar canal, as is shown in Text-figure 3. This uplifting of the germ is rendered possible by the dome-shaped outpocketing in the egg-membrane. Although the germinal region is thus somewhat segregated from the yolk, there is no sharp line of demarcation between cytoplasm and yolk. The germinal hillock contains the egg nucleus.

CLEAVAGE

Since the male possesses no copulatory organs, fertilization must be presumed to be external. We cannot go into the much discussed question of hermaphroditism in *Bdellostoma*. Suffice it to say that internal impregnation has never been alleged for it. Fertilization then probably takes place at the time of spawning or immediately thereafter. Dean notes that the micropylar canal is so small that only one spermatozoon can enter at a time, hence he thinks that monospermy is invariable.

Of the early development of this myxinoid, Dean wrote in his 1899 memoir as follows:—

> The large egg of *Bdellostoma* gives . . . evidence of a partial discoidal cleavage. . . . Fertilization takes place within the protoplasmic cap, which lies immediately below the micropylar funnel. In this cap occur also the early stages of segmentation. During later divisions, the cell cap increases in size and its margins extend downward around the [animal] end of the egg. At a late stage of the blastula the cell cap occupies the entire operculate end. . . .
>
> At the animal pole the germinal area is distinctly lighter in color. . . . Its uppermost point, a minute hillock which projects toward the micropylar funnel, is the germinal cap in which the earlier cleavages appear. The cell cap [in the blastula stage] . . . extends downward to nearly the limits of the operculum.
>
> It can be said, in summary, that segmentation first appears within the protoplasmic cap, that it later extends into the yolk-filled subgerminal zone, that yolk nuclei are then present and that the cellular mass becomes asymmetrical as it encroaches upon and surrounds the yolk region.

In the collection of *Bdellostoma* material left by Dean, all the eggs in segmentation stages have been sectioned; but owing, no doubt, to long preservation of the eggs in alcohol before the sectioning was done, these sections do not show details of cytological structure. Our description of the cleavage is therefore confined to surface features as revealed by Dean's drawings of the fresh or recently preserved eggs.

FIRST CLEAVAGE STAGE

The germinal hillock previously referred to (Text-figure 3) is now shown in lateral surface view in Plate I, figure 1, drawn with the shell removed. It is a nipple-shaped cone of densely aggregated protoplasm with the sides sloping gently at the base and is continuous with a pellicle of cytoplasm surrounding the remainder of the egg. This structure is the protoplasmic cap previously referred to as found at the animal pole of the elliptical egg. The first cleavage furrow is vertical. It appears on top of the hillock and according to Dean lies in the plane of the micropylar canal. In Plate I, figure 1, the plane of first cleavage is somewhat oblique to the observer, the egg being rotated slightly to the left.

The first cleavage furrow is further shown in polar view in Plate I, figures 2 and 3. In these drawings the region traversed by the first cleavage furrow is the summit of the germinal hillock shown in Plate I, figure 1, whose gently sloping base is here represented by the more softly shaded area which appears like a halo in the background. Plate I, figure 2, apparently shows the first cleavage furrow in an early stage of development while Plate I, figure 3, represents the same cleavage furrow in a later stage. We deduce this from our observations of other vertebrate eggs studied in the living condition, in which the first cleavage furrow is in the beginning broad in the region of the animal pole but later becomes constricted in this region but broad and shallow at the ends. As shown in the figures, this cleavage plane does not extend marginally to the base of the hillock. These conclusions drawn from the figures and based on the study of other and living eggs, are definitely confirmed by Dean who writes "In a stage of late first cleavage which my material has afforded the blastomeres are drawn closely together at the sides of the cleavage plane [furrow?]; but even here this has not extended quite to the rim of the germinal cap."

SECOND CLEAVAGE STAGE

The second plane of cleavage is also vertical and is approximately at right angles to the first. The resulting blastomeres are of nearly equal size. In Plate I, figure 4, showing the polar hillock in lateral view, is portrayed an early phase of the four-celled stage. Figure 5 on this plate shows a polar view of an egg in practically the same stage. Plate I, figure 6, gives a polar view of an egg in a slightly later four-celled stage, in which the furrows are broad at their outer extremities but slightly constricted in mid-course. At the center of the germinal hillock there is a slight depression.

Figure 7, plate I, is a lateral view of a late phase of second cleavage in which the furrows are broad and shallow at their outer and lower extremities and the inner angles of the blastomeres have withdrawn slightly from contact with one another. By comparison with Figure 1, plate I, we note that in the second cleavage stage the germinal hillock is no longer nipple-shaped but is now dome-shaped. Figure 8 is a polar view of the same stage of cleavage as that protrayed in Figure 7, and according to Dean's notes is drawn from the same egg. Here is shown the same widening at the outer ends of the furrows and the same retraction of the blastomeres where the planes of cleavage cross leaving a pit which presumably leads into the beginning of a segmentation cavity. In Figure 9 the distinctive features already noted in Figure 8 are still more marked. Here the most striking characteristic is the rounding up of the individual blastomeres resulting in the appearance of constriction from the underlying protoplasm and also in the formation of an unusually large segmentation cavity.

Thus far we have been dealing with eggs in which the cleavage pattern is very regular. However, beginning with the second cleavage stage irregularities occur as shown in figures now to be considered. The slightest irregularity which Dean portrays is that shown in Figure 10, where the cleavage furrows are sinuous in the region of intersection. At the intersection is a slight depression of the surface of the germinal hillock.

The irregularity of the cleavage pattern in the eggs represented in Figures 11 and 12 is in our opinion the result of the failure of the second cleavage furrows to meet each other where they join the first. In their initial formation they evidently met the first furrow at right angles but a shifting of furrows occurred to enable the blastomeres to assume a more compact form. This interpretation is based on the study of the living eggs of other vertebrates as well as on the examination of these figures.

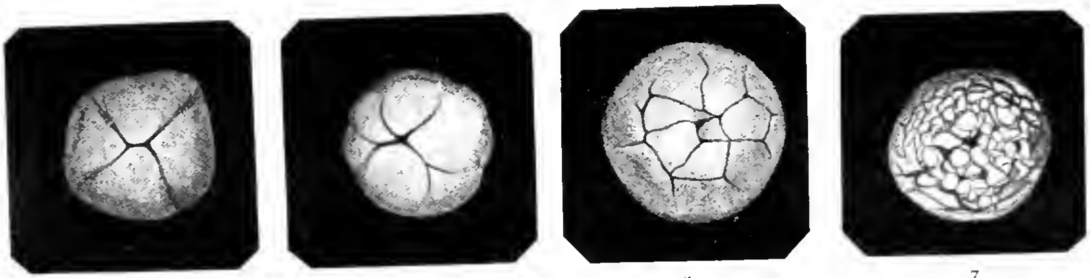
That such a slightly irregular cleavage pattern is not uncommon in the egg of *Bdellostoma* is evidenced by the fact that we have another example in Text-figure 4 reproduced from Dean's drawing of a wax-plate reconstruction from sections of another egg. This figure practically duplicates numbers 11 and 12 of Plate I.

THIRD CLEAVAGE STAGE

The third cleavage furrows are usually vertical and at right angles to one of the preceding furrows, ordinarily the second. In Plate II, figure 13, is shown in lateral view the beginning of the third division which will result in the formation of eight blastomeres. The third furrows on the side of the egg next the observer are plainly shown but the corresponding ones on the further side are not visible. Figure 14 on the same plate shows in polar view an egg in the same stage of cleavage. This drawing was possibly made from the same egg as Figure 13 of plate II, since on the side of the figures toward the observer the furrows are identical. The irregularities in the egg shown in Figure 14 are due to the fact that the third cleavage furrows shown in the upper part of the figure extend horizontally or circularly whereas the others are vertical. In the upper left hand part of this figure there is shown the beginning of a vertical cleavage furrow which probably belongs to the fourth generation.

Figure 15 on plate II shows a still more irregular cleavage pattern, which seems to us to be derived from an earlier condition of irregular cleavage such as is shown in Figures 11 and 12 of plate·I. In all three figures the first and second cleavage furrows meet to form obtuse angles, but we cannot certainly distinguish the second from the first. In Figure 15, plate II, we find cleavage furrows extending horizontally cutting off two complete micromeres near the center of the blastodisc; these furrows are presumably third and fourth cleavage furrows but they cannot be identified with certainty. The blastoderms shown in Figures 14 and 15 of plate II resemble each other in the general character of their cleavage patterns, and in the fact that each contains nine blastomeres.

Text-figure 5 shows an eight-celled stage reproduced from Dean's 1899 memoir. This figure was drawn from reconstructions of serial sections, and concerning it Dean says—"In three of the blastomeres of a preceding stage vertical cleavage has occurred, while in the fourth (that at the right of the figure) a nearly horizontal cleavage is demonstrated by sections." This blastodisc illustrates the general tendency for the third cleavage furrows to form vertically.



4 5 6 7

DEAN'S DRAWINGS (IN POLAR VIEW) OF WAX-PLATE RECONSTRUCTIONS FROM SERIAL SECTIONS OF BLASTODERMS OF *BDELLOSTOMA STOUTI*, REPRODUCED FROM HIS 1899 MEMOIR

Text-figure 4.	Second cleavage stage, slightly irregular.
Text-figure 5.	Third cleavage stage, somewhat irregular. Of the third cleavage furrows, two do not show in the figure.
Text-figure 6.	Early fourth cleavage, rather irregular.
Text-figure 7.	Late cleavage, micromeres somewhat unequal in size.

The germinal hillock shown in lateral view in Figure 16, plate II, has evidently reached a late third cleavage stage. So far as can be determined from this lateral view the cleavage pattern is somewhat irregular. In both Figures 13 and 16 of this plate it is plainly noticeable that the form of the germinal hillock is now that of a very much flattened dome. Study of all the figures drawn in lateral view reveals a process of reduction in the height of the hillock and a broadening of its base which presumably continues throughout the later segmentation stages. This elevation of the germinal region in the form of a conspicuous hillock, which only gradually flattens out, is one of the most unique features in the early development of *Bdellostoma*. Neither of us has ever encountered such a structure in any other animal egg.

The cleavage pattern portrayed in Figure 17, plate II, is more irregular than any yet studied—so much so that the cleavage furrows cannot be identified. There are four or possibly five micromeres completely outlined in the blastodisc. Two of these are exceedingly small, the others are about normal size. The side of the egg toward the observer appears to be more developed than the opposite side.

The conditions shown in Figure 18, plate II, are probably abnormal. We here find at least eight blastomeres of which only one is completely separated from its neighbors. The chief peculiarity, however, of the egg shown in this figure is the presence of a large open segmentation cavity. This may possibly be a development of the conditions shown in Figures 8 and 9, plate I; or it may be due to the death and disappearance of a central micromere. In this matter, we find in the brief notes appended to Dean's list of "Segmentation Stages" a reference to an egg as follows "seven c[ells], one central lost." This is the only figure we find approximating seven cells, and it is the only one in which we find a blastomere missing. Morever, Dean (1899 memoir) notes that occasionally a blastomere is torn away from a blastoderm in the process of removing the egg-shell.

FOURTH CLEAVAGE STAGE

Beginning with this stage we find in all the drawings left by Dean marked irregularities in the cleavage pattern. Of these drawings we have selected for description and publication those which seem to us most typical. The earliest of these, which shows the beginning of this stage, is seen in Figure 19, plate II. In this blastodisc some of the fourth cleavage furrows are horizontal or circular, cutting off five irregularly shaped micromeres of unequal size; the remaining fourth cleavage furrows are vertical. It is notable that the radiating furrows have not extended very far from the center of the germinal hillock. This retardation we interpret as due to the fact that the outlying protoplasm of the blastodisc is considerably laden with yolk.

Similar in the stage of its development to the blastoderm just described is the one shown in Text-figure 6 drawn from a reconstruction of a sectioned blastodisc and published by Dean in his 1899 memoir. This blastoderm consists of four micromeres of moderate and nearly equal size, of two very small ones, and of nine macromeres partially separated from each other. Such a cleavage pattern might readily arise by further development of such a blastodisc as that portrayed in Figure 15, plate II. It is evident that some, at least, of the fourth cleavage planes are circularly arranged.

The drawing that seems to us to show the greatest regularity in the fourth cleavage furrows is the one reproduced as Figure 20 of plate II. The entire group of 14 micromeres is cut off from the surrounding and underlying macromeres by circular or horizontal furrows which belong presumably to the fourth generation. Within this mass of micromeres some divisions have occurred by means of the fifth cleavage furrows which are variously circular, diagonal, or vertical. It is noticeable that the micromeres vary considerably in size, and that development is excentric since the micromeres extend farther from the animal pole on one side of the germinal hillock.

FIFTH CLEAVAGE STAGE

This stage might be expected to have sixteen micromeres. We find drawings of two eggs which we determine as approximately of this stage. The first of these is reproduced as Figure 21, plate II. Here are shown twelve micromeres surrounded by about as many macromeres incompletely separated from each other.

The next figure (Number 22), apparently drawn under a greater magnification, has a larger number of micromeres—eighteen or nineteen—supported by apparently only twelve macromeres. In the upper right region of the micromeres are two rather unusually large intercellular spaces presumably opening into the segmentation cavity. It is interesting to note that in each egg there are at least twelve vertical furrows separating the macromeres, a close approach to sixteen, the theoretical number if the segmentation were complete and regular.

LATER CLEAVAGE STAGES

Of eggs in later stages we find only two drawings, here reproduced as Figures 23 and 24, plate II. In the stages represented in these figures, the discoidal character of the cleavage is more clearly apparent.

In Figure 23 the smaller micromeres are aggregated at the center of the blastoderm. On the left side of this the blastomeres are larger and are also fewer than on the right side and among them are what appear to be unusually large micromeres, possibly unsegmented regions of the outer edge of the blastodisc, or possibly projecting macromeres in which segmentation for some unknown cause has been delayed. In the surrounding and supporting mass of protoplasm, only two or three cleavage furrows are visible in the drawing.

The other egg, shown in Figure 24, differs from the preceding in that large and small micromeres are mingled indiscriminately but there are lacking the unusually large cells and the peninsula-like projections noted in the former. Further, almost the entire surface of the blastodisc visible in polar view is segmented—i.e., there is, unlike the condition in the preceding drawing, only a narrow surrounding rim of partially segmented protoplasm visible.

The conditions in the marginal partially segmented portions of both these blastodiscs agree with what Dean found in sections of a stage approximately corresponding to them. Of it he writes: "No traces of cleavage could be found on the yolk region of the egg, the entire series of the larger marginal blastomeres being but faintly indicated." His figure of the blastoderm, reconstructed from sections of the stage just referred to, is reproduced herein as Text-figure 7. This bears a marked resemblance to our latest stage shown in Figure 24, plate II.

Inspection of Dean's figures in his 1899 memoir discloses the fact that, during the latest segmentation leading up to the gastrula stage, the blastoderm overgrows the whole animal end of the egg, extending excentrically on the side of the future blastopore a little beyond the opercular groove. It is our impression that these changes are accompanied by a complete obliteration of the germinal hillock, whose progressive flattening has been illustrated so far as there are drawings available. We are confirmed in this conclusion by Dean's figure of a gastrula (1899 memoir, p. 252) which shows not the least trace of such a hillock.

It is very obvious from an inspection of the plates that the drawings of the blastodiscs vary considerably in size. There is no record of the magnifications at which these drawings were made. Part, at least, of this discrepancy can be accounted for by the variations in the size of the eggs as previously noted, and there is, of course, a possibility that the drawings were not all made to the same scale.

SUMMARY

In the early history of the egg of *Bdellostoma stouti* we find four things especially worthy of note.

1. The egg is very large, varying in length from 14.3 to 29 mm., the average of 70 eggs being 22.8 mm. with a width of about 8 mm.
2. The egg is strongly telolecithal: i.e., most of the protoplasm is segregated into a disc at the animal pole but it extends as a thin mantle over the entire surface of the egg which is mainly composed of yolk.
3. The disc of protoplasm at the animal pole is upraised to form the germinal hillock, which at first is nipple-shaped, but through a gradual reduction in height and broadening of the base it becomes dome-shaped or helmet-shaped. Its later history is obscure but it probably flattens out to conform to the general contour of the egg since it is entirely absent at the time of gastrulation. We do not know of any other vertebrate egg having such a germinal hillock.
4. The mode of cleavage is discoidal but the marginal blastomeres are incompletely separated from each other and from the general protoplasmic mass by radial furrows. Early cleavage is limited to the germinal hillock but in later stages extends beyond its site.

PLATE I

SEGMENTATION OF THE EGG OF *BDELLOSTOMA STOUTI*

PLATE I

Fig. 1. Lateral view of germinal hillock showing first cleavage furrow.

Fig. 2. Polar view of first cleavage furrow, early stage.

Fig. 3. Polar view of later first cleavage with furrow broad and shallow at ends.

Fig. 4. Lateral view of germinal hillock in second cleavage. Note change in height and width compared with Fig. 1.

Fig. 5. Polar view of early four-celled stage.

Fig. 6. Polar view of later four-celled stage, showing depression at intersection of furrows and widenings at their outer ends.

Fig. 7. Lateral view of germinal hillock in late four-celled stage. Note the rounded dome-shape of the germinal hillock.

Fig. 8. Polar view of the same blastodisc in late four-celled stage. Note the large intercellular space at the intersection of the furrows.

Fig. 9. Polar view of unique four-celled blastodisc.

Fig. 10. Polar view of slightly irregular four-celled stage, showing depression at the intersection of furrows.

Fig. 11. Polar view of an egg in four-celled stage in which the second cleavage furrows do not meet.

Fig. 12. Polar view of a blastodisc in four-celled stage, showing the same variation in cleavage pattern as in the proceeding figure.

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SEGMENTATION OF EGG OF BDELLOSTOMA

PLATE II

SEGMENTATION OF THE EGG OF *BDELLOSTOMA STOUTI*

PLATE II

Fig. 13. Lateral view of germinal hillock in third cleavage stage.

Fig. 14. Polar view of blastodisc in third cleavage showing formation of micromeres.

Fig. 15. A blastodisc in approximately the same stage as the preceding.

Fig. 16. Lateral view of germinal hillock in late third cleavage. Note that the hillock is reduced in height and broadened at base. It is now helmet-shaped.

Fig. 17. Polar view of blastodisc showing irregular pattern of third cleavage.

Fig. 18. Blastodisc in third cleavage with central blastomere missing.

Fig. 19. Example of irregular fourth cleavage.

Fig. 20. Typical blastodisc showing completion of fourth cleavage and beginning of fifth. This figure is drawn either from an unusually large egg or in greater magnification than the others.

Fig. 21. Typical example of fifth cleavage.

Fig. 22. Blastodisc in late fifth or beginning sixth cleavage.

Fig. 23. Late segmentation showing retarded division (possibly abnormal) in the lower left segment of the blastoderm.

Fig. 24. Blastoderm in late cleavage showing intermingling of large and small micromeres.


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SEGMENTATION OF EGG OF BDELLOSTOMA

A. Hoen & Co. Lith.

THE
BASHFORD DEAN MEMORIAL VOLUME
ARCHAIC FISHES

Edited By
EUGENE WILLIS GUDGER

ARTICLE III

THE GENITAL SYSTEM OF THE MYXINOIDEA: A STUDY BASED ON NOTES AND DRAWINGS OF THESE ORGANS IN *BDELLOSTOMA* MADE BY BASHFORD DEAN

By J. LEROY CONEL
Professor of Anatomy
Boston University School of Medicine

NEW YORK
PUBLISHED BY ORDER OF THE TRUSTEES
Issued September 25, 1931

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THE GENITAL SYSTEM OF THE MYXINOIDEA: A STUDY BASED ON NOTES AND DRAWINGS OF THESE ORGANS IN *BDELLOSTOMA* MADE BY BASHFORD DEAN

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CONTENTS

THE GENITAL SYSTEM OF THE MYXINOIDEA: A STUDY BASED ON NOTES AND DRAWINGS OF THESE ORGANS IN *BDELLOSTOMA* MADE BY BASHFORD DEAN

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Professor of Anatomy
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INTRODUCTION

The Myxinoids, or slime eels, have been the subject of a considerable amount of inquiry and discussion by many investigators in Europe and America. The interest of investigators has been challenged by these eels because they are the lowest living vertebrates. Some of the earliest authors believed that the Myxinoids practice parasitic or semiparasitic habits of living on the bodies of fishes, therefore much controversy has arisen as to whether these animals are primitive or degenerate, and whether they should be classified as Gnathostomata or Agnathostomata. The excretory system has been characterized by some writers as a pronephros, by others as a pronephros in the early stages of development but later becoming transformed into a mesonephros except at the anterior end, and by others as a very small anterior pronephros and a posterior segmental mesonephros which develops in the usual manner. The homologies of the different parts of the brain, also, have been variously interpreted.

The genital system in particular has been extensively investigated, with considerable difference of opinion both as to facts and interpretation. Because of peculiarities in the structure of the genital organ, the Myxinoids were believed by some of the early investigators to be hermaphrodites, and this opinion continues to be incorporated in modern text-books. The egg and its membranes have received much attention, resulting in a variety of interpretations, and the time when the eggs are spawned has long been a matter of speculation.

For many years the assistance of embryology in solving these and other problems was denied because no one was able either to find the embryos developing in the natural environment or to obtain them by keeping the eels in captivity. Neither could paleontology contribute toward the elucidation of any of the many obscure problems, for until very recently no fossil of a myxinoid has been found with the single exception of *Palaeospondylus*, supposed by some to be a Devonian lamprey, but this is denied by Dr. Bashford Dean.

Many important contributions toward a solution of some of the problems regarding the Myxinoidea were made by Doctor Dean while he was Professor of Zoology in Columbia University. Many of the observations which he made during his investigations at that time, however, have never been published. Doctor Dean spent the summer and fall of 1896 in searching for the embryos of *Bdellostoma stouti* in Monterey Bay at Pacific Grove, California. He succeeded in collecting the first fairly complete series of myxinoid embryos that had ever been taken, and in 1899 he published an account of the development of *Bdellostoma stouti*, which was the first description of the general embryology of a myxinoid. During the time he was searching for embryos, he examined several thousand specimens of *Bdellostoma stouti*, and while engaged in a similar quest off the coast of Japan in 1900 1901, he examined many specimens of *Bdellostoma (Homea) burgeri*. Doctor Dean made many notes of his observations at the time he was catching the eels in California and Japan. Also, he made sixteen excellent drawings for the purpose of illustrating some of his observations on the growth of the genital system both male and female.

That Dean intended to write further regarding the genital system of *Bdellostoma* is evident from the fact that most of the notes and drawings which he left unpublished refer to this subject. On several occasions he expressed to me the desire to publish the results of his investigations; but his life was so full of urgent tasks that he could never find the time to do this.

Inasmuch as I have been associated with Doctor Dean during the past several years while working with his collection of *Bdellostoma* embryos, and have already published a paper on the urogenital system of the Myxinoidea, I have been asked to prepare his data on the genital system of *Bdellostoma* for publication in the Dean Memorial Volume. I am very happy, indeed, in having this privilege. It gives me special pleasure because I know that Doctor Dean earnestly desired to publish the results of his investigations, and by doing this for him I shall have the opportunity to indicate my appreciation for a very pleasant friendship with a man for whom I had the highest regard and respect.

This paper is based chiefly upon the notes and drawings which Dean made at the time he was examining the specimens of *Bdellostoma*. There are four notebooks labelled "Bdellostoma." One of these contains the rough draft of his paper on the embryology of *Bdellostoma* (1899); another contains written descriptions, sketches, and other information regarding the embryos which he collected. The other two notebooks, a smaller and a larger (marked IV) have furnished most of the information for the present paper, for in them Dean recorded his observations.

Here and there in this paper I have added the results of my own investigations. During the summer of 1930, from June 18th to August 28th, I caught and examined more than six thousand specimens of *Bdellostoma stouti* in Monterey Bay at Pacific Grove, California. The special purpose of this work was to collect embryos of *Bdellostoma*, and the results in this respect will be presented later. While catching the eels, however, I made the observations which will be referred to in the present paper.

For the opportunity of making my investigations, I gratefully acknowledge my indebtedness to the National Research Council, to the Bashford Dean Memorial Committee of the American Museum of Natural History, and to the Committee on the Permanent Science Fund of the American Academy of Arts and Sciences. I desire to express my gratitude to Professor W. K. Fisher, Director of the Hopkins Marine Station, for generously placing at my disposal the facilities of the Station, and to Professor G. E. MacGinitie for much assistance courteously and willingly given.

The data which Doctor Dean accumulated indicate that he was especially interested in the questions of hermaphroditism, time of spawning, and the descent and relationships of the Myxinoidea. These subjects in particular will be discussed; in each case the literature will be reviewed briefly in order to summarize for the reader the results of previous investigations, thereby enabling him to orient himself in the subject under consideration.

HERMAPHRODITISM IN THE MYXINOIDEA

Because the myxinoids have been so little understood, they have been more misrepresented and maligned than any other vertebrates. The earliest investigators classified them with the worms. Even after this error had been corrected, and the slime eels accorded a place with the vertebrates, complete enjoyment of their new position was denied them on account of their round, leech-like mouths, indicated by the word "Bdellostoma." The shape of the mouth coupled with the fact that the eels were often brought to the surface of the water with their heads, and even their entire bodies, buried in the flesh of fish caught on hooks or in traps, misled many investigators to believe that the myxinoids are parasites, and therefore are degenerate. I am convinced, however, that the myxinoids are not parasites. They do not attack free-living fishes, but only fishes caught on hooks just as other predatory fishes do. The eel feeds by rasping into the flesh of the large hooked fish and may bore its way into the body of this fish and eat everything but the skin and the bones, being found inside the remains of its prey when this is brought to the surface. Many students of the myxinoids have found that the eel does this to fishes on lines set over night or even left for a few hours where these eels are plentiful. However, the eel was not living as a parasite either on the outside or in the inside of its prey before this was hooked.

In spite of the fact that many observers have proved that the myxinoids are free-living bottom feeders and not parasites in any sense of the word, some authors continue to stigmatize them as being the only parasites among the vertebrates. Hence many writers are still discussing the pros and cons of this form of degeneracy in these lowest vertebrates. Furthermore another charge filed against the Myxinoidea of conduct unbecoming vertebrates is the alleged practice of the lowly method of reproduction hermaphroditism. The origin and development of this idea in the minds of certain investigators can best be presented by giving a resum´ of the literature.

REVIEW OF THE LITERATURE

The earliest recorded discussion of the structure of the reproductive organs in the myxinoid fishes was written by Johannes Müller in 1843. He briefly described the male and female genital systems in *Myxine glutinosa* and *Bdellostoma forsteri*, giving an account of the structure of the testis and ovary.

Evidently the reproduction of these eels later became a subject of lively interest, for in 1862 the Academy of Sciences of Copenhagen offered a prize for the discovery of the manner of reproduction and development of *Myxine glutinosa*. Though many investigators have tried, no one has ever been able to solve this problem in the case of *Myxine*. Dean, however, as has been stated above, succeeded in collecting the embryos of *Bdellostoma stouti* in sufficient numbers to work out the general development of this myxinoid.

HERMAPHRODITISM IN *MYXINE GLUTINOSA*

After J. Müller (1843), Steenstrup (1863) of Denmark wrote the next paper pertaining to the genital system of *Myxine glutinosa*. He described eggs of various sizes in the ovary, as well as a naturally deposited egg of *Myxine* which he found in a museum at Copenhagen. The label in the jar stated that the egg had been recovered from the stomach of a cod. In the one text-figure he illustrated the filaments, with their anchor-shaped hooks, at each end of the egg, and also represented the operculum in one egg.

W. Müller (1875) was the next writer upon this subject. He was of the opinion that "*Myxine* ist gleich *Amphioxus* getrennten Geschlects," and described the testis, as well as the ovary, as extending along the gut on the right side only, attached by a mesorchium and mesovarium, respectively, to the mesentery. The ovary could be identified by the eggs, the youngest of which were round, and the older ones ellipsoidal. He doubted if J. Muller really saw the testis. He found the males occurring much more rarely than the females, and somewhat smaller in size. According to him the testis has the same position as the ovary, and can be recognized as such at the first glance, forming a flat, gray, lobed mass along the free border of the mesorchium, and consisting of a large number of follicles. Müller found no spermatozoa in the testicular follicles. His figures, while not detailed, indicate that he undoubtedly saw the testis.

J. T. Cunningham, of Edinburgh, published (1886.1) the results of his extensive observations made upon numerous specimens of *Myxine glutinosa* which had been caught for him in the Firth of Forth. As one result of his investigations Cunningham concluded that *Myxine* is a protandric hermaphrodite. He thought that *Myxine glutinosa* while young is an immature male, then later becomes a mature male with small eggs in the anterior part of the sexual organ, i.e., a functional male hermaphrodite, and finally that the testis atrophies, the eggs become larger and the animal then is a female. The change from a mature male hermaphrodite to the female was thought to occur when the eel reached a body length of 32 or 33 centimeters. Cunningham (1886.2, p. 71) stated that in "nearly all specimens with very immature eggs the posterior portion of the sexual organ had the same structure as the testis," and that (p. 73) "in all specimens with well developed ovarian eggs . . . with one exception, no testicular portion was present in the sexual organs." Therefore, he decided that in the young state the females are nearly, but not quite always hermaphrodites, and that the testicular portion normally disappears as the eggs become more mature. It seemed to him probable that fertilization is normally effected by hermaphrodites, since true males are so rare.

In his paper of 1886.2 (p. 70), Cunningham wrote as follows:

> Among the hundreds of specimens which have passed through my hands I have only succeeded in identifying eight males, and these are all very immature. It is a matter of difficulty to recognize the immature testes in these young males, and some few young male specimens may have escaped my recognition, as the matter requires careful examination with the microscope.

He published figures of the testis after sectioning, and as they agree with illustrations shown by other authors, he was undoubtedly correct in his identification of the testis. He wrote further (1886.2, p. 71):—

> After identifying the male organ and investigating its structure, I was surprised to find that in nearly all specimens with very immature eggs the posterior portion of the sexual organ had the same structure as the testis. This testicular portion occupies about two inches of the posterior end of the sexual organ, and I have only found it in specimens in which the eggs were very small, that is, less than 4 mm. in length.

Cunningham illustrated sections of the posterior end of the sexual organ in these latter specimens, and they revealed the same follicular structure as the testes in the young males. In one of these specimens he found spermatozoa which he illustrated in his Fig. 14; but spermatozoa were not present in quantities which he thought sufficient for fertilization.

In February, Max Weber (1887.1) presented a paper before the Nederlandsche Dierkundige Vereeniging regarding the sexual organs of *Myxine glutinosa* in which he criticised Cunningham for not giving credit to W. Muller for his contributions upon this subject. Weber doubted the abundance of hermaphrodites claimed by Cunningham to be present among *Myxine* and the occurrence of active spermatozoa in the specimens examined by Cunningham. Weber made his investigations upon eels caught at Alvarströmmen, near Bergen, Norway.

In March, Cunningham (1887.1) replied to Weber, admitting that he had overlooked W. Müller's paper and the fact that the latter author had described the testis in *Myxine glutinosa*. He added (p. 243):

> But the discovery of hermaphroditism in *Myxine*, of the abundance of hermaphrodite individuals and the probability of nearly all females being hermaphrodite when young, was made by me; and the spermatozoa, with stages in their development were also described by me for the first time.

In a later paper, in June of the same year, Cunningham (1887.2) stated that any doubt regarding the abundance of hermaphrodites and the presence of living active spermatozoa in them could be dispelled by the examination of any dozen *Myxine* taken at random. Weber replied in May of the same year (1887.2), stating that his investigations were not sufficiently complete to justify taking a position either for or against the existence of hermaphroditism in *Myxine glutinosa*.

Nansen (1887) examined a "great many specimens" of *Myxine*, caught near Bergen, and observed that, "females only came under review, as I could not discover a single male in spite of diligent search." He was of the opinion that Cunningham did not see the real spermatozoa, but the abnormal product in this respect of an abnormal specimen. In 1886 Nansen (1887) visited Cunningham in Edinburgh, and examined the latter's specimens; at that time he thought they resembled spermatozoa, but he saw only a few follicles which had this appearance. Later, in his own specimens of *Myxine*, Nansen (1887) found spermatozoa in the greatest abundance, and then did "not know what to say about those found by Cunningham." Among several hundred specimens of *Myxine* examined by him, Nansen recognized only very few males, and even these were unripe. In quite early stages he found little difference between testes and ovaries. He generally found that large specimens were females with well developed eggs; but in eels of about twenty-eight to thirty-two centimeters in length the sexual organ anteriorly was but slightly prominent and contained very many young ova, while the posterior portion was often very broad and prominent, and had the appearance and structure of a testis. Upon teasing this tissue in the fresh condition, Nansen found an abundance of spermatozoa in various stages of development, and illustrated some of them in his Fig. 4. The spermatozoa were more evident in the tissue after it was sectioned and stained. He concluded that, "those young specimens (28–32 cm. in length) are, consequently, hermaphrodites, with quite immature ovaries, but well developed testes: and they must be able to perform male functions."

Nansen observed that in the large specimens of slime eels, which generally contained a number of large and well developed ova, there were no reproductive elements, neither ova nor testes, in the posterior portion of the generative organ, which here was very narrow. Eels in size between that of the large females and that of the hermaphrodites possessed sexual organs which were prominent in the anterior portion and contained oblong young ova, whilst in the posterior portion they were of testicular nature and not very prominent. These eels were, consequently, in a transition stage between the hermaphrodite male and the female condition. "Indeed," wrote Nansen, "on examining a sufficient number of specimens, we will easily be able to find every transition stage from hermaphrodite males to fully developed females: and the rule seems to be that the larger the specimen is, the more are the female organs developed, and the more do the male organs disappear." He concludes then, "that *Myxine* is generally, or always (?), in its young state, a male; whilst at a more advanced age it becomes transformed into a female. Indeed, I have not yet found a single female that did not show traces of the early male stage." Nansen found eels in which testicular follicles occurred along the free margin of the whole reproductive organ (especially developed in the posterior portion, 6.7 cm. in length); while in its anterior portion (7.4 cm. in length) young ova were present in the mesorchium proximal to the testicular follicles, or mixed with the latter. He believed that the few true males which he found were really transformed hermaphrodites, since he could identify all the transitional stages between true males and hermaphrodites. Nansen ends his discussion of hermaphroditism with these words:

> Upon the whole, it must be admitted that there is a strange irregularity in the occurrence and extension of the male and female organs in *Myxine*. *Myxine* seems to me to be an animal which, in sexual respects, is just at present in a transition-stage; from what and to what, it is however not easy to say. It seems still to be seeking, without yet reaching, that mode of reproduction which is most profitable for it in the struggle for existence.

A few years later Cunningham (1891) published the results of further investigations upon spermatogenesis in *Myxine*. For the purpose of making this study he spent several weeks at Alvarströmmen, Norway, and was supplied with eels caught in traps. He wrote as follows (p. 170):

> In the morning the specimens caught were brought to me. The number varied from about fifty to ninety, and out of these I found rarely more than two or three in the required condition. . . . All the testicular elements which I am about to describe were obtained from hermaphrodite specimens, individuals in which the whole of the generative organ is male being exceedingly rare. The numerous specimens of the animal which I examined were from 25 to 42 cm. in length. In all the larger specimens ova in various stages of growth were found, but no testicular tissues, the posterior 5–7 cm. of the generative organ being sterile. In all the smaller specimens only very young ova were found in the anterior part of the generative organ; these young ova are usually round, not ellipsoidal as they become when more developed, and only about 2 mm. in diameter. In such specimens the posterior 5 to 7 cm. of the organ is male, consisting of testicular tissue in various stages of development. The limit of size, between the functionally male hermaphrodites and the larger female specimens in which the testis has atrophied, is, of course, not absolutely constant. I found no testicular tissue in specimens more than 35 cm. (about 14 inches) in length, and it was sometimes absent in specimens smaller than this. On the other hand, I rarely found traces of actual spermatogenesis in specimens less than 30 cm. long. Specimens containing mature testicular tissue are thus usually between 30 and 35 cm. in length, and after a little practice I was able, by simply comparing the sizes, to select from a large batch of specimens all the individuals in which mature testes were likely to occur.

In this paper Cunningham illustrated "perfect ripe spermatozoa" which he had observed "in motion" under the microscope, but he found that only a small number of the capsules contained ripe spermatozoa. This was the last publication by Cunningham in regard to this subject.

Between 1904 and 1908, A. and K. E. Schreiner published several papers presenting the results of extensive investigations made upon *Myxine glutinosa* at the Biological Station of the University of Christiania, now Oslo, at Dröbak, Norway, with particular reference to the development of the male sex cells. From their references it is evident that these authors were influenced by Professor Dean, who visited Dröbak during that time. They stated that the hypothesis of protandric hermaphroditism for the condition in *Myxine* as advanced by Cunningham and Nansen was at that time generally accepted and had been printed in all modern text-books, and that only Bashford Dean (1899) expressed strong doubts as to the truth of this hypothesis. After two years' work, in which time they examined very thoroughly, both macroscopically and microscopically, many hundreds of specimens, the Schreiners decided that all Myxines are to be placed in three groups, viz., male, female and sterile individuals.

In the males the testis is well developed, occupying a greater or lesser portion of the posterior end of the sex organ, while an ovary is either not at all developed, or if present is more or less rudimentary and always shows signs of degeneration. Ovaries present in ripe males are always abnormal and not well developed. As a rule, in the males the anterior portion of the sex organ consists of a rudimentary ovary which contains quite small eggs. The number of pure males, i.e., individuals with only a testis in the sex organ, was found to be insignificant. All transition stages of males were found between those in which the testis occupied only the posterior 0.7 cm. of the sex band, and those in which the testis extended the entire length of the band.

In the females the anterior portion of the sex organ always consists of an ovary with normal eggs, while the posterior end is either entirely lacking in sex elements, or consists of testicular tissue which is slightly developed and shows signs of degeneration or other abnormalities. As a rule, the females have nothing in the posterior part of the mesovarium; in many young females, however, and in some of the older ones, the posterior part of the mesovarium is not entirely empty, but contains an abnormal testis which never becomes functional. The testis present in specimens having well developed ovaries in the anterior portion of the sex band is always abnormal and non-functional, whether in an old (33 cm. long) female or in a young one (25.5 cm. long), and it shows no indications of ever having produced spermatozoa in either young or old females. The Schreiners found all transition stages of females from those in which the ovary contained a single small egg to those in which the entire ovary was filled with eggs up to the posterior 7 mm. of the mesovarium.

The sterile individuals are those in which the posterior end of the sex organ consists of an abnormal, degenerate testis, and the anterior portion is an abnormal, degenerate ovary. These individuals never attain sexual maturity, either as males or females, i.e., they are sterile throughout the entire extent of their lives. They fall into two main groups: (1) the completely sterile, in which there is no trace of either testicular tissue or of eggs; (2) those whose sex organs consist of both testis and ovaries both of which are abnormal and attacked by degeneration processes. Among 1690 eels examined, 13.1 per cent were sterile individuals.

Unlike Cunningham and Nansen, the Schreiners observed no relation between body length and sex. They found males in great numbers 25 cm. long with almost ripe spermatozoa, and males 29-30 cm. long which were not ripe and which, according to the structure of the testis, apparently had not produced sperm at any earlier time. They found females 26-27 cm. long which had large empty egg cases (corpora lutea) hanging to the ovary, clear proof that they had deposited eggs, and they also found good females over 31 cm. long which had never laid eggs. They found large ripe males (30 cm. long), large females (37 cm. long) and large sterile individuals. As a rule, however, the females were larger than the males, most of which were 30-31 cm. long, and seldom more than 33 cm in length.

The Schreiners agreed with Cunningham and Nansen that there is a condition of hermaphroditism in *Myxine glutinosa*. They observed that in most individuals the sex organ is hermaphrodite in structure, being a testis in its posterior one-fourth or one-third, and containing eggs in the anterior portion. They believed, however, that protandric hermaphroditism is impossible in these animals; that the hermaphroditism is of a rudimentary, functionless nature, and that the eels are functionally dioecious. They stated that, with his permission, they were permitted to declare that Doctor Dean had come to the same conclusion after examining 200 specimens of *Myxine* taken at Bergen.

These authors offered the following explanation of the present condition of the sex organ in *Myxine*. An effective hermaphroditism really existed in the ancestors of the myxinoids, and self-fertilization occurred. When larger and larger numbers of individuals assembled in the same locality, there arose the necessity for cross fertilization; this was first effected by means of the posterior testicular part of the sex organ developing and functioning at a different time from the anterior ovarian portion. Gradually a dioecious condition prevailed, resulting in pure males and females, but with many intermediate sterile individuals which were functionless either as males or females, during the entire extent of their lives.

Conel (1917) found a testis present in the posterior portion and small, round eggs in the anterior part of the sex organ in some young specimens (31-36.5 cm. long) of *Myxine glutinosa* caught at South Harpswell, Maine. Sections of the testis showed that in structure it resembled the young testis as described by Cunningham, Nansen and the Schreiners. An older specimen (62 cm. long) had a testis in the posterior 9.5 cm., and numerous brown bodies in the entire length of the anterior portion of the sex band. These brown bodies represented atrophied eggs. Microscopical examination of sections of the testis revealed many mitotic figures in the cells of about one-half the follicles, but no spermatozoa in any of the follicles. In two older specimens (63 and 67 cm. long) the testicular tissue had been converted by a process of degeneration into a palisade layer of columnar cells, enclosing a central core of fibrous connective tissue; there were no follicles containing sex cells anywhere in the testis; these individuals were sterile, probably because of old age. In the adult females with well developed eggs the posterior end of the sex organ sometimes contained a few small eggs or brown bodies (atrophied eggs), but it was usually without any reproductive elements. Females with large eggs measured from 59 to 64 cm. long; adult males were from 62 to 67 cm. long. From these facts it was concluded that *Myxine* could not be a protandric hermaphrodite.

The results of the investigations of Cunningham, Nansen and the Schreiners may be tabulated as follows:

Cunningham	Nansen	The Schreiners
Found but eight individuals having only a testis in the sex organ (true males), and these were young and immature.	Saw only very few true males, and these were immature.	Found that true males are insignificant in number.
Mature males with motile spermatozoa are between 30 and 35 cm. in length, and have young, round ova about 2 mm. in diameter in the anterior portion of the sex organ.	Mature males with spermatozoa are 28–32 cm. long and have very many young ova in the anterior portion of the sex organ.	Mature males with ripe spermatozoa vary from 25 to 33 cm. in length. In anterior part of sex organ in most males there is a rudimentary ovary containing quite small eggs which are always abnormal and never develop to maturity, but degenerate.
A testis is never present in specimens with eggs more than 4 mm. long. As the eggs grow larger, the testis atrophies. No testicular tissue remains in specimens more than 35 cm. long.	The testis is not prominent in individuals with oblong young ova. As the animal grows larger, the testis disappears, and the ovary increases in development.	If a testis is present in females having normal eggs, it is always abnormal and degenerate, and never was functional.
Animals over 35 cm. long are females in which the testis has completely atrophied (this length is not absolutely constant). The longest individuals have well developed ova. Does not describe the structure of the atrophied testes.	The largest animals generally contain large, well developed ova in anterior portion of sex organ, and nothing whatever in posterior portion. All females show traces of early male stage. Does not discuss these traces.	Females with mature ova vary in length from 26 to 37 cm. As a rule, females have nothing in posterior part of the sex organ. Any testicular tissue present in posterior part of sex band is always abnormal and degenerate. Do not discuss degenerate elements.
		Of all the eels examined 13.1 per cent were sterile. Some of these sterile individuals lacked both testis and ovary; others possessed these in an abnormal, degenerate condition, and were never functional either as males or as females.
Myxine is functionally a protandric hermaphrodite.	*Myxine* is functionally a protandric hermaphrodite.	*Myxine* is structurally hermaphrodite, but functionally dioecious.

From the review of the literature as given above it can be seen that true male specimens of *Myxine glutinosa* have been but rarely taken in European waters. This fact led Cunningham to believe that the males change into females after functioning as males, and Nansen corroborated him in this. The Schreiners confirmed the presence of a morphological hermaphroditism, but decided that it is not functional. Why functional males are not caught more frequently in the North Sea is certainly very strange. Females exist in large numbers, and since each female deposits from 25 to 45 eggs at a time, many males and much sperm would be required to insure fertilization, especially if, as is believed by all investigators, fertilization occurs after the eggs are extruded from the female.

HERMAPHRODITISM IN *BDELLOSTOMA FORSTERI* AND *BDELLOSTOMA BURGERI*

In view of the uncertainty as to hermaphroditism in *Myxine glutinosa*, an investigation into the condition of the genital system of *Bdellostoma* would be of special interest, and this needs to be prefaced with a brief review of the literature in order to indicate what observations have been recorded by previous authors. The investigators of the question of hermaphroditism in the genital system of *Bdellostoma* are fewer in number than those who have examined *Myxine*; only four writers have published accounts of their observations.

HERMAPHRODITISM IN *Bdellostoma forsteri*.—In July 1886, Cunningham read a paper before the Royal Society of Edinburgh in which he discussed briefly the reproductive organs of a number of specimens of *Bdellostoma forsteri* from Cape Town, Africa, which were in the museum at Oxford. Strange to say no other student of the Myxinoidea has made any further observations on *B. forsteri*. Regarding his specimens Cunningham (1886.1) wrote as follows:

> I have not yet made a microscopic examination of the reproductive organs of *Bdellostoma*, but from what I could see by ordinary dissection, it is evident that all the peculiarities which exist in the reproductive system in *Myxine* occur also in *Bdellostoma*. A number of specimens possessed sexual organs, in the anterior part of which were minute ova, while the posterior part was evidently testicular tissue; and in one or two other specimens the whole organ seemed to be testicular. The small quantity of testicular tissue in a given specimen was also noticeable, as in *Myxine*.

HERMAPHRODITISM IN *Bdellostoma stouti*.—As a result of observations made on *Bdellostoma stouti* at Pacific Grove, California, Ayers (1894) concluded that "in all cases each individual is potentially bisexual." He observed that the anterior region of the peritoneal fold is always ovary, while the much smaller posterior region of the fold is the testis. He found spermatozoa in the testicular follicles of many individuals, but found very few females containing eggs in the last stages of ripening. Among the specimens taken by him were some young, as well as large and old, males and females. He wrote as follows:

> Some individuals of *Bdellostoma* are truly hermaphroditic, having at the same time a genuine testis with ripe sperm and an ovary with eggs nearly or quite ripe [his Fig. 12]. These individuals are rare, so far as my experience goes, but others with the two organs in a more unequal state of development are more numerous. However, by far the largest number of individuals are genuinely male or female.

He found a preponderance of males among the specimens taken by him; of 309 eels, 182 were true males, 121 were females, and 6 were hermaphrodites. Ayers, therefore, believed that functional hermaphrodites exist in small numbers.

In his excellent paper describing the general embryology of *Bdellostoma stouti*, Dean (1899) discussed at some length the question of hermaphroditism in *Myxine* and *Bdellostoma*. He offered the following objections to the hypothesis that *Myxine* is a protandric hermaphrodite. (1) *Bdellostoma* and *Myxine* are admitted to be closely related. If, therefore, there are found in *Bdellostoma* small females which do not have testes, and large functional males without any traces of eggs, the hypothesis of protandric hermaphroditism would be disproved. Dean observed among large specimens of *Bdellostoma* (38 to 40 cm. in length) that males are about as abundant as females, and that males are by no means uncommon among the larger specimens. He also found small females (30 cm. long). (2) Dean contended that on general grounds it is highly improbable that *Myxine* is a protandric hermaphrodite. He believed the evidence is not sufficient to show that Cunningham's and Nansen's hermaphrodites were other than young males; he called attention to the fact that, "it is not an uncommon thing to find immature eggs in the testis of a number of vertebrates, Teleosts, Petromyzonts, Amphibia, where the assumption of hermaphroditism to say nothing of its protandric form is entirely unwarranted."

As an explanation of the presence of both male and female sex elements in young specimens of *Myxine*, Dean suggested that because one side (the left) of the genital ridge is usually lacking, the remaining side is precociously developed; therefore the early undifferentiated condition of the sex elements, which obtains in all vertebrates to a greater or lesser degree, is carried along further in the myxinoids before differentiation into either ovary or testis commences. Consequently, both immature ova and testicular tissue are present in the sex organ simultaneously, the former in the anterior, the latter in the posterior part. He says:

> But this condition does not, I believe, imply that the individual is hermaphrodite, except in the sense that an embryo afterwards a male may be regarded as potentially hermaphrodite during a time when its genital epithelium is undifferentiated. It merely implies that the hagfish is carried further along the road of developmental specialization; so that when the time comes for sex-differentiation, the animal may become promptly female or male.

This explanation is supported by the observations of all investigators of the generative organs in myxinoids, that when both testicular and ovarian tissues are present in an individual, the eggs are always very small, and may be involved in a process of degeneration; or, as the Schreiners observed, if the eggs are good, the testicular tissue will be abnormal and degenerating. Ayers alone reported finding some individuals which contained simultaneously a testis with ripe spermatozoa and an ovary with nearly ripe eggs. Dean was unable to verify Ayers' statement, nor could he agree with Ayers' view that in *Bdellostoma* each individual is essentially bisexual.

Conel (1917) examined twenty-four specimens of *Bdellostoma stouti* which were caught in Monterey Bay, at Pacific Grove, California; they consisted of one immature male 33 cm. long, nine adult males, ranging in length from 36 to 42 cm., and fifteen adult females varying from 34 to 40 cm. in length. No female sex elements were found in any of the males, and none of the mesorchia presented the appearance of ever having contained eggs. No testicular tissue was found in any part of the mesovarium of any female. Since the adult males were larger than the adult females, it was concluded that *Bdellostoma stouti* is not a protandric hermaphrodite.

OBSERVATIONS ON *BDELLOSTOMA STOUTI* AND *BDELLOSTOMA BURGERI*

From the above review of the literature it is evident that there is a division of opinion among investigators as to whether the Myxinoidea reproduce by means of hermaphroditism. Of those who have investigated this subject extensively, Cunningham and Nansen believed that in *Myxine glutinosa* the method of reproduction is protandric hermaphroditism; the Schreiners agree that most specimens of this eel are hermaphrodites in structure, but found that minute examination of the sex organs in each hermaphroditic individual proves either the male or female sex elements to be sterile; these two investigators concluded, therefore, that *Myxine* is not functionally hermaphroditic. Cunningham believed *Bdellostoma forsteri* to be a protandric hermaphrodite, and Ayers claimed to have found some specimens of *Bdellostoma stouti* containing both ripe spermatozoa and almost mature ova. Dean was unable to find any specimens of *Bdellostoma stouti* which were hermaphroditic in the structure of their sex organs, and raised grave doubts as to a functional hermaphroditism in *Myxine*.

Since the question of hermaphroditism in the Myxinoidea remains in this unsettled condition, additional contributions to this subject are most welcome. By far the largest amount of the information presented in the following pages is based upon observations made by Dean on *Bdellostoma stouti* at Pacific Grove, California, in 1896; and on *Bdellostoma burgeri* at Misaki, Japan, in 1900 and 1901. My own contributions consist chiefly of corroborations of Dean's observations. While fishing for *Bdellostoma stouti* at Pacific Grove, California, during the summer of 1930, I did not keep any detailed record of observations on the genital system, but limited myself to checking Dean's statements. I have had no opportunity to examine *Bdellostoma burgeri*.

HABITAT OF *BDELLOSTOMA STOUTI* IN MONTEREY BAY

While fishing in Monterey Bay for *Bdellostoma stouti*, Dean learned that the hagfish, as it is called, is "curiously local in distribution." Sometimes his fisherman would catch from two to three hundred specimens in one place on six lines of trawl, each line being about 400 feet long and holding 200 hooks; while within one-quarter of a mile from that place, few or no eels would be caught on the same number of hooks. Lines set in a seagoing direction, i.e., at right angles to the shore, would catch an eel on every hook where the line lay over favorable spots. Dean concluded that these favorable spots extend parallel to the shore, and represent a series of large steps leading away from the shore into successively deeper water.

The bottom in such places was mud, gravel or rock, the eels seeming to prefer mud, as more were caught on that kind of bottom. In some places mostly males were caught, many of them ripe; in other localities principally females were taken. Dean observed that the males were most frequently taken in places where young females abounded. Four-fifths of the eels examined by Dean measured from 38 to 60 cm. in body length; most of them were caught in water from ten to twenty fathoms deep, twelve fathoms being the most favorable depth. I can corroborate Dean in all these statements, excepting only that I caught all my eels in water measuring from thirty to thirty-five fathoms deep, and failed to catch any in shallower water.

DATA PERTAINING TO *BDELLOSTOMA BURGERI* COLLECTED BY BASHFORD DEAN ON THE COAST OF JAPAN

During the year 1900–1901 Dean was fishing along the coast of Japan, searching for the embryos of *Bdellostoma burgeri*. He tabulated the daily catches of hagfish in his notebook, listing information as follows for each of 569 specimens:

TABLE I

DATA FOR *BDELLOSTOMA BURGERI*. AUG. 29, 18-20 FATHOMS

Eel No.	Length in cm.	No. of Gills	Sex	No. of Eggs	Length of Eggs in mm.	Remarks
39	41	6-6	Male			Ripe
40	47	6-6	"			Ripe
41	45	6-6	Female	24	25	
42	42	6-6	Male			Ripe
43	54.5	6-6	"			Ripe
44	45	6-6	"			Ripe (Gonad extending far forward)
45	50	6-6	"			Ripe
46	42	6-6	"			Ripe (Gonad far back)
47	46	6-6	"			Ripe (Gonad far back)
48	40	6-6	"			
49	47.5	6-6	"			Ripe (Gonad far back)
50	39	6-6	"			Ripe
51	46	6-6	"			Ripe
52	41	6-7	"			Gonad very small
53	37	6-6	Female	5	22	Spawned
54	38	6-7	"	13	22	Partly spawned?
55	47	6-7	Male			
56	46	6-7	"			Gonad small, ripe, far back

Dean wrote these tables in the same notebook (the smaller one) which he used for recording observations on *Bdellostoma stouti* while fishing in Monterey Bay. For instance, on two pages of the notebook he wrote an outline, evidently for titles of paragraphs, with the caption: "Bdellostoma. Habitat in Bay of Monterey"; following that are two pages of notes, then two blank pages; the next eleven pages are used for the tabulations illustrated above. In these tables the day of the month is indicated, but not the year. In the larger notebook marked "Bdellostoma Notes, IV," is a table which was evidently compiled from the data given in the tables recorded in the smaller notebook. This table is reproduced here:

TABLE II

DATA FOR *BDELLOSTOMA BURGERI* CONTAINED IN DOCTOR DEAN'S LARGE NOTEBOOK, IV

Date	No. examined	Percentage		Approx. percentages Immat., i.e., those in which sex elements cannot be distinguished.	Size				Percentage of females with eggs of nearly uniform size.	Number of eggs			Size of Eggs in mm.			Remarks
		Male	Female		Male Max. (in cm.)	Male Min. (in cm.)	Female Max. (in cm.)	Female Min. (in cm.)		Max.	Min.	Aver.	Max.	Min.	Aver.	
1900																
July 18	37	62%	33%	5%	45	30	45	30	50%	23	13	18	23	22	22.9	After the large eggs—uniform—came next size 3 mm. long.
Aug. 27																1 immature male, 14 inches—put out 6 trawl lines. All gone to sea.
Aug. 29	41	83%	14%	3%	54.5	29	45	33	60%	24	5	15	25	22	23	Many large males, average about 48 cm.
September																4 times—failed to get specimens.
Oct. 28	16	13%	87%	.	41.5	32	46	32	63%	27	17	23				Empty capsules from 9–10 mm. long.
Oct. 30	29	24%	76%	.	45	29	46.5	30.5	90%							All mature males spent.
Nov. 25	96	37%	63%		50	28	60	24	98%							Large females, about 98% of, with empty capsules.
Dec. 15	40	45%	55%	.	47	29	47.5	32	85%				8	3	4.4	2 females, eggs 11–14.
1901																
Jan. 15	33	45%	55%		48	28	26	30	95%				7.2	2	4.2	1 female, eggs 12.
March 30	96	31%	65%	4%	47	30	48	32	81%	36	2	17	20	5	11.9	1 female, 2 mm.—2 females, 5 mm.—rest between 7–14
June 5	60	42%	58%		45	31	45	29	63%	24	5	17	22	16	18.9	2 females—5 and 4 mm.
June 18	14	60%	40%		49	35	40	37	83%	28	9	14	22	3	20	1 female, small eggs.
June 30	59	50%	46%	4%	52	30	50	35	87%	27	4	17	23	19	20	6 " " "
July 25	91	78%	22%	..	54	30	52	27	80%	32	10	19	25	3	22	2 " " " 1 male ripe.

In order to present the data contained in the tabulations in Doctor Dean's small notebook, I have compiled the following table:

TABLE III

DATA FOR *BDELLOSTOMA BURGERI* FROM DOCTOR DEAN'S SMALL NOTEBOOK

Date	Total eels caught	Males					Females				
		Immature		Mature			Immature		Mature		
		No.	Lgth. in cm.	No.	Lgth. in cm.	Aver. lgth	No.	Length	No.	Length	Av. lgth.
July 18	37	16	27–36	8	37–45	41	6	28–37	7	40–45	42
July 25	92	13	29–34	60	35–53	44.5	3	27–35	16	37–49	42
			Aver. 32								
Aug. 29	40	1	29	33	32–54.5	45	3	32–37	3	32–46	39.6
Oct. 28	16	2	29–32	1	41.5	41.5	3	32–37	10	37–46	40.3
Oct. 30	29	0		7	39–45	41.5	4	35–39	18	37–45	41.8
Nov. 25	99	8	28–35	29	36–50	44	0		62	24–50	41.4
			Aver. 32								
Jan. 15	34	2	28–35	13	35–48	41	18	30–41	1	39	39
Apr. 2	97	16	26–35	35	35–55	41	10	33–37	36	32–48	39
			Aver. 31.5					Aver. 35			
June 5	65	7	31–36	21	35–48	41	12	29–42	25	35–43	39.6
			Aver. 33					Aver. 33			
June 30	60	7	29–34	23	37–52	43	4	36–40	26	35–48	41
			Aver. 33					Aver. 38			
Totals	569	72		230		42.5	63		204		40.5

The reader will observe that the years 1900 and 1901 are recorded in Dean's table, Number II above. During this time he was fishing in Japan, therefore the data contained in Table II refer to *Bdellostoma burgeri*. That these data are compiled from those in the tables in the small notebook is made evident by comparing Tables II and III. The dates are almost identical; in the notebook a line has been drawn through Mar. 30, and Apr. 2 has been written below; the numbers, lengths and sizes of eels caught on the same dates, the sizes of eggs, and other data correspond quite closely. Therefore, it seems quite evident that the data in the tables shown in Dean's small notebook are for *Bdellostoma burgeri*, caught on the coast of Japan in 1900–1901.

Table III was compiled from Dean's data in order to show the sizes of immature and mature males and females. The immature males average about 33 cm. in length, and the immature females average from 33 to 38 cm. The average length of mature males is 42.5 cm., and that of mature females is 40.5 cm. The immature males and females are approximately of the same length, the females being a little the larger; the mature males are larger than the mature females. In view of these facts it is impossible that *Bdellostoma burgeri* is a protandric hermaphrodite in the sense that Cunningham and Nansen meant in regard to *Myxine*, namely, that during the young stages the eels function as males, and when older become females, the transformation occurring when the individual reaches a body length of about 32 cm.

SIZES OF *BDELLOSTOMA STOUTI* TAKEN IN MONTEREY BAY BY J. LEROY CONEL

During the summer of 1930 I caught more than six thousand specimens of *Bdellostoma stouti* in Monterey Bay at Pacific Grove, California, and examined them with special consideration as to the question of hermaphroditism. I found that the mature males, containing ripe spermatozoa, were usually longer than females which contained nearly mature eggs. Some females with eggs almost ready to be deposited were only one-half as long as adult males. The largest individuals were usually found to be males; the largest eel caught was a male measuring 82 cm., and its testis was full of ripe spermatozoa. I also observed many very small young females which had no indications of a testis in any part of the ovary. In Dean's small notebook are five loose leaves containing the sizes of 38 females and 100 males of *Bdellostoma stouti.* The figures have been added, and the averages computed; the average length of the females is 41.5 cm., and that of the males is 42 cm. As a result of my own observations I feel quite positive that the California hagfish is not a protandric hermaphrodite. Whether either *Bdellostoma stouti* or *B. burgeri* shows any form of hermaphroditism will become apparent from an examination of their sex organs.

GROWTH OF THE MALE GENITAL ORGANS OF *BDELLOSTOMA BURGERI* AND *BDELLOSTOMA STOUTI*

The testis is usually confined to the posterior part of the mesorchium, but patches of testicular tissue are occasionally scattered along the entire length of the mesorchium; rarely does the testicular tissue form a continuous band extending along the free margin of the mesorchium from the most anterior to the most posterior ends (Conel, 1917; Fig. 83). Microscopic examination reveals that the testis band consists of follicles of various sizes which are filled with the germ cells. All the cells in any one follicle are in approximately the same stage of development (Conel, 1917; Fig. 77).

Under the heading of "remarks" in his notebook, Dean usually indicated whether a male hagfish was mature or immature by such words as "ripe," "mature," "not quite ripe," "unripe," "immature," "young ." He recorded the testis as being located at the posterior end of the mesorchium, occasionally with the notation, "far back," and in some specimens "extending far forward." Under remarks for specimen No. 393, which is a male 34 cm. long, are written the words, "with young eggs." This is the only male which he has recorded as having eggs in the gonad, and nowhere in the notes does he mention having seen specimens which contained both testis and ovary. Dean made five drawings to illustrate progressive stages in the development of the testis from the very young to the adult condition; these drawings are reproduced in Figures 1 to 5 of plate I.

Dean did not label any of the sixteen drawings which he made to indicate whether they represent *Bdellostoma stouti* or *burgeri.* A list with descriptions of these drawings is pasted in the large notebook on the back of the page which contains Table II; this table bears the dates 1900 and 1901, and at the top of the table is written "H. burgeri," crossed with two lines. This leads me to think that the drawings illustrate specimens of *Bdellostoma burgeri.* I know by comparison, however, that corresponding specimens of *Bdellostoma stouti* present exactly the same appearances as shown in the drawings, and therefore the latter might well illustrate either of these two species of hagfish.

In all the males represented in the drawings the testis is confined to the posterior one-fifth or less of the mesorchium. The gonad in the youngest male illustrated (Figure 1, plate I) shows very little differentiation. In this specimen the mesorchium is narrowest at the anterior and posterior ends where it is merely a ridge along the mesentery; it is widest in the central part. The testis is indicated by a slight thickening along the free (outer) margin of the mesorchium in its posterior part. A slightly older stage of development is shown in Figure 2. The mesorchium is wider than in the preceding specimen, and is slightly waved in its posterior part. In the specimen illustrated in Figure 3 the waved condition in the posterior portion of the mesorchium is increased, and a definite band can be seen in its free margin. This band consists of numerous small follicles closely packed together, giving the free margin of the mesorchium a beaded appearance. This is now the widest part of the mesorchium; the anterior portion has not increased in width, and contains no sex elements whatever.

The testis in the specimen illustrated in Figure 4 is considerably more advanced in development. The posterior part of the testis band is quite thick and is thrown into short, deep folds, indicating increased growth in a limited area. The anterior portion of the mesorchium shows no change over the condition in the last specimen, and contains no sex elements.

The adult appearance of the male gonad is illustrated in Figure 5. The testis occupies the posterior one-fourth of the mesorchium; the anterior portion of the latter is wider than it is in the preceding specimens, and is entirely free of sex elements. The testis has increased in width and in thickness, and is considerably more lobulated and folded.

All the specimens illustrated in Figures 1 to 5 are true males, with no trace of eggs anywhere in the genital fold. As stated above, Dean recorded only one specimen which had both ova and testicular tissue in the genital fold, and this he interpreted to be a young male, 34 cm. long, "with young eggs."

Among the many specimens of *Bdellostoma stouti* which I examined in 1930, I found no male individuals in which there were any indications of eggs anywhere in the mesorchium. In some of the males there were scattered testicular follicles in the anterior portion of the mesorchium, and in a very few specimens a narrow band of testicular tissue extended along the entire length of the mesorchium from the gall bladder to the caudal end of the body cavity. I carefully examined the testis in numerous males while they were still living, and was impressed by the scantiness of the spermatic fluid in the gonads. Microscopic examinations revealed myriads of active spermatozoa in the spermatic fluid, but the total amount of fluid secured from a testis seemed very small, only about two or three cubic centimeters. If, as is believed by all investigators, fertilization of the eggs occurs after they have been extruded from the body cavity of the female, the amount of spermatic fluid seems very slight to insure bringing spermatozoa into contact with all the eggs. This may account for the fact that both Dean and I, in collecting the naturally deposited eggs of *Bdellostoma stouti* found so many unfertilized ones; Dean recovered many unfertilized eggs, and I observed that only about one in every five collected was fertilized. When squeezed out of the testis the fluid was milky-white, and slightly sticky. The entire gonad was usually creamy-white in color. In some males the testicular follicles were bulging with their contents, while in others, the testis presented a shrunken, spent appearance, and yielded very little fluid when squeezed between the fingers. When these latter gonads were sectioned, stained and examined under the microscope many of the large follicles were found to be empty.

Since there are no genital ducts in either the male or female, the spermatozoa apparently escape into the body cavity upon rupture of the follicles, and are extruded to the exterior through the genital pore. I observed that males can be identified upon external examination by means of a gland located on each side of the genital pore. This gland is present in both males and females but is much larger in the males, and can be felt as a hard lump when pressed between the thumb and forefinger.

By consulting Table III, which has been compiled from Dean's data, the reader will see that the males which he caught varied from 27 to 55 cm. in body length; the immature males measured from 27 to 35 cm., and the mature males were 32 to 55 cm. long. The average length of the mature males was 42.5 cm. I caught many males longer than 55 cm., measured soon after they were taken from the hook, while they were still alive; the longest one was 82 cm. from tip of the nose to tip of the tail, the two points used for measuring the length of the eels. The testis in this male occupied the posterior one-fourth of the genital fold, was very large, and was of a creamy-white color. The follicles were bulging with their contents. When examined under the microscope many of the follicles were found to be filled with active spermatozoa. Sections of this testis were made later, and revealed that many of the large follicles were packed with spermatozoa resembling in structure those so excellently illustrated by the Schreiners (1905, 1908). These authors have very thoroughly described spermatogenesis in *Myxine*. I have seen no evidence to lead me to believe that the formation of the spermatozoa is any different in *Bdellostoma*.

All the male specimens of *Bdellostoma burgeri* examined by Dean, with the single exception of the young male No. 393, and all the male individuals of *Bdellostoma stouti* examined by me, without exception, were true males, having no traces whatever of eggs in the sex organ. Small, immature males, and large males with ripe spermatozoa were found in great numbers. Cunningham, Nansen and the Schreiners (page 76) all reported that true males were observed but rarely, and were always young and immature. In the case of *Bdellostoma*, both Dean and I found males and females occurring in approximately equal numbers. Among 569 specimens of *Bdellostoma burgeri* caught by Dean (Table III), there were 72 young males and 63 young females, 230 adult males and 204 adult females. I observed that the two sexes are about evenly distributed in number in *Bdellostoma stouti*.

GROWTH OF THE FEMALE GENITAL ORGANS OF *BDELLOSTOMA BURGERI* AND *BDELLOSTOMA STOUTI*

Both Dean and I caught females showing all stages of development of ova from mere dots in the free margin of the mesovarium to eggs which were almost ready to be deposited, measuring as much as 29 mm. in length. Dean made nine drawings of dissected females to illustrate various stages in the growth of the eggs; these drawings are shown in Figures 6 to 14, plates II, III, and IV.

The youngest female illustrated is shown in Figure 6, plate II. The ovary in this individual contains many eggs, closely packed together, all spherical in shape, varying in size from mere dots to eggs 0.8 mm. in diameter. In all the females the smallest eggs are located in the outermost part of the ovary along its free margin; successively larger eggs lie internal to these, i.e., nearer the attached border of the mesovarium, the largest being the most internal in position. The eggs in the specimen shown in Figure 6, plate II, are distributed fairly evenly along the entire length of the ovary from the gall bladder to within a few millimeters of the caudal end.

A slightly older female is illustrated in Figure 7. The largest eggs in this specimen are spherical, and measure about one millimeter in diameter. The mesovarium is a little broader in this individual. Figure 8 illustrates an older female, in which the largest eggs, still spherical in shape, are about 1.5 mm. in diameter. The mesovarium is broader and somewhat more folded. With progressive development the mesovarium increases in breadth and becomes more folded, reaching the maximum condition in both these respects in those females which have the largest eggs.

In the ovary of a slightly older female than the one shown in Figure 8, the largest eggs are beginning to assume a spindle shape by tapering at each end (Figure 9). The eggs elongate as they develop further, as illustrated in Figure 10, plate II. The largest eggs in this individual measure from 4 to 7 millimeters in length, and occupy a position in the ovary internal to all the other eggs. The next smaller eggs are about 2 mm. long and lie immediately external to the largest eggs. Ova of successive gradations of diminishing sizes occupy successively external positions in the ovary, with the smallest, which are mere dots, in the extreme external or free margin.

The largest eggs in the next older specimen (Figure 11, plate III) measure from 7 to 10 mm. long. They have grown in circumference as well as in length, and now are so heavy that they have stretched the mesovarium where they are attached, and hang down into the body cavity, each suspended by a narrow strand of mesovarium. The large eggs in this specimen are not very numerous; some were probably lost while the eel was being handled.

In the next older female selected by Dean to illustrate the development of the ova (Figure 12), the eggs are from 11 to 13 mm. in length, but are much larger than the largest in the specimen shown in Figure 11; the increase in growth has been more in circumference than in length. The ends are not as pointed as they are in younger eggs. The increased weight of the eggs has stretched the mesovarium in the vicinity of each egg into a longer strand.

A female with older eggs is shown in Figure 13, plate III. The largest of these eggs are from 15 to 18 mm. long, and they are likewise larger in the transverse diameter than those shown in Figure 12. A female with eggs that are almost ready to be deposited is shown in Figure 14, plate IV. The eggs are from 20 to 22 mm. long, and 7 to 8 mm. wide. The largest eggs recorded by Dean were 29 mm. long by 9 mm. wide. The average length of seventy eggs was 22.8 mm. The mesovarium in females containing eggs almost ripe is very broad, and is stretched into long, narrow, twisted strands at the places where the large eggs are attached. Sometimes adjacent strands of the mesovarium become tangled together, and may even be tied in loose knots. A female containing large eggs usually has from 25 to 45 or more, and their contours can easily be seen from the exterior. The mass of the numerous mature eggs causes the body cavity to be slightly enlarged by expansion of its walls. Neither Dean nor I succeeded in catching any females with eggs lying in the body cavity, free from the ruptured ovarian capsules, ready to be deposited. European investigators likewise record that they have been unable to get any females of *Myxine* containing fully mature eggs. It has been suggested by some authors that the females do not eat during the time they are ready to deposit eggs, consequently cannot be taken on hooks or in traps. Dean suggested that possibly they hide under rocks or in holes at this time. From my experience in collecting naturally deposited eggs, I believe this is probable.

Nowhere in his notes does Dean make any mention of having observed testicular tissue in the ovary of any female. None of his drawings shows a female individual having a testis anywhere in the sex organ. It is reasonable to infer, therefore, that he did not find any female specimen whose sex organ contained any male sex elements. Among all the females of *Bdellostoma stouti* which I examined in the summer of 1930 there was not one which had any testicular tissue in the posterior part, or in any other part of the mesovarium. In its posterior two or three centimeters the mesovarium was usually entirely without any sex elements, but occasionally it contained a few quite small eggs.

In *Bdellostoma burgeri* and *B. stouti*, then, both Dean and I found the sex organ in each individual hagfish examined, excepting one (Dean's specimen No. 393), to be distinctly either a testis or an ovary; that is, each individual hagfish was either a true male or a true female, with no indications whatever of any elements of the opposite sex in the genital fold. As a result of our observations on the structure of the sex organ in both males and females, therefore, it is quite evident that *Bdellostoma burgeri* and *Bdellostoma stouti* are very rarely, if ever, hermaphrodite, either in the young or in the adult condition. As Dean suggested (1899, p. 228), it is, therefore, quite improbable that the closely related *Myxine* is functionally hermaphrodite; the extensive observations of the Schreiners seem to have established this negative. That the sex organ in *Myxine* is frequently hermaphroditic in structure there can be no doubt. All the European investigators have observed that in the case of *Myxine* true males are very rarely found, true females are often caught, but the preponderant majority of specimens taken are morphologically hermaphrodites. This difference in the frequency of occurrence of hermaphroditism in *Myxine* and *Bdellostoma* indicates that the genital organ of the former has proceeded in sex specialization to a lesser degree than that of the latter. As suggested by the Schreiners, the ancestors of the Myxinoidea may have been hermaphrodite; if so, *Myxine* is more primitive than *Bdellostoma* in the structure of the genital organ.

DEVELOPMENT TO MATURITY OF THE EGGS OF *BDELLOSTOMA*

Although several investigators have studied the structure and formation of the membranes which surround each egg during the time when it is developing in the ovary, no one has recorded any observations pertaining to the development of the eggs themselves. That Dean's interest was aroused by certain phenomena related to the growth of the eggs is attested by certain data which he recorded and some of the drawings which he made. He made no descriptive notes in regard to this subject, however, and his ideas can only be surmised from studying the tables and drawings.

One striking fact that I observed in 1917 (p. 122), and also while examining hundreds of specimens of *Bdellostoma stouti* at Pacific Grove in the summer of 1930, was that in almost every female with large eggs in the ovary, the eggs next smaller in size measured about 1.5 to 2 mm. in length, with no intermediate sizes between them and the largest eggs. All the latter were almost always within from one to three millimeters of being uniform in size. It is quite probable that Dean also observed this fact in 1900. In Table II, which he compiled from the data recorded in his small notebook, there is a column marked "Percentage of females with eggs of nearly uniform size." Under "Remarks" for the first entry in this table are written the words: "After the large eggs—uniform—comes next size, 3 mm. long." In the last two columns in the table are shown the number and length of eggs in the specimens which have eggs of nearly uniform size. When the figures in these last two columns are inspected in connection with the notations opposite them under the heading "Remarks," it becomes evident that Dean very probably made in 1900 the observation which I made independently in 1917 and again in 1930.

In 1917 (p. 124) I wrote further regarding this subject as follows:

> The fact that, as noted above, there are no intermediate stages between eggs about 2 mm. long and the large ones, and that also in animals which have corpora lutea, the eggs present do not exceed 2 mm., is interpreted to mean that as soon as some eggs exceed 2 mm. in length all the other eggs are arrested in development until the larger ones have matured and have passed from the body, and their corpora lutea are well along in the process of degeneration.

A short list of data written by Dean on the margin of one page in his small notebook indicates that he also noticed that when corpora lutea are present in the ovary there are no large eggs. His list is reproduced here, designated as Table IV:

TABLE IV

NOTES FOR PRESERVED SPECIMENS OF *BDELLOSTOMA BURGERI* EXAMINED BY DOCTOR DEAN

Individual	Length in cm.	Number of spent follicles	Eggs No.	Eggs Length	Number of brown bodies
1	44	25	27	6 mm.	95
2	40	25	48	5 mm.	10
3	37.5	19	42	5 mm.	13 noticeable
4	37.5	17	19	5 mm.	51 "
5	47	28	74	5 mm.	124 "
6		35	22	4 mm.	7 very small
7	37.5	16	29	5 mm.	
8	41		42	7 mm.	

According to this table, the largest eggs in females with corpora lutea were about 5 mm. in length, whereas the largest eggs in females with corpora lutea examined by me were about 2 mm. long. The eels listed in Tables II and IV are specimens of *Bdellostoma burgeri*, while those which I examined in 1917 were specimens of *Bdellostoma stouti* and *Myxine glutinosa*. With one exception (Figure 13) Dean's drawings of adult females, shown in Figures 6 to 14, inclusive, bear evidence of the fact that in the ovary of each female with either corpora lutea or large eggs the next longest eggs measure about 5 mm. in length, with no intermediate sizes.

Nowhere in his notes did Dean offer any explanation for this phenomenon; my conclusions, however, may be stated as follows. When the largest eggs in a female have reached a length of about 2 to 5 mm., only a comparatively few continue to enlarge, while growth processes are arrested in all other eggs in the ovary until the large eggs have developed to maturity, have been extruded, and their empty egg follicles (corpora lutea) have been almost completely resorbed. I venture to offer the suggestion that a more or less remote explanation for these growth phenomena may be found in the blood supply to the ovary; but, of course, this will not explain ultimate causes.

In all females containing eggs longer than 2 to 5 mm. the larger eggs number from about 25 to 45, more or less, and are distributed rather uniformly along the entire length of the mesovarium, excepting in the posterior two or three centimeters (Figures 10 to 14, plates II, III and IV inclusive). In fact, the large eggs are approximately segmentally distributed, one egg for each segment in the muscle of the abdominal wall or in the mesonephros. If the arteries in the mesovarium of a female which contains large eggs are examined, especially in an individual whose arteries have been injected with a color mass, they also will be found to be approximately segmental, one ovarian artery to each muscle segment. Dean made one drawing to illustrate the ovarian arteries in a female whose arteries had been injected with a red mass, Figure 12, plate III. The ovarian arteries are also shown in Figures 13—16, drawn from specimens whose arteries were not injected. Each ovarian artery arises directly from the aorta, extends downward between the two layers of the mesentery to the line of attachment of the mesovarium then continues between the two layers of the latter to within a short distance of the ovary and there divides into two or more branches. Some of the smaller branches supply the smaller eggs, while the larger branches go to the large eggs and spread out upon the surfaces of the ovarian capsule by means of further branching. Microscopic examination reveals that the arteries and their branches are contained within the connective tissue sheath of the capsule.

The approximate segmental distribution of the large eggs is probably determined by the location of the ovarian arteries, and the eggs favored with a direct stream of arterial blood through these arteries doubtless outstrip their neighbors in the accumulation of yolk material. Usually each large egg is supplied with blood by a single ovarian artery; and there is a corresponding ovarian vein for each egg. Each ovarian artery increases in size as its corresponding egg grows larger. After the mature eggs have been extruded from the body, the ovarian vessels remain large for a time, then gradually become smaller coincidentally with the decrease in size of the corpora lutea. The blood in the ovarian vessels is undoubtedly involved in the processes of resorption of the corpora lutea; it is possible, therefore, that other eggs do not receive a sufficiently large supply of blood to commence growing until the corpora lutea are almost or completely resorbed. Nothing is known regarding the factors which control the entire series of events concerned in the development of the eggs. Also the time required for the larger eggs to grow to the size and condition of maturity is unknown: Dean (1899) expressed the opinion that it is one year.

FATE OF THE EGGS WHICH DO NOT DEVELOP TO MATURITY

In the ovary of every female specimen of *Myxine* and *Bdellostoma* are very many eggs which are smaller than 2 to 5 mm. in length. These small eggs are so numerous that probably many of them do not develop to the mature condition. When the mesovarium of an adult female is examined closely, small brown nodules can be seen scattered throughout the ovary, usually toward the inner, or attached margin of the mesovarium. I observed these structures (Conel, 1917, p. 124) in adult females of *Myxine*, called them "brown bodies," and briefly described them. I interpreted them as degenerate eggs and corpora lutea which had been almost entirely resorbed. Very probably these brown bodies do represent the remains of those small eggs which are less favored than their neighbors as to blood supply and which do not enlarge but atrophy. Table IV shows that Dean saw these small structures in *Bdellostoma burgeri*, and also called them brown bodies. He did not write any notes regarding them; however, and therefore his interpretation of their significance is not known.

RELEASE OF THE MATURE EGGS FROM THE OVARY

When the large eggs in the ovary have attained maturity and are enveloped in their membranes, the follicle, consisting of ovarian tissue which surrounds each egg, bursts thus permitting the egg to escape into the body cavity. Cunningham (1886.2, p. 69) was the first investigator to report the manner in which the mature eggs are released from the ovary. He found several females which had recently discharged their ova. In place of the eggs there was present in the ovary a corresponding number of collapsed follicles, each of which had a slit-like aperture at one end, through which the ripe ovum had been expelled. Cunningham called the burst follicles "corpora lutea," but gave no description of their structure. He found them in old females, and observed various intermediate stages in the process of their absorption, "the last stage being that of minute yellow nodules in the mesovarium."

Schreiner (1904) caught many "spent" females of *Myxine glutinosa* which had corpora lutea in their ovaries, but he did not describe the ruptured follicles. Likewise Dean (1899) did not describe the corpora lutea in the spent females of *Bdellostoma stouti* which he observed. Conel (1917) found two females of *Bdellostoma stouti* and four of *Myxine glutinosa* which had corpora lutea in their ovaries. One specimen of *Myxine* had 27 large eggs and two empty ovarian follicles which had been ruptured along one side, not at one end, as Cunningham (1886.2) observed; it is probable that these two follicles had been ruptured by rough handling of the eel. Another specimen of *Myxine* had 33 empty follicles which measured 6 mm. long by 4 mm. wide; another female had 30 smaller (3×2 mm.) empty follicles, and a fourth individual had several corpora lutea which were smaller still. The presence of large ruptured follicles in some spent females and very small ones in others was interpreted to mean that the corpora lutea are resorbed. Traces of them, however, remain permanently in the mesovarium as some of the brown bodies.

Dean left no records in his notes as to his ideas regarding either the manner in which the mature eggs are released from the ovarian follicles, or the fate of the corpora lutea. He made two drawings, however, which clearly indicate his views regarding both these questions. These drawings are shown in Figures 15 and 16, plate IV, and illustrate two female specimens of *Bdellostoma* (probably *B. burgeri*) whose ovaries contain many corpora lutea. The large size of the ruptured follicles in the female illustrated in Figure 15 is evidence that in this individual the eggs had but recently been released from the ovary; and the opening in one end of each corpus luteum shows the place and manner of escape. Figure 16 illustrates a specimen in which the corpora lutea are smaller and somewhat wrinkled; they are evidently involved in a process of resorption. Dean referred to this drawing in the list mentioned on page 83 by two words, "capsules retracted"; it is therefore, very probable that he, too, believed that resorption is the ultimate fate of the corpora lutea. Whether he thought the brown bodies in the ovaries represent either atrophied eggs or corpora lutea, or both, is of course problematical. He recorded the number of these brown bodies in each of six females which had corpora lutea (Table IV), but left no suggestion as to what he thought they signify. In one individual (Number 5) he counted 124 brown bodies; if they are atrophied corpora lutea, such a large number of them would represent at least two, and possibly three, different deposits of eggs by that female. If, as Dean believed probable, a female deposits eggs only once each year, female Number 5 had been an adult for three and possibly four years, at the time she was caught.

In this, Doctor Dean has furnished the only suggestion in all the literature as to the normal extent of the life of a myxinoid. The time required for an embryo hagfish to develop to the hatching stage is unknown, nor is the time known which elapses between the hatching stage and the earliest appearance of sexual maturity. Furthermore, no one has been able to gather any definite information regarding the length of time required for eggs to develop to the mature condition; it may be more or less than one year.

TIME OF SPAWNING

Having been released from the ovary by the rupture of the ovarian follicles, the eggs lie free in the body cavity of the female. They are probably immediately extruded to the exterior, being forced through the genital pore by contractions of the musculature in the abdominal wall. No investigator has been able to observe either the act of depositing or fertilizing the eggs. As Dean (1899) has suggested, since the males have no clasping or ejaculatory organs, fertilization very probably occurs after the ova have been extruded from the body cavity of the female. The spermatozoa enter the eggs through the micropyle (Cunningham, 1886.2; Dean, 1899). Dean found the canal to be about the same size as a spermatozoon, and therefore concluded that monospermy is the type of fertilization in the Myxinoidea.

Attempts to solve the many unknown questions concerning spawning have been made by keeping the hagfish in aquaria. Ayers (1893) and Dean (1899) tried this method with *Bdellostoma stouti*, but learned that the eels will not take food while in captivity and soon die. Two pages in Dean's small notebook are filled with notes and small sketches regarding movements of the eels in aquaria, and he made the following entry in regard to feeding: "Food. Dead fish put in—not touched, the specimen had been kept foodless for 10 days. Usually die overnight. If little injured they remain for days. Even healthy lie on side." Cunningham (1886.2) placed some specimens of *Myxine* in an aquarium, and some of them lived there for six months, but they refused to feed. European investigators have spent much time and money in attempts to keep *Myxine* alive in aquaria for observation; some have even constructed elaborate apparatus for experimentally duplicating the temperature, pressure, and other conditions of the water in which the eels live while in their natural habitat. All such attempts, however, have been unsuccessful: the eels will not deposit eggs while in captivity, and refuse to feed, therefore do not live very long.

Putnam (1873) first recorded observations regarding the spawning time. He concluded that the time when eggs are deposited is not the same with all females, for in each lot of specimens of *Myxine* collected in the Straits of Magellan during March there were females with eggs in all the different stages of development. This was also true of females of *Myxine* collected at Grand Manan, Nova Scotia, from August to October. He concluded, therefore, that in the Straits of Magellan eggs are probably deposited by April or May, and about the first of the winter at Grand Manan.

Cunningham (1886.2), after collecting *Myxine* in large numbers, first concluded that, in the North Sea, the eggs are deposited in December, January and February. Later during the same year he wrote:

> Amongst the specimens obtained on January 29th, I recognized for the first time a female which had recently discharged its ova. In place of the 19-25 large ova which are usually present there were a corresponding number of collapsed follicles; each of these had a slitlike aperture at one end, through which the ovum had been extruded. I found afterwards that similar 'spent' specimens were present among a lot obtained on Dec. 24, 1885, and I have obtained them on several occasions since. Thus it is proved that the deposition of ova occurs in *Myxine* in the neighborhood of the Firth of Forth during the months of December, January, February, and March.

Weber (1887.1), in collecting *Myxine* at Alvarströmmen, Norway, and Bohuslän, Sweden, observed that various stages of ova are present at all seasons, and suggested that oviposition is not limited to any certain months in the year.

In March, Cunningham (1887.1) stated, "after examining large numbers of specimens every month in a year I found newly spent specimens only from November till March." Later in the same year (1887.2, June 23rd) he stated that he had taken "spent" females containing ruptured egg follicles in April, May and the first half of June, adding:

> So that there are now six months of the year, November to June inclusive, in which it is, in my opinion, certain that eggs of Myxine are deposited near St. Abb's Head. . . . I now expect to find that recently spent females can be captured in any month of the year, and that oviposition is therefore not limited to a particular season.

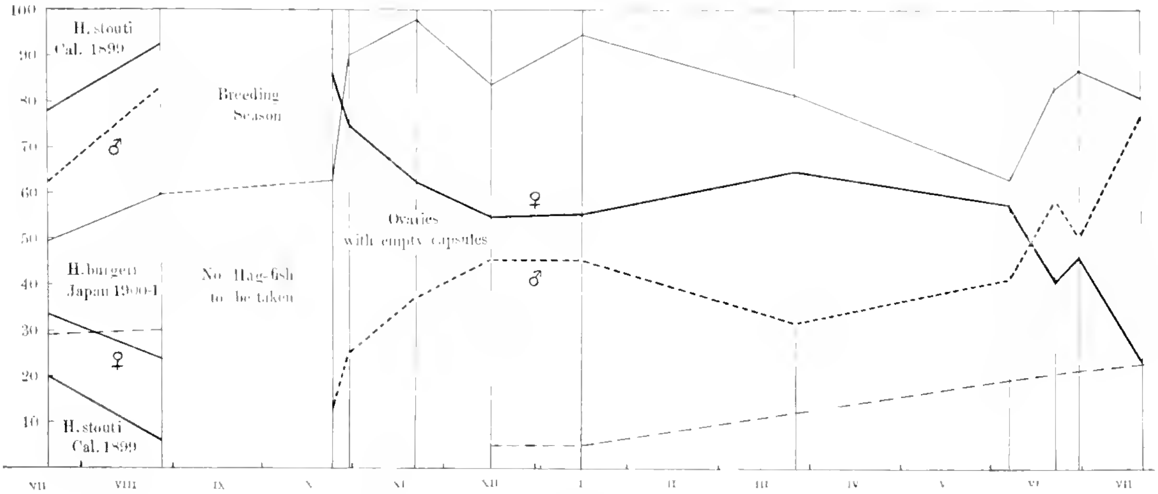
Nansen (1887), in collecting *Myxine* at Alvarströmmen, Norway, caught eels at all seasons of the year with very large (up to 24 mm.) and nearly mature ova, and at the same time found specimens with ova of every smaller size. In addition, he found recently spent females with large empty ovarian capsules at various seasons of the year, in the autumn as well as in the winter and summer. Also, he observed nearly ripe testes in hermaphrodite males at all seasons. He concluded, therefore, "that *Myxine* has no limited breeding season, but breeds at every season of the year."

Price (1896.1) collected ripe females of *Bdellostoma stouti* in Monterey Bay, California, in late winter and early spring on the same ground where Dean (1899) obtained embryos of

Bdellostoma during the late fall and early winter in stages which enabled him "to extend the known season of ovulation throughout the entire year." Dean stated, however, that the last of spring and the first month of summer represented a time of optimum spawning.

The Schreiners (1905, 1908) collected females of *Myxine glutinosa* containing nearly ripe eggs or fresh corpora lutea, and males with ripe or almost ripe spermatozoa at all seasons of the year. They concluded, therefore, that the deposition of eggs is not limited to any special time in the year.

While collecting *Bdellostoma stouti* in California in 1899 and *Bdellostoma burgeri* in Japan in 1900 and 1901 Doctor Dean recorded in his notes many observations which contribute toward answering the question of the spawning time. The most significant of these data he incorporated in a graph which he left with his notes and drawings. This graph is reproduced here.



Text-figure 1. A graph drawn by Doctor Dean to show the data contained in Table II.

The graph is an illustration of the data contained in Dean's Table II (p. 81); the percentages in the graph and in the table correspond exactly, with the single exception that the figures for July 18, 1900, and July 25, 1901, are interchanged in the case of both the heavy solid line and the heavy broken line (short dashes). In the graph Dean has used the name *Homea* instead of *Bdellostoma*.

The abscissa represents the various months of the year, shown in Roman numerals; the vertical lines represent the dates of fishing trips as shown in Table II, beginning with July 18, 1900, at the left and ending at the extreme right with July 25, 1901. The ordinate represents percentages, written in arabic numerals.

The graph shows data for *H. stouti*, collected in California in 1899, for the months of July and August only. The double line in the upper left corner of the graph represents the percentages of males to the total number of specimens of *H. stouti* caught during July and August, 1899; the double line in the lower left corner represents the percentages of females caught during the same months.

The heavy broken line (short dashes) represents the percentages of males of *H. burgeri* taken in the various catches made in Japan from July 18, 1900, to July 25, 1901. The heavy solid line represents the percentages of all females to the total catches of *H. burgeri* made in the various months of 1900 and 1901.

The thin solid line represents the percentages of females of *H. burgeri* which contained eggs of approximately uniform sizes, taken in the various catches from July 18, 1900, to July 25, 1901, as shown in column ten of Table II (p. 81). The thin broken line (long dashes) represents the predominating sizes of eggs in females of *H. burgeri* taken in the various catches throughout the year from July 18, 1900, to July 25, 1901. The ordinate in this case represents the length of eggs in millimeters, written in arabic numerals.

Between the dates of August 29 and October 28, 1900, Dean was unable to catch any eels, although the lines were set several times. He believed that his failure to get any specimens during this time was due to the fact that the eels were breeding; it is well known that many different kinds of fish do not feed during the spawning season.

Further evidence that the spawning season may be during the months indicated by Dean in his graph is furnished by the fact that, immediately after the spawning season, a very high percentage of the females taken had empty ovarian follicles (capsules), as is shown in the graph. Table II (page 81) shows the percentages of females having empty follicles in the ovaries to be as follows: on October 28, 1900, 63 per cent; on October 30th, 90 per cent; on November 25, 98 per cent. The presence of empty ovarian follicles in the ovary of a female is positive proof that ova had been recently deposited.

Additional support for Dean's opinion as to the breeding season is to be found in his data regarding the sizes of eggs in females taken in the various months of the year. In Table II (page 81) it will be seen that on December 15, 1900, one month after the catch which contained the highest percentage of empty ovarian follicles, the average length of the eggs in the females was 4.4 mm.; on January 15, 1901, one month later, the average length of the eggs was 4.2 mm., or practically the same. This lack of increase in size can be explained by the hypothesis which I advanced (1917, p. 124), namely, that the eggs in an ovary containing corpora lutea are arrested in development until the latter are almost completely resorbed. On March 30th, two and one-half months later, the average length of the eggs was 11.9 mm. From that date on there was a gradual increase in the size of the eggs, the largest ones being in females caught on August 29th, shortly before the spawning season. These eggs in females taken on that date averaged 23 mm. in length, which is approximately the size of mature eggs. These facts in regard to the gradual increase in the size of eggs from December to late August are shown in the graph (page 94) by means of the long dashes. In this case the abscissa, as before, represents the months of the year, while the ordinate indicates the average length of eggs in millimeters.

Very significant also, in respect to the breeding season, are the data in Dean's notebooks regarding the males caught in the different months of the year. These data are shown by Dean in condensed form in Table II (page 81) and in this graph. During the months immediately preceding the breeding season, when the eggs in females were approaching the size and condition of maturity, a very large percentage of the eels caught were males, as can be seen in Table II (page 81). On July 18th the males constituted 62 per cent of the total catch; on July 25th, 78 per cent, and on August 29th, immediately before the eels began breeding activities, 83 per cent were males. Under "Remarks" for this date Dean wrote: "Many large males, average about 48 cm." Immediately after the breeding season fewer males were taken, 13 per cent of the catch on October 28th and 24 per cent on October 30th. The notation under "Remarks" for the latter date states: "All mature males spent." The proportion of males increased to 37 per cent on Nov. 25th: during the months from December to June, inclusive, while the eggs in the females were developing, approximately equal numbers of males and females were taken in each day's catch. These months may be a period of sexual quiescence.

The conclusion which Dean drew from his observations, namely, that the spawning season for *Bdellostoma* is during late August, all of September, and the first three weeks of October, is at variance with his statements in 1899 (p. 224):

> I find, furthermore, that embryos can be obtained during the late fall and early winter, in stages which enable me to extend the known season of ovulation throughout the entire year. A time representing the optimum spawning probably occurs; and this I believe to be the last of spring and the first month of summer, basing this view upon the uniform size of embryos collected during the months of August and September, and upon the growth rate of embryos which I attempted to rear.

It is possible that Dean changed his opinion regarding the time of spawning after making observations on *Bdellostoma burgeri* in 1900 and 1901. The two differing views emphasize the fact that the spawning time for the Myxinoidea is not yet known.

My own experience has been too limited to be of assistance in solving this question. Like other investigators, I have in every month of the year collected females of *Myxine* with large eggs which had the appearance of being almost ready to be extruded. But the time required for the eggs to grow to the mature condition is not known; it is possible that a female carries large eggs for almost a year before they are ready for depositing. One cannot be positive, therefore, that the presence of large eggs in females taken in every month means that there is no definite season for ovulation, and that eggs are deposited at all times of the year. More significant, perhaps, than the presence of large eggs in females at all seasons, is the condition of development of embryos recovered from the bottom of the ocean in different months. During each of the months of June, July and August, 1930, I collected embryos of *Bdellostoma stouti* in all stages of development from blastodermic discs to embryos almost ready to hatch. This would indicate that spawning occurs before and during those three months. On almost every day of this time I caught females representing all stages in the growth of the eggs, from the smallest to the largest. Very interesting, however, is the fact that during this time I did not find any females with corpora lutea in the ovary; the presence of large corpora lutea is positive proof that mature eggs had been recently deposited. Another very interesting fact is that, like Dean, I was unable to catch any eels during the last week in August. I fished from June 18th to August 28th, and up to the last ten days was catching one hundred or more specimens every day; then on the succeeding two or three days the number of eels caught decreased, and during the last week none was taken, even though the lines were shifted to many different places. I am entirely at loss to state any conclusion regarding the time of spawning, excepting that it is not definitely known.

THE PROBLEM OF THE DESCENT AND RELATIONSHIPS OF THE MYXINOIDEA

Dean was also greatly interested in the problem of the descent and relationships of the myxinoids, and he discussed some phases of this question in his description of the general embryology of *Bdellostoma stouti* (1899, pp. 222 and 272). In this paper he wrote as follows:

> And one can, I believe, say justly that upon this question there is no uniformity of belief even among the few specialists who at present deserve to be ranked as the most competent judges. The critics will at the best agree in but the single proposition that the cyclostomes are a degenerate group—but they all will disagree as to the limits of this degeneration. . . . It is clearly evident that before any definite conclusions can be reached in these matters a wide range of data must yet be forthcoming. But on what side should this be sought? Will it be obtained on the sides of the morphology of fossil and recent forms? Is this additional evidence to be forthcoming on the side of development?

It was Dean's belief that the developmental history of the myxinoids would be of some value in solving these general problems. As to paleontology, he expressed the opinion that the cyclostomes "are such unfavorable subjects for preservation that their lack of occurrence as fossils is in no way remarkable: but that their remains may be found and ultimately prove of the greatest value in general determination no one can gainsay." Subsequent investigations in the realms of morphology, embryology and paleontology have demonstrated the correctness of Dean's predictions.

The contributions from embryology toward solving the problem of the descent and relationships of the *Myxinoidea* have been confined to studies of embryos of *Bdellostoma stouti* alone, for the embryos of no other myxinoid have been found. Possibly Dean succeeded in collecting a few embryos of *Bdellostoma burgeri* in Japan in 1900 and 1901: at any rate he made the following entry in his small notebook. This is the only reference in his notebooks as to obtaining eggs of *Bdellostoma burgeri*.

> Eggs from boat for Kuma [head fisherman and collector at Misaki]. From slime of a lump from several individuals all together gather animals just as in Cal."

In another place he wrote:

> In the night of 25th Nov. Kuma went out for longlining to collect *Bdellostoma*, and got two masses of eggs, and 102 individuals. At this number he said he stopped letting down his lines again. Early in the morning (26th Nov.) I measured the length of the fish and Bun noted down.

Mass A consists of 7 eggs, perhaps at very young stage

Number	Length	Width
1	20 mm.	7.5 mm.
2	20	7.5
3	22	9
4	20	7.5
5	20.1	7.7
6	24.5	9.5
7	20	8.5

Mass B consists of 8 eggs.

Number	Length	Width
1	23 mm.	10 mm.
2	20	7
3	21	9.5
4	19	9.7
5	20	10
6	22	11
7	20	7.5
8	22	9.5

Eggs from No. 3.

Number	Length	Width
1	23 mm.	9 mm.
2	21	9.5
3	27	9
4	Empty shells	
5	" "	
6	" "	

G. C. Price (1896.1), of Stanford University, California, made the first contribution to our knowledge of the embryology of the Myxinoidea. From a few embryos of *Bdellostoma stouti*, collected at Pacific Grove, California, and representing but three stages of development, Price described some phases in the development of the excretory system. Later (1904), having succeeded in obtaining more embryos, he was able to make a more extensive study of the ontogeny of the excretory system. As a result of his investigations Price concluded that the entire excretory organ develops like the pronephros of other vertebrates; that a very small anterior part remains a pronephros in the adult, but the long, segmental posterior portion becomes transformed into a mesonephros before the definitive condition is reached. Price states:

> If the view above expressed be correct, the mesonephros of the Myxinoids is primitive in a much more fundamental sense than has hitherto been supposed, and the natural inference would be that it represents the ancestral condition, from which the mesonephros of other vertebrates has been derived. . . . I should like to say, however, that embryology teaches that the excretory system of the Myxinoids is not only more primitive, but much more primitive than that of any other known vertebrate except *Amphioxus*.

Dean (1899) made the next contribution to our knowledge of the developmental history of a myxinoid. He gave a very excellent description of the general embryology of *Bdellostoma stouti* from segmentation stages to hatching, "based upon material collected in the Bay of Monterey, California, mainly during the months of August and September, 1896." As to evidences of relationships furnished by embryology he concluded that "the Myxinoids are not to be looked upon as forms which have become greatly degenerate," and that the presence in the embryos of a transversely directed mouth and the mode of origin of the barbels around the mouth indicate clearly that *Bdellostoma* belongs to the Gnathostomes.

During the summer of 1896, while Dean was collecting embryos of *Bdellostoma stouti* at Pacific Grove, California, Franz Doflein (1898, 1899), then of München University, Germany, was also at Pacific Grove and obtained some embryos of *Bdellostoma* from the same fisherman who was collecting embryos for Dean. Professor Carl von Kupffer, of

München University, used the embryos obtained by Doflein for studying the development of the head of *Bdellostoma stouti* (1899, 1900; 1906). He did not, however, express any opinion as to the descent and relationships of the Myxinoidea. He believed the nose developed from an unpaired "Reichplakode" (1900, p. 11), whereas Dean (1899, p. 273) was of the opinion "that the embryonic nasal sacs arise from the early 'Nasenrachengang' as distinctly paired structures." The adult nose shows no indication of ever having been paired; but a paired nose in the embryonic stages of development would link the Myxinoidea with the Gnathostomes.

Stockard (1906.2) wrote an excellent paper on the development of the mouth and gills in *Bdellostoma stouti*, using Dean's collection of embryos for this purpose. He concluded that the myxinoids are gnathostomatous vertebrates, the so-called "tongue" being the homologue of the gnathostome jaw. Furthermore he considered the myxinoids as "undoubtedly primitive," but decidedly specialized in some respects. Neumayer (1910), however, in a short discussion on the development of the cranium of *Bdellostoma stouti* based on a study of a few embryos from Dean's collection, expressed the opinion that the complete absence of an articulating jaw and the presence of an unpaired nose separate the myxinoids from the Gnathostomes.

My investigations on the development of the brain of *Bdellostoma stouti* (Conel, 1929, 1931) based on Dean's collection of embryos, lead me to the conclusion that the myxinoids are primitive, but, like all living vertebrates, have undergone some modifications as to structure. In early embryonic stages the brain follows the developmental changes which occur in the ontogeny of all generalized vertebrates, at one stage resembling especially closely the brain of *Necturus*. The eye is somewhat modified in the adult, but develops in the manner typical of vertebrates. After an extensive and excellent study of the fiber tracts in the adult brain of *Myxine glutinosa*, Jansen (1930) concluded that "in spite of striking morphological differences, an analysis of the functional relations of the nuclear masses in the brain of *Myxine* reveals great concordance with the conditions in generalized vertebrate brains, like those of petromyzonts and Amphibia." As a result of these studies upon the development and adult structure of the brain, it seems reasonable to conclude that the Myxinoidea, in respect to this organ at least, are primitive.

As Dean (1899, p. 222) suggested might sometime occur, paleontology also has recently furnished an important contribution toward solving the problem of descent and relationships of the Myxinoidea. Fossil remains of Ostracoderms (Cyclostomes) have been discovered in Spitsbergen by Norwegian expeditions from 1906 to 1925, and have been excellently described and discussed by Stensiö (1927). His studies upon these fossils led him to the following conclusions (1927, p. 373):

> Thus the Ostracoderms had already very early separated into two main branches, one of which includes the Osteostraci, Anaspida and Petromyzontia, while the other consists of the Heterostraci and Myxinoidea. To make it easy to refer to these two branches it will of course be necessary to name them, and I therefore propose for the first mentioned branch the term

> Cephalaspidomorphi and for the other the term Pteraspidomorphi. The knowledge which we now possess concerning their phylogeny and relationships shows that the Petromyzontia and Myxinoidea have degenerated in certain respects, as, for instance, with regard to the degree of development of the skeleton and the absence at least of pectoral fins and shoulder-girdle, but that otherwise on the whole they remain in a very lowly organized stage of evolution and that they are primarily agnathous forms.

Stensiö believes that the Myxinoidea are "descendants either from *Palaeospondylus* or from primitive Heterostraci." He suggests the following classification to express the interrelationship of the Ostracodermi:

VERTEBRATA CRANIATA
BRANCH I AGNATHI
  CLASS OSTRACODERMI (CYCLOSTOMATA)
    SUB CLASS A PTERASPIDOMORPHI
      ORDER 1 HETEROSTRACI
      ORDER 2 PALAEOSPONDYLOIDEA
      ORDER 3 MYXINOIDEA
    SUB CLASS B CEPHALASPIDOMORPHI
      ORDER 1 OSTEOSTRACI
      ORDER 2 ANASPIDA
      ORDER 3 PETROMYZONTIA
BRANCH II GNATHOSTOMI.

From the above brief resumé of the literature it is evident that the investigators in the two fields which Dean believed would yield the most informative evidence, namely embryology and paleontology, agree that the Myxinoidea are primitive; but there is a difference of opinion as to whether these low vertebrates belong to the Gnathostomes or to the Agnathostomes.

SUMMARY

A general summary of the entire paper is hardly necessary, as a discussion and resumé have been given within each section. The data which Doctor Dean left in the form of notes, tables, graphs, and sixteen excellent drawings, which have formed the chief basis of this paper, have made many important contributions to our knowledge of the Myxinoidea. The information which he has supplied makes it inexcusable to continue publishing in text-books the statement that some of the myxinoids are protandric hermaphrodites. He has shown that *Bdellostoma* is certainly not hermaphroditic in any respect, and has raised grave doubts as to whether *Myxine* is functionally hermaphroditic, even though it is structurally. The extensive investigations of the Schreiners have proved that Dean was correct in doubting that *Myxine* is functionally an hermaphrodite.

Dean's data regarding the eggs are very interesting and instructive, and furnish us with much information concerning phenomena related to the development of the ova, their escape from the ovary, and the time of spawning. The following points seem almost, if not quite established as facts:

1. When some eggs have grown to a length of 2–5 mm., all the smaller eggs are arrested in growth while a favored few continue to develop to maturity; the favored eggs are approximately segmental, one to each myomere, and continue to develop to the condi-

tion of maturity because each egg receives most of the blood in the corresponding segmental ovarian artery.

2. After escape of the mature ova, the ruptured ovarian follicles (corpora lutea) are resorbed.
3. All eggs in the ovary are arrested in development until the corpora lutea are almost completely resorbed.
4. Traces of corpora lutea and atrophied eggs remain in the ovary as "brown bodies."
5. The spawning time is not definitely known.

The preponderance of evidence based on embryology, contributed by various investigators, indicates that the Myxinoidea are primitive, and belong to the Gnathostomes. Stensiö, the sole investigator in the field of paleontology, regards the Myxinoidea as primitive, but classes them with the Agnathostomes.

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PLATE I

GENITAL SYSTEM OF THE MYXINOIDEA

GENERAL EXPLANATION OF PLATE FIGURES

All of these figures were drawn by Doctor Dean from dissections, probably of specimens of *Bdellostoma burgeri*, although they may represent *Bdellostoma stouti* (see pp. 83 and 84). Doctor Dean gave no information to indicate the proportions of the drawings to the actual specimens; they are probably life size.

In all the males the testis is located in the posterior part of the mesorchium. In all the females the smallest eggs are nearest the free (outer) margin of the ovary, while the successively larger eggs occupy positions successively nearer the attached (inner) edge of the mesovarium, the largest eggs being the most internal, i.e., nearest the attached margin.

PLATE I

A SERIES OF STAGES IN THE DIFFERENTIATION OF THE TESTIS OF *BDELLOSTOMA BURGERI*

Fig. 1. Youngest male; testis scarcely differentiated.

Fig. 2. Slightly older male; testis more distinct. Mesorchium slightly waved in posterior part.

Fig. 3. Somewhat older than the preceding; follicles can be seen in the testis, which is larger and more waved.

Fig. 4. Testis band broad, thick, and much folded; follicles more evident.

Fig. 5. An adult specimen. Testis increased in width and breadth, and very much folded and lobulated.

All the figures on this plate are one sixth smaller than the original drawings.

PLATE II

GENITAL SYSTEM OF THE MYXINOIDEA

PLATE II

FIVE STAGES IN THE DEVELOPMENT OF THE OVARY AND OVA OF *BDELLOSTOMA BURGERI*

Fig. 6. A very young female. All the eggs are spherical and vary in size from mere dots to 0.8 mm. in diameter.

Fig. 7. A slightly older female. All the eggs are spherical and are of all sizes from 1 mm. in diameter to mere dots.

Fig. 8. The next older female. All the eggs are spherical in shape, the largest measuring 1.5 mm. in diameter.

Fig. 9. The largest eggs are slightly tapered at each end; all smaller eggs are spherical.

Fig. 10. The largest eggs are spindle-shaped and measure from 4 to 7 mm. in length. The next smaller are eggs 2 mm. long.

Figures 6, 7, 8 and 9 are the same size as the original drawings. Figure 10 is reduced by one-fourth.

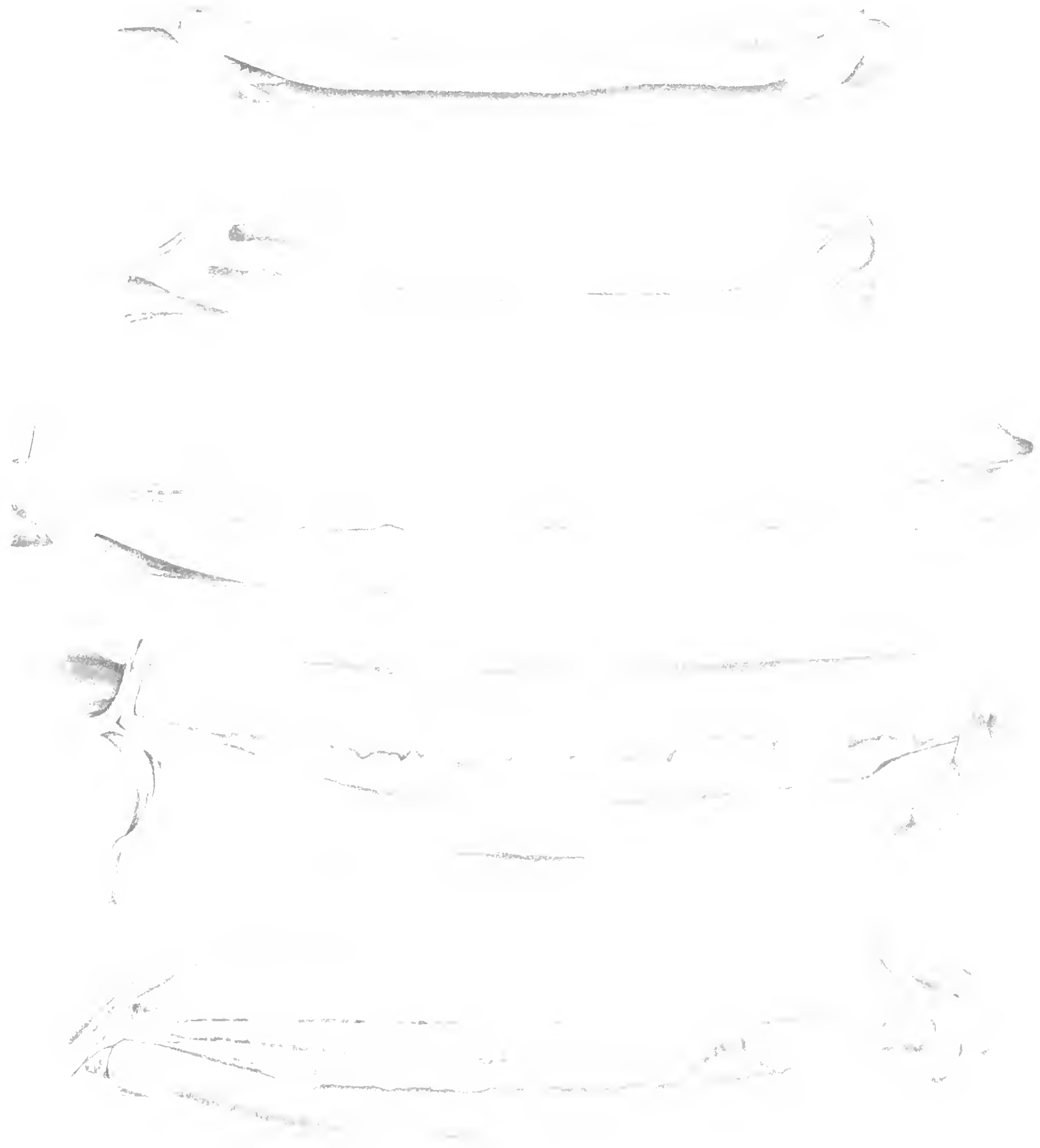

PLATE III

GENITAL SYSTEM OF THE MYXINOIDEA

PLATE III

LATE STAGES IN THE GROWTH OF THE EGGS OF *BDELLOSTOMA BURGERI*

Fig. 11. The largest eggs measure from 7 to 10 mm. in length.

Fig. 12. The largest eggs are 11 to 13 mm. in length, and are proportionately thicker. The arteries have been injected with a red mass; the ovarian arteries are indicated in red.

Fig. 13. A female in which the largest eggs measure from 15 to 18 mm. in length, and have increased in diameter.

Figure 11 is the same size as the original drawing, while figures 12 and 13 are reduced by approximately one-fourth.

PLATE IV

GENITAL SYSTEM OF THE MYXINOIDEA

PLATE IV

RIPE AND SPENT OVARIES OF *BDELLOSTOMA BURGERI*

Fig. 14. A female with eggs almost mature, measuring from 20 to 22 mm. in length, and 7 to 8 mm. in width.

Fig. 15. A female which has recently discharged her ova. Each ovarian follicle is ruptured at one end.

Fig. 16. A female with empty ovarian follicles (corpora lutea) which are "retracted." The follicles present a shrunken and wrinkled appearance indicating that they are being resorbed.

All the figures on this plate are about one fourth off the original size.

THE

BASHFORD DEAN MEMORIAL VOLUME

ARCHAIC FISHES

Edited By
EUGENE WILLIS GUDGER

ARTICLE IV

THE STRUCTURE OF *DINICHTHYS* A CONTRIBUTION TO OUR KNOWLEDGE OF THE ARTHRODIRA

By ANATOL HEINTZ
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Oslo, Norway

THE
AMERICAN
MUSEUM
OF
NATURAL
HISTORY
SCIENCE
EDUCATION

NEW YORK
PUBLISHED BY ORDER OF THE TRUSTEES

Issued June 15, 1932

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A CONTRIBUTION TO OUR KNOWLEDGE OF THE ARTHRODIRA

BY ANATOL HEINTZ

CONTENTS

Warum ich am liebsten mit der Natur verkehre ist weil sie immer Recht hat, und der Irrthum bloss auf meiner Seite sein kann.

(Goethe. Zur Natur)

THE STRUCTURE OF *DINICHTHYS*
A CONTRIBUTION TO OUR KNOWLEDGE OF THE ARTHRODIRA

By Anatol Heintz
Curator of the Paleontological Museum,
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INTRODUCTION

As we know, Newberry, in 1868, described the first fragments of *Dinichthys* (*D. herzeri*). Since that time, nearly ninety larger and smaller papers on *Dinichthys* have been published by various American scientists. Of these Newberry published 15; Adams, 1; Branson, 4; Bryant, 1; J. M. Clarke, 3; W. Clark, 1; Claypole, 11; Dean, 12; Eastman, 18; Hussakof, 10; Moodie, 1; Ringeberg, 1; Smith, 2; Stetson, 1, and Wright, 2. Among these publications, nearly all of Newberry's and Dean's, and many of Hussakof's, are descriptions of and observations on the material preserved in the American Museum of Natural History.

I also have had the privilege of studying these remarkable collections and have been successful in finding some new points in the structure of *Dinichthys*, and have been able to make a new reconstruction of this form. Doctor William King Gregory, Professor of Vertebrate Palaeontology in Columbia University and Curator of Ichthyology in the American Museum of Natural History has been good enough to propose to me this publication of the results of my investigations.

In this place I wish to express my deep gratitude to my teacher and friend, Professor Johan Kiaer, of the University of Oslo, for all the kindness he has shown me, and for his constant help. Only through his efforts was I able to come to America.

I also desire to express my best thanks to Professor Gregory for the privilege of studying in the American Museum and for all the benevolent interest he has shown my work, and I am also obliged to Dr. L. Hussakof, Research Associate in Devonian Fishes in the Museum, for his friendliness during my studies in America. I am especially grateful to Miss Francesca La Monte, Assistant Curator, for the constant help and unusual kindness she has shown me.

During the summer of 1930, I visited the Cleveland Museum of Natural History, the Museum of the Buffalo Society of Natural Sciences, and the Museum of Comparative Zoology at Harvard University. In all these institutions I was permitted to study the collections of Arthrodira, and I here wish to express my gratitude to the authorities of these museums for their courtesies.

The material in Cleveland, Ohio, gathered under the direction of Professor J. E. Hyde, is the most perfect collection of Arthrodira I know. However, since it is going to be described in a monograph by Professor Hyde, nothing I saw in Cleveland is included in this work. I might only mention here, however, that in spite of Professor Hyde's far superior material, and in spite of some new plates of *Dinichthys* he has found, the descriptions given in this paper correlate perfectly with the new material in Cleveland. I am glad to have the opportunity of expressing my thanks to Doctor Hyde for the great kindness he showed me during my Cleveland visit.

The collection in the Buffalo Museum, Buffalo, New York, includes some very well preserved plates of *Dinichthys* gathered by Professor W. Bryant of Providence, Rhode Island. I wish to express to him my gratitude for permission to describe and figure some plates of his material. For the same privilege, I am obliged to Professor Charles Fish, Director of the Buffalo Museum. For the privilege of studying the collection in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, I am grateful to Dr. H. C. Stetson.

The majority of the photographs illustrating this work are by Mr. H. S. Rice of the American Museum of Natural History. Two of the spinal plate from the Buffalo Museum, are by Mr. Schneckenburger. All microphotographs and drawings are by the author himself.

DINICHTHYID MATERIAL

The beautiful collection of *Dinichthys* fragments in the American Museum of Natural History is mostly very old. The major part of it consists of Newberry's material, including all the originals used in his works. This collection, the property of Columbia University, has been kept on deposit in the American Museum since 1911. The rest of the collection belongs to the American Museum and was partly bought from J. Terrell, in 1901, and partly collected in 1914–15 by Doctors Hussakof and Bungart. The whole collection consists of some hundred pieces of very different quality, ranging from nearly complete head shields to the smallest indeterminable fragments of bone. All the specimens of *Dinichthys* in the collection of the American Museum are from the Cleveland shale of Ohio (Upper Devonian).

The bones are usually preserved in concretions of hard, dark limestone. The fossils themselves are also dark, nearly black, but microsection shows very well preserved bone structure. One finds in the concretions mostly separate bones of the body carapace or fragments of the head shield, and plates of the same individual are very seldom found together. Moreover, as Hussakof (1905.1) writes:

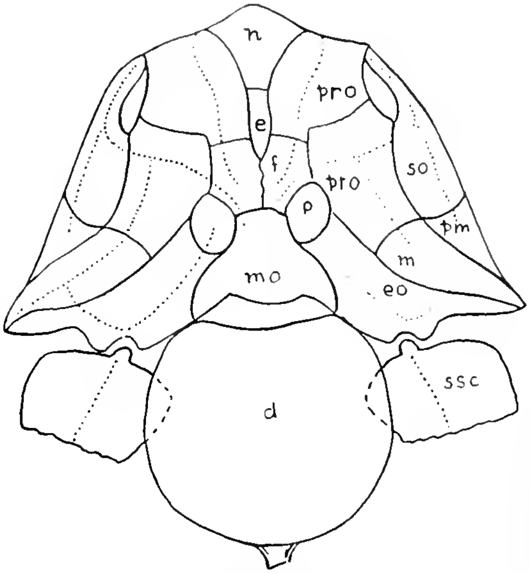
> Some of the best material from the classical Ohio localities has been lost through the vagaries of enthusiastic local collectors, who would detach from a concretion only the larger plates, casting out all other parts, and then shuffle together the detached elements so that it is well-nigh impossible to bring together again the parts from the same concretion.

Because of this, most of the remains of *Dinichthys* in the Museum's collection represent isolated plates of the body carapace of different individuals and some more or less complete head shields. Both the head shield and the big body plates are for the most part broken and crushed. Especially the larger and strongly curved plates such as the median-dorsal, antero-lateral and the posterior part of the head shield, are greatly destroyed by pressure.

It is therefore clear that the reconstruction of a carapace of *Dinichthys* is a difficult task. Many have tried it, but up to now no satisfactory reconstruction has been made.

THE OLDER RECONSTRUCTIONS OF *DINICHTHYS*

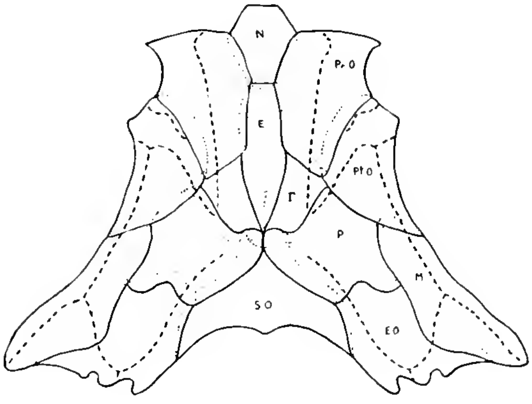
The first attempt in this direction was made by Newberry. In his paper (1875.1) we find a reconstruction of a *Dinichthys* "plastron," that is, the ventral shield. In this reconstruction he has placed the sub-orbital in the position of the postero-ventro-lateral, a mistake he himself corrected later in "Palaeozoic Fishes of North America" (1889).



Text-figure 1.
Newberry's reconstruction of *Dinichthys intermedius* Nwb. (1889).
d, dorso-median; *e*, ethmoid; *eo*, external-occipital; *f*, frontal; *m*, marginal; *mo*, middle-occcpital; *n*, nasal; *p*, parietal; *pm*, post-maxillary; *pro*, pre-orbital; *pto*, post-orbital; *so*, sub-orbital; *ssc*, supra-scapula.

In the latter paper he also gives the first reconstruction of the head shield and part of the dorsal shield (Text-figure 1). The drawing of the head is nearly correct but the limits between the plates are too schematic. The "central" is divided into two plates, and the external-occipital (*eo*) is too large. Besides this, we find a very interesting detail,—a small triangular plate behind the sub-orbital. Newberry called it the post-maxillary but did not describe it in the text. We shall return later to this plate.

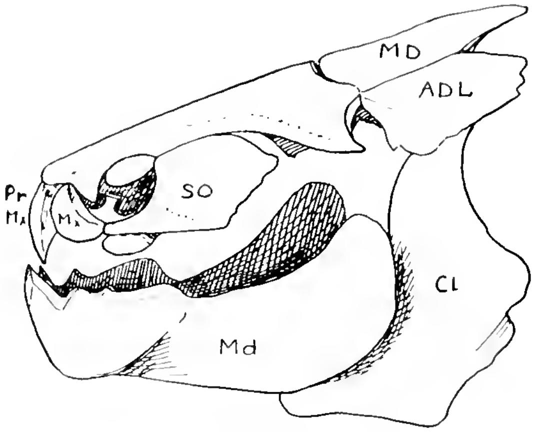
Of the dorsal body carapace we find only the median-dorsal and antero-dorso-lateral in the Newberry reconstruction. The median-dorsal is too round and placed too far forward, so that it comes in contact with the posterior part of the head shield and covers the opening between the head and body carapace. The antero-dorso-lateral only touches the median-dorsal. Of the other body plates, Newberry recognized the antero-ventro-lateral, median-ventral, antero-median-ventral, antero-lateral (clavicular) and postero-dorso-lateral, but he could not clearly define their position.



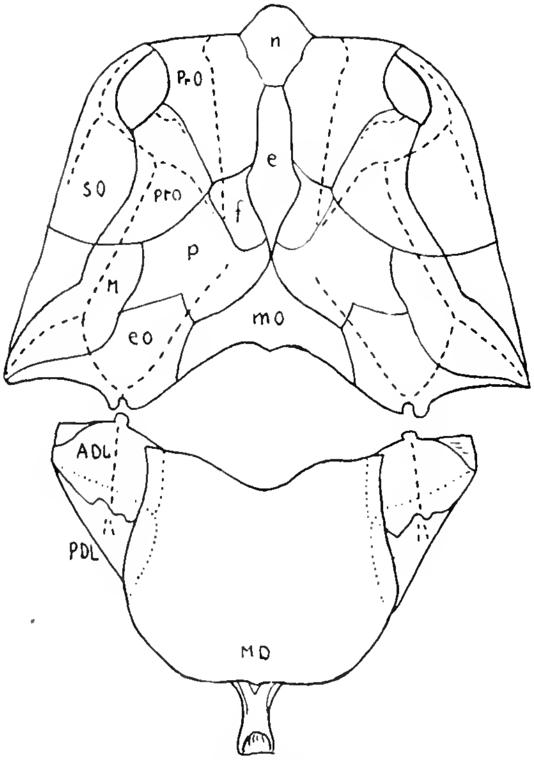
Text-figure 2.
Claypole's reconstruction of *Dinichthys intermedius* Nwb. (1892).
E, ethmoid; *EO*, external-occipital; *F*, frontal; *M*, marginal; *Ṅ*, nasal; *P*, parietal; *PrO*, pre-orbital; *PtO*, post-orbital; *SO*, supra-occipital.

We find in Dean's paper (1891), dealing with the pineal fontanelle of *Dinichthys*, a redrawing of Newberry's reconstruction with the one difference that the above mentioned plate, the post-maxillary, is here called hyomandibular.

Next, Claypole (1892.2) published a paper on *Dinichthys* with a very good figure of its head from outside and inside (Text-figure 2). The limits between the single plates are correctly drawn, but he, like Newberry, has divided the "central" into two plates, "frontal" and "parietal." Claypole's section of the head is especially interesting since he correctly shows the strong curving of the head shield.



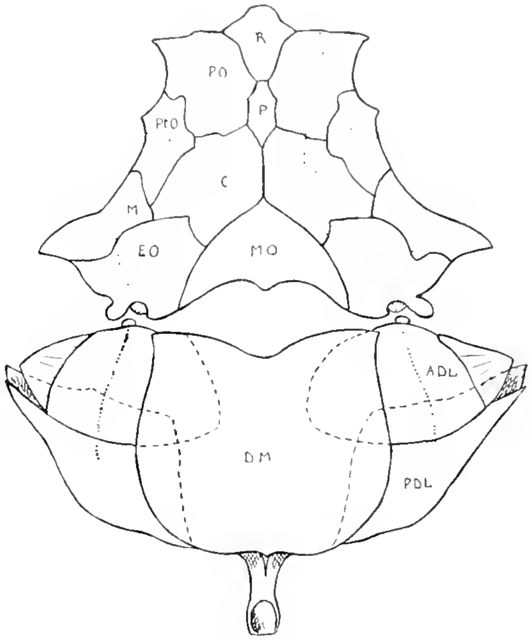
Text-figure 3.
Dean's reconstruction of *Dinichthys intermedius* Nwb. (1895).
ADL, antero-dorso-lateral; *Cl*, clavicular; *MD*, median-dorsal; *Md*, mandible; *Mx*, maxilla; *PrM*, premaxilla; *SO*, sub-orbital.



Text-figure 4.
Eastman's reconstruction of *Dinichthys intermedius* Nwb. (1897).
ADL, antero-dorso-lateral, *e*, ethmoid; *eo*, external-occipital; *f*, frontal, *M*, marginal; *MD*, median-dorsal, *mo*, middle-occipital; *n*, nasal; *p*, parietal; *PDL*, postero-dorso-lateral; *PrO*, pre-orbital; *PtO*, post-orbital; *SO*, sub-orbital.

Dean, in his "Fishes Living and Fossil" (1895) reproduces a photograph of the first more complete reconstruction of *Dinichthys intermedius* Nwb. (Text-figure 3). This reconstruction consists of the whole head shield with sub-orbital and jaw elements and the median-dorsal, antero-dorso-lateral and antero-lateral of the body carapace. Because of imperfect knowledge of the osteology of *Dinichthys*, this reconstruction shows many mistakes. The head shield is not strongly enough curved. The orbit openings are too large. All the jaw elements, especially the mandibles, are taken from larger examples than are the other parts of the carapace. The maxilla is incorrectly placed in relation to the sub-orbital. The median-dorsal, congruent with Newberry's drawing, is set too far forward. The contact between median-dorsal and antero-dorso-lateral is too short and too weak. The antero-dorso-lateral itself is placed too horizontally. The antero-lateral, which also is taken from larger specimens, touches the antero-dorso-lateral from the underside. (As we know in reality the antero-lateral overlaps the antero-dorso-lateral). The posterior part of the mandible rests on the antero-lateral, a mistake we find in many other reconstructions.

Besides these photographs, we find in the same book two drawings of *Dinichthys*. The first is a redrawing of Newberry's reconstruction of 1889, the only difference being that the "post-maxilla" is omitted and the sub-orbital is made correspondingly larger. The other picture is an attempt to make a total reconstruction of the whole *Dinichthys*. This drawing is not successful; the position of the antero-dorso-lateral is wrong; there is no contact between the dorsal and ventral carapace, etc.

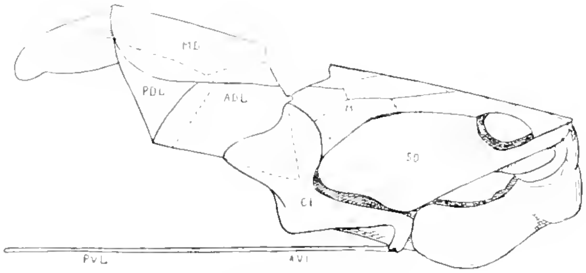


Text-figure 5.
Hussakof's reconstruction of *Dinichthys intermedius* (1905).
ADL, antero-dorso-lateral; *C*, central; *DM*, dorso-median; *EO*, external-occipital; *M*, marginal; *MO*, median-occipital; *P*, pineal; *PDL*, postero-dorso-lateral; *PO*, pre-orbital; *PtO*, post-orbital; *R*, rostral.

Two years later Eastman (1897.2) published his first reconstruction of *Dinichthys* (*D. intermedius* Nwb, Text-figure 4). Like Newberry he placed a plate at the back of the sub-orbital and divided the central into two plates. Here, for the first time, the dorsal part of the body carapace (median-dorsal, antero-dorso-lateral and postero-dorso-lateral) is correctly figured, but it is too small in relation to the head shield. The next year Eastman (1898.3) made a little change in the reconstruction. He did not divide the central into two plates. The sub-orbital is excluded. Of the body carapace he figured the same five plates, but they are now larger than in the reconstruction of 1897— nevertheless still too small. Eastman's method of drawing reconstructions became a standard type for later works on *Dinichthys*. We find it used by Eastman himself, Dean, Hussakof, and others.

The same year Clark (1898) tried to give some new points of the fine attachments of *Dinichthys*, but his reconstruction is incorrect for he placed the "clavicular" upside down. The first true relation between head and body plates is to be found in Hussakof's reconstruction of 1905 (Text-figure 5).

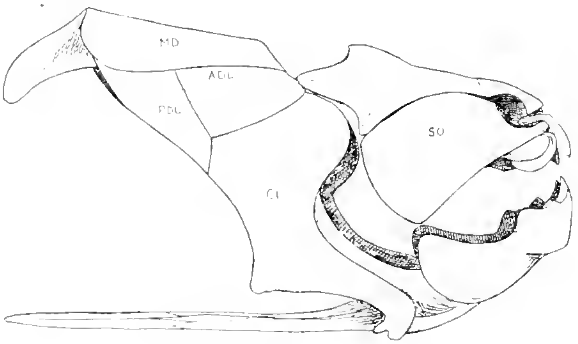
Although the structure of the ventral armor in *Dinichthys* has been studied by many authors (Newberry, 1875, 1889; Wright, 1894; Dean, 1896 and 1897, Eastman, 1897.2, .3; Hussakof, 1905.1, .2) nobody has been especially interested in the attachment of the dorsal and ventral carapace. The first attempts in this direction were made by Branson in 1908 and 1911. His reconstruction of *Dinichthys terrelli* (Text-figure 6) showed some new and correct alterations. In it the fore part of the "clavicular" covered the posterior part of



Text figure 6.
Branson's reconstruction of *Dinichthys terrelli* Nwb. (1908).
ADL, antero-dorso-lateral, *AVL*, antero-ventro-lateral; *Cl*, clavicle; *M*, marginal; *MD*, median-dorsal, *PDL*, postero-dorso-lateral; *PVL*, postero-ventro-lateral, *SO*, sub-orbital.

the exoccipital and marginal. In the posterior corner of the marginal he figured a new sensory canal, nearly perpendicular to the marginal canal. As we shall see later, Branson has here mistaken the limit between two plates for a canal. The sub-orbital is very large since his sub-orbital was in reality three plates. He also made several other mistakes. The ventral carapace came in contact with the lower part of the "clavicular" and was nearly parallel to its narrow lower part. In consequence, the distance between the ventral and dorsal part of the body was too short and the whole fish too flat. The size and position of the antero-dorso-lateral were also incorrect, and the postero lateral was not figured at all. Nevertheless, Branson's reconstruction is one of the best, for it is based on fragments of only one specimen. Therefore the relation between the size and position of the single plates is more or less correct.

The next year, 1909, Dean gave a short description with six photographs of a reconstruction of *Dinichthys terrelli*, Nwb. (Text-figure 7), which is now on exhibit in the American Museum of Natural History. This is the most complete reconstruction of *Dinichthys* known to me.[1] Unfortunately, in making it, plates from four different specimens were used and some of these were made of plaster. Therefore the relation between the single plates is not entirely correct. As a whole this reconstruction, was very which good for its time, shows many mistakes:



Text-figure 7.
Dean's reconstruction of *Dinichthys terrelli* Nwb. (1909).
ADL, antero-dorso-lateral, *Cl*, clavicle; *MD*, median-dorsal, *PDL*, postero-dorso-lateral; *SO*, sub-orbital.

1. The entire carapace is too flat and too broad, especially the head shield and the median-dorsal plare which are not sufficiently curved.
2. The ventral shield is not related to the dorsal shield. This circumstance alone makes the reconstruction improbable.
3. The clavicular (made of plaster) is too big in relation to other plates. The spinal and intero-lateral are not shown. They are included in the clavicular, and are incorrectly placed.
4. The postero-lateral is absent. Later the reconstruction was changed a

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[1] According to Dean, two other Museums (Harvard and South Kensington) have made attempts to reconstruct *Dinichthys*, but the present writer has been unable to find anything about these two reconstructions in the literature.

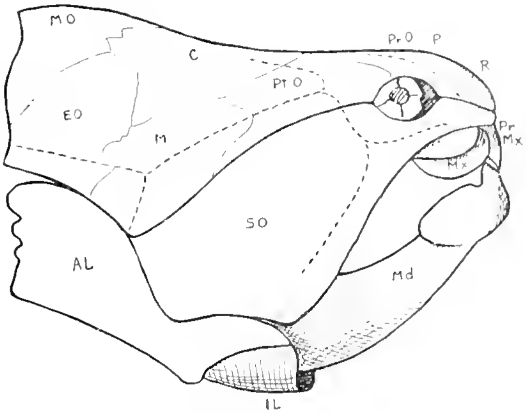
little and the postero-lateral was included in the carapace, but its size and position are wrong.

5. The condyle and the fossa condyli are not placed horizontally. This makes movement of the head absolutely impossible.

6. The sub-orbital is not connected with the pre-orbital.

7. The maxilla and pre-maxilla are not correctly placed in relation to each other and to the sub-orbital.

8. The position of the mandible is incorrect. It is placed too low down and comes in contact with the clavicular.



Text figure 8.

Bryant's reconstruction of *Dinichthys mirabilis* Huss. & Br. (1918).

AL, antero-lateral; *C*, central; *EO*, external-occipital; *IL*, intero-lateral; *M*, marginal, *Md*, mandible; *MO*, median-occipital, *Mx*, maxillary, *P*, pineal; *PrMx*, pre-maxillary; *PrO*, pre-orbital; *PtO*, post-orbital; *R*, rostral; *SO*, sub-orbital.

(After the present author's sketch made in the Buffalo Museum.)

The next figure of a reconstruction of *Dinichthys* is found in Hussakof and Bryant's "Catalogue of the Fossil Fishes in the Museum of the Buffalo Society of Natural Sciences" (1918). The present writer was able to study this reconstruction (made by Bryant) during his visit to the Buffalo Museum. It is a reconstruction of *Dinichthys magnificus* n.sp. (Text-figure 8). It can only be regarded as an unsatisfactory attempt, and gives an incorrect picture of *Dinichthys*. I will merely point out here that the whole head carapace is too flat, the median part of the head is depressed instead of being arched, the sub-orbital is wrong in its outlines and position, and the mandible is too strongly curved and is fixed to the lower part of the antero-lateral (clavicular). Besides this reconstruction, there is exhibited in the Buffalo Museum, a plaster model of the fore part of *Dinichthys mirabilis* in natural size. This model, which also includes the body carapace, shows still more mistakes. It is enough to state that the position of the head shield in relation to the body carapace makes all movement between head and body totally impossible.

In the American Museum of Natural History there is a model of *Dinichthys intermedius* made by Hussakof. Here the whole fish is shown in natural size. This model is much better than the one in the Buffalo Museum, but here also the head is too flat. Another mistake worth mentioning is that the distance between the right and left parts of the upper and lower jaws is too great.

In 1919, Adams gave a sketch (Text-figure 76) of *Dinichthys* in his book "A Memoir on the Phylogeny of the Jaw Muscles in Recent and Fossil Vertebrates." He has here briefly given the first description of a new plate placed at the posterior corner of the mandible. This plate shows a joint impression and, according to Adams, by its aid the mandible was suspended to the sub-orbital. We shall return to Adams' new theory of jaw movement in the Arthrodira in another part of this work.

A paper on *Dinichthys* was published by Woodward in 1922. He gave here the first more detailed drawing (unhappily on a very small scale) of a *Dinichthys* head shield from the inside. In the same paper we also find a drawing showing the relative position of the jaw elements of *Dinichthys*.

The most recent paper (Stetson 1930) describes a new reconstruction of *Dinichthys terrelli* Nwb. exhibited in the Museum of Comparative Zoology, Harvard College. The mounted specimen is nearly complete (only the ventral shield is absent), and the whole reconstruction must be accepted as the best one. Nevertheless it shows some mistakes The front part of the head is concave instead of being convex. The pre-maxilla is too small in relation to the maxilla and to the whole head. It certainly belongs to another and smaller individual. Both the combinations proposed by Stetson of placing pre-maxilla and maxilla in relation to the sub-orbital are in the present author's opinion incorrect. Especially that combination shown on his Pl. II must be regarded as wrong, as we shall see later when describing the gnathal elements in *Dinichthys*. The mandible is too strongly curved and comes too near the antero-lateral plate. Possibly it belongs to another specimen. The body carapace lacks the postero-lateral plate.

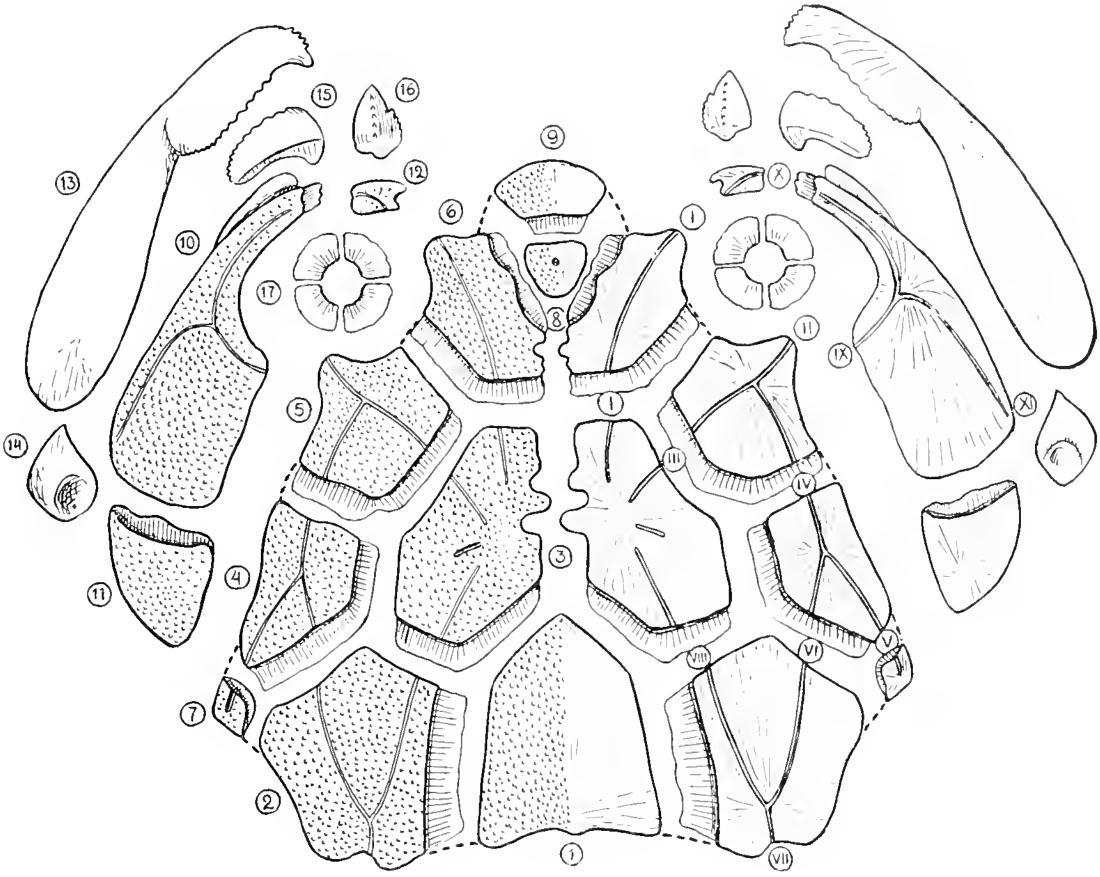
Since all attempts to rebuild *Dinichthys* have been more or less incorrect or incomplete, the present writer will try to give a new reconstruction of this animal, based on his latest investigations, leaving its acceptance or rejection to the judgment of others.

NOMENCLATURE OF HEAD AND BODY PLATES AND SENSORY CANALS IN THE ARTHRODIRA

If we look at the carapace structure of different Arthrodires, we find that in spite of the great difference in form, adaptation and size, the number and relative arrangement of the single plates are unusually constant. Such a constant arrangement of skeletal elements is hard to find in other primitive fishes even when they belong to one order. This shows that the Arthrodira are a group of very closely related forms and are also a very conservative group, since their structure changed very little during the enormously long time from Lower to Upper Devonian.

For this reason, it is possible to make a schematic drawing of an "ideal arthrodire," showing all the plates typical of the Arthrodira in their characteristic positions. Such a drawing might be a great help in the study of new and unsatisfactorily known forms or fragments.

In Text-figures 9, 10, and 11, I have tried to make such schematic drawings of the plates of the head and of the ventral and dorsal body carapace of such an "ideal arthrodire." These represent not a definite form, but a composite— in which the most characteristic points of all known forms have been assembled. The single plates are separated to show the overlapping margins. (In reality the head plates of the Arthrodira were seldom found isolated). All the sensory canals found in the various forms are included. The ossification centers and ossification rays are also indicated on the plates at the right side of the drawings.



Text-figure 9.
The head armor of the "Ideal Arthrodire" with the plates separated.

PLATES: 1, median-basal (*MB*); 2, externo-basal (*EB*); 3, central (*C*); 4, marginal (*M*); 5, post-orbital (*PtO*), 6, pre-orbital (*PrO*); 7, post-marginal (*PM*); 8, pineal (*P*); 9, rostral (*R*), 10, sub-orbital (*SO*); 11, post-sub-orbital (*PsO*); 12, post-nasal (*PN*); 13, infero-gnathal (*IG*); 14, postero-infero gnathal (*PIG*); 15, postero-supra-gnathal (*PSG*); 16, antero-supra-gnathal (*ASG*).
CANALS: I, pre-orbital (*Proc.*); II, III, IX, X, sub-post-orbital (*Sptoc*); IV, VI, VII, marginal (*Mc*); V, post-marginal (*Pmc*); VIII, externo-basal (*Ebc*); XI, gnathal (*Gnc*).

It is possible that later investigations will show that in the Arthrodira the head shield included some more plates. Nevertheless I am quite sure that the picture of this Arthrodiran head will not be altered in any particular way.[2]

As we see, the head contains 37 single plates (Text-figure 9). Among them are 3 symmetrically placed in the median line, while 34 others form 17 pairs of unsymmetrical side plates (right and left). The body carapace has only 19 plates; 3 symmetrical median plates, and 8 pairs of unsymmetrical side plates (Text-figures 10 and 11). Thus the whole carapace of the "ideal arthrodire" is built of 56 single plates (6 unpaired and 25 paired).

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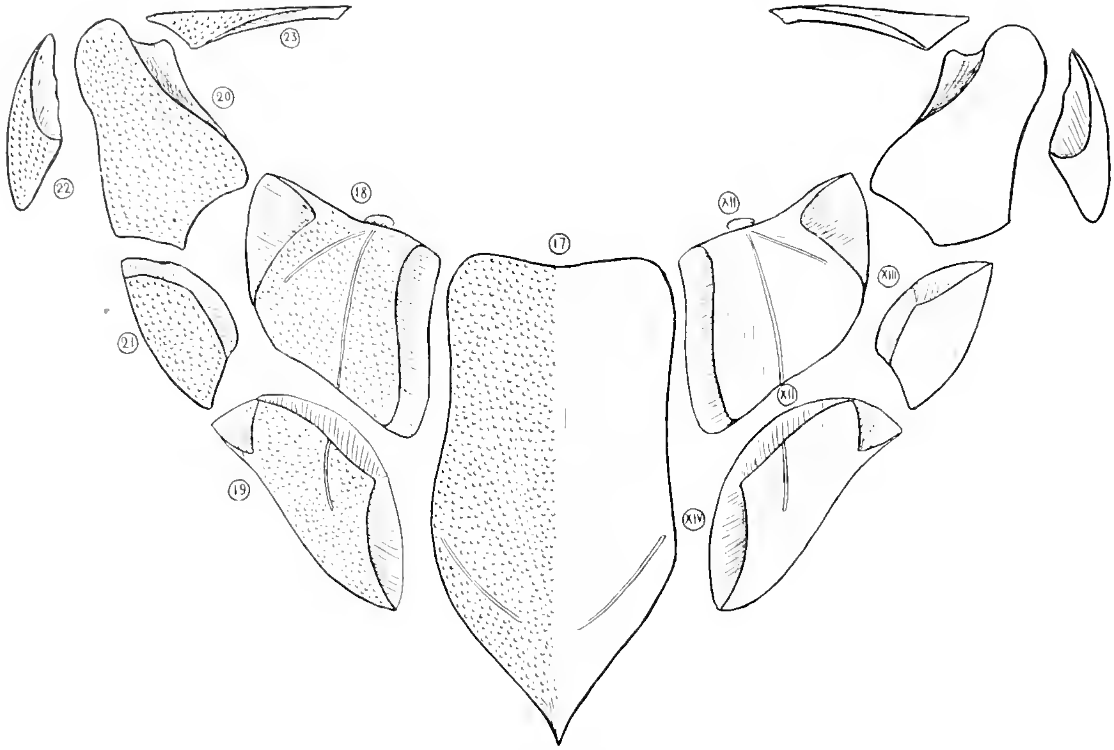
[2] This supposition proves to be correct. The author has been convinced that Professor Hyde has found four new plates in the head of *Dinichthys*. Nevertheless, the picture of the whole head is not changed. These four new plates will be described in Professor Hyde's monograph on *Dinichthys*.



Text-figure 10.
The dorsal shield of the "Ideal Arthrodire" with bones separated

PLATES: 17, median-dorsal (*MD*); 18, antero-dorsal-lateral (*ADL*); 19, postero-dorso-lateral (*PDL*); 20, antero-lateral (*AL*), 21, postero-lateral (*PL*); 22, spinal (*Sp*); 23, intero-lateral (*IL*).
CANALS: XII, anterior lateral (*Aslc*); XIII, posterior lateral (*Pslc*); XIV dorsal (*Dc*).

The nomenclature of the single plates in the carapace of an Arthrodire is very varied according to the different writers. In the works of Dean (1901) and Heintz (1929.1) are found tables giving the names used by various authors.

It is usually acknowledged that a mistake is made in calling the different plates in the Arthrodire armor by the same names given to the bones in the cranium and shoulder girdle of the fishes. The Arthrodira are so isolated in their systematic position that the homology between their carapace plates and the cranial bones of the fishes is too uncertain. Therefore it is better to change such names as "frontal," "parietal," "occipital," "quadratum," "mandible," etc., especially used in Germany by Jaekel, to more neutral names. For this reason, the names given to Arthrodiran plates in England and America are the best. They are based on the position of the plates in the carapace and are therefore more neutral (e.g., pre-orbital, central, median-dorsal, antero-ventro-lateral, etc.).

In 1925, Stensiö proposed naming the single plates of the Arthrodiran head with capital letters, as B, M, M_2, L, P, etc. This method of nomenclature, notwithstanding its many advantages, is, in my opinion, unsatisfactory. The single letters give no characteristic of the plate's position or relation to other plates, as do the English-American names.

Moreover, the latter nomenclature is very common and has been used in more than one hundred papers on the Arthrodira.

In this work, the English-American nomenclature will be applied with a slight alteration, so that the names will not remind one of the bone names of the fishes. This nomenclature has been worked out by Professor J. E. Hyde of Cleveland and the present writer. It will be used by Professor Hyde in his series of monographic descriptions of the Arthrodiran material from the Cleveland shale. This new nomenclature is shown below. The abbreviations used in this work are placed in parentheses; the numbers refer to the various plates shown in the drawings (Text-figures 9, 10, and 11).

NOMENCLATURE OF THE PLATES IN THE ARTHRODIRA

HEAD SHIELD

1. Median-Basal (MB)
2. Externo-Basal (EB)
3. Central (C)
4. Marginal (M)
5. Post-Orbital (PtO)
6. Pre-Orbital (PrO)
7. Post-Marginal (PM)
8. Pineal (P)
9. Rostral (R)
10. Sub-Orbital SO)
11. Post-Sub-Orbital (PSO)
12. Post-Nasal (PN)
13. Infero-Gnathal (IG)
14. Postero-Infero-Gnathal (PIG)
15. Postero-Supra-Gnathal (PSG)
16. Antero-Supra-Gnathal (ASG)

BODY CARAPACE

17. Median-Dorsal (MD)
18. Antero-Dorso-Lateral (ADL)
19. Postero-Dorso-Lateral (PDL)
20. Antero-Lateral (AL)
21. Postero-Lateral (PL)
22. Spinal (Sp)
23. Intero-Lateral (IL)
24. Antero-Ventro-Lateral (AVL)
25. Postero-Ventro-Lateral (PVL)
26. Antero-Median-Ventral (AMV)
27. Median-Ventral (MV)

As can be seen, the alterations are not great. The name "occipital," used for cranial bones of other animals, is replaced by the more neutral name basal. The little plate, No. 7, is called post-marginal, being behind the marginal. This plate has been called "angular" by Traquair (1894) and Heintz (1930.2)—an unsuitable name because the plate has nothing to do with the "angular" in the fishes. Jaekel (1902) called it "Supra-temporale."

The name post-sub-orbital is given to a plate which has had many names before. Pander (1857) called it "Opercul"; Newberry (1889) called it "post-maxillary"; Dean (1895), "hyomandibular"; Woodward (1898), "operculum"; Traquair (1889), "jugal or post-maxillary"; and Jaekel (1902), "Quadrato-jugale."

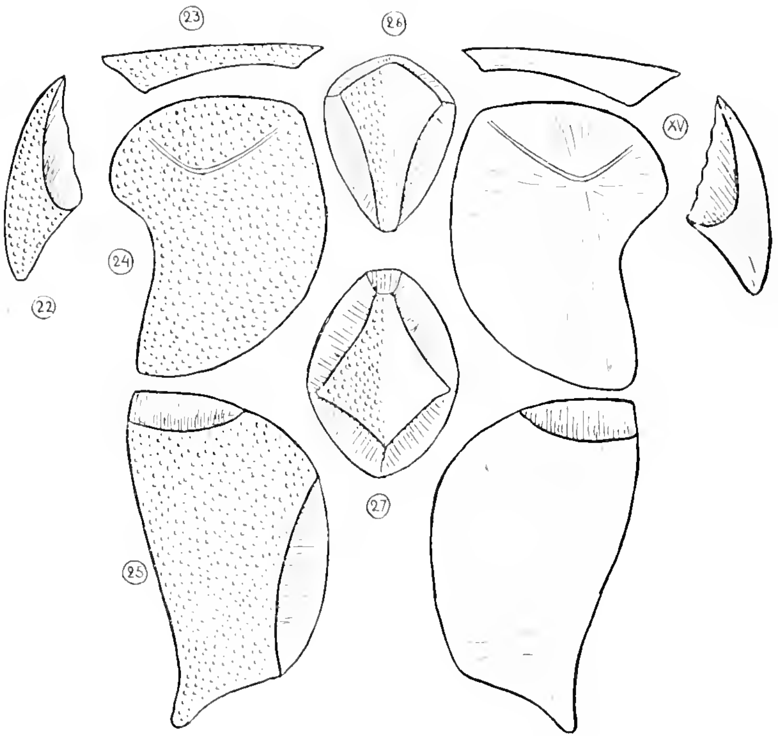
The post-nasal is a small plate in front of the head and surrounds the nasal opening. Traquair (1889) calls this the "pre-maxilla"; and Jaekel (1902) once refers to it as the "Lacrymale," and later (1906.1) calls it the "Post-nasale."

The jaw elements have the names Hussakof proposed in 1906, instead of maxillary, pre-maxillary and mandible, all names well known from the fishes. Plate No. 14 is called postero-infero-gnathal. Jaekel called this plate the "Articulare" in *Pholidosteus*.

With that exception, it has hitherto only been known in *Dinomylostoma* (Eastman 1906.1).

No changes have been made in the names of the plates of the body carapace.

Finally, let us consider the sensory canals. These canals in the Arthrodira show the same constancy as the plates. We find the same fundamental plan of arrangement in all the forms.[3] Different authors have proposed different names for these canals, but most frequently they have been named from the plates on which they were situated. The most detailed nomenclature has been proposed by Claypole (1892.2) and Stensiö (1925). Stensiö's nomenclature is based on a comparison of the course of the sensory canals of the Arthrodira with that in *Macropetalichthys* and other fishes. He suggests calling them by the names used for other fishes.



Text-figure 11.

The ventral shield of the "Ideal Arthrodire" with plates separated.

PLATES: 22, spinal (*Sp*); 23, intero-lateral (*IL*); 24, antero-ventro-lateral (*AVL*); 25, postero-ventro-lateral (*PVL*); 26, antero-median-ventral (*AMV*); 27, median-ventral (*MV*).

CANALS: XV, ventral canal (*Vc*).

The present writer prefers the more neutral names shown in the following table in which the abbreviations are placed in parentheses; the numbers relate to the different canals on the drawing (Text-figure 9).

NOMENCLATURE OF THE SENSORY CANALS IN THE ARTHRODIRA

I.	Pre-orbital canal (Proc)	V.	Post marginal canal (Pmc)
II. III. IX. X.	Sub-post-orbital canal (Sptoc)	VIII.	Externo-basal canal (Ebc)
		XI.	Gnathal canal (Gnc)
		XII.	Anterior sensory canal (Aslc)
		XIII.	Posterior sensory canal (Pslc)
IV. VI. VII.	Marginal canal (Mc)	XIV.	Dorsal canal (Dc)
		XV.	Ventral canal (Vc)

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[3] In one form of Acanthaspida from Germany (*Lunaspis*), described by Broili (1929), it was impossible to indicate any sensory canals despite the very well preserved material.

DESCRIPTION OF THE ARMOR OF *DINICHTHYS*

In this section are given detailed descriptions and drawings not only of new or hitherto imperfectly known plates of *Dinichthys*, but also of all the well known ones.

Remarkably enough, after Newberry, in Claypole only do we find more thorough descriptions of the single plates of the head of *Dinichthys*. The other authors have been satisfied with schematic drawings and partial reconstructions on a small scale, and very seldom do we find detailed pictures of plates of the carapace of *Dinichthys*. Nevertheless, *Dinichthys* is an especially favorable object for thorough description. It is one of the largest of the known Arthrodires and is often very well preserved. It is not too highly specialized in any one direction and shows, therefore, all the more typical characters of the Arthrodira. The single plates of the carapace can be worked out from the matrix and observed from all sides. For these reasons, *Dinichthys* is much more suitable to take as a type for the Arthrodira than is *Coccosteus decipiens* Ag., which was for many years the best known form.

In the following pages I have tried to give a detailed description of *Dinichthys*, with as many drawings and photographs as possible, realizing that drawings are the most perfect descriptions. This work is based chiefly on the fragments of *Dinichthys intermedius* Nwb. which are best represented in the collection of the American Museum of Natural History, but all the other specimens of *Dinichthys* are also considered. It is my hope that this paper may be of help in studying other less well preserved Arthrodira, and may perhaps contribute to a better understanding of this remarkable group.

THE HEAD SHIELD

As we known, the head shield of *Dinichthys* is composed of not less than 37 single plates. These plates cover nearly the whole head like a perfect armor, leaving only the openings for the eyes, nostrils and mouth. The only region unprotected by plates is the under part, between the lower jaws. The whole head can be divided very naturally into two parts: the central part, or roof of the head; and the side parts, or the plates around the mouth.

THE HEAD ROOF

The single plates of the head roof[4]; as we shall call this part, are for the most part strongly connected with one another and form a compact, well limited shield. This is the case in all Arthrodira, and as a result this head roof has often been described for the whole head (*e.g.* in *Acanthaspis*, *Phlyctaenaspis*). The 15 plates which compose the head roof (Text-figures 12 and 13, and Plates I, II) are connected with one another by more or less complicated sutures, all of which must be characterized as squamosal sutures. The margins of all the plates overlap each other, but the limits between the single plates may be very unlevel, with large and extensive indentations fitting into one another. Furthermore, the margin of some plates may show spines, long crests, etc., which fit into corresponding excavations in the margins of the neighboring plates As a result, the plates in

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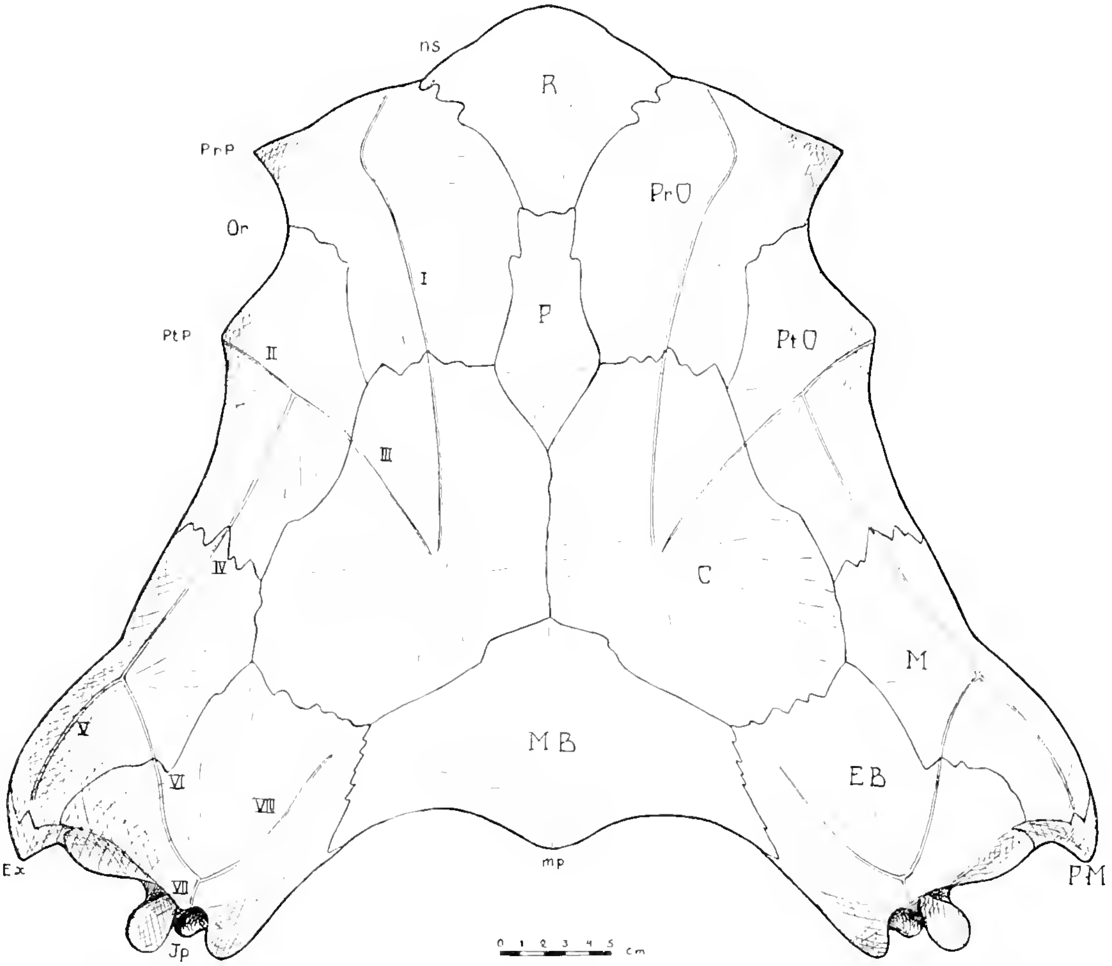
[4] In the following description, the letters in parentheses refer to Text-figures 12, 13 and 14 unless otherwise indicated.



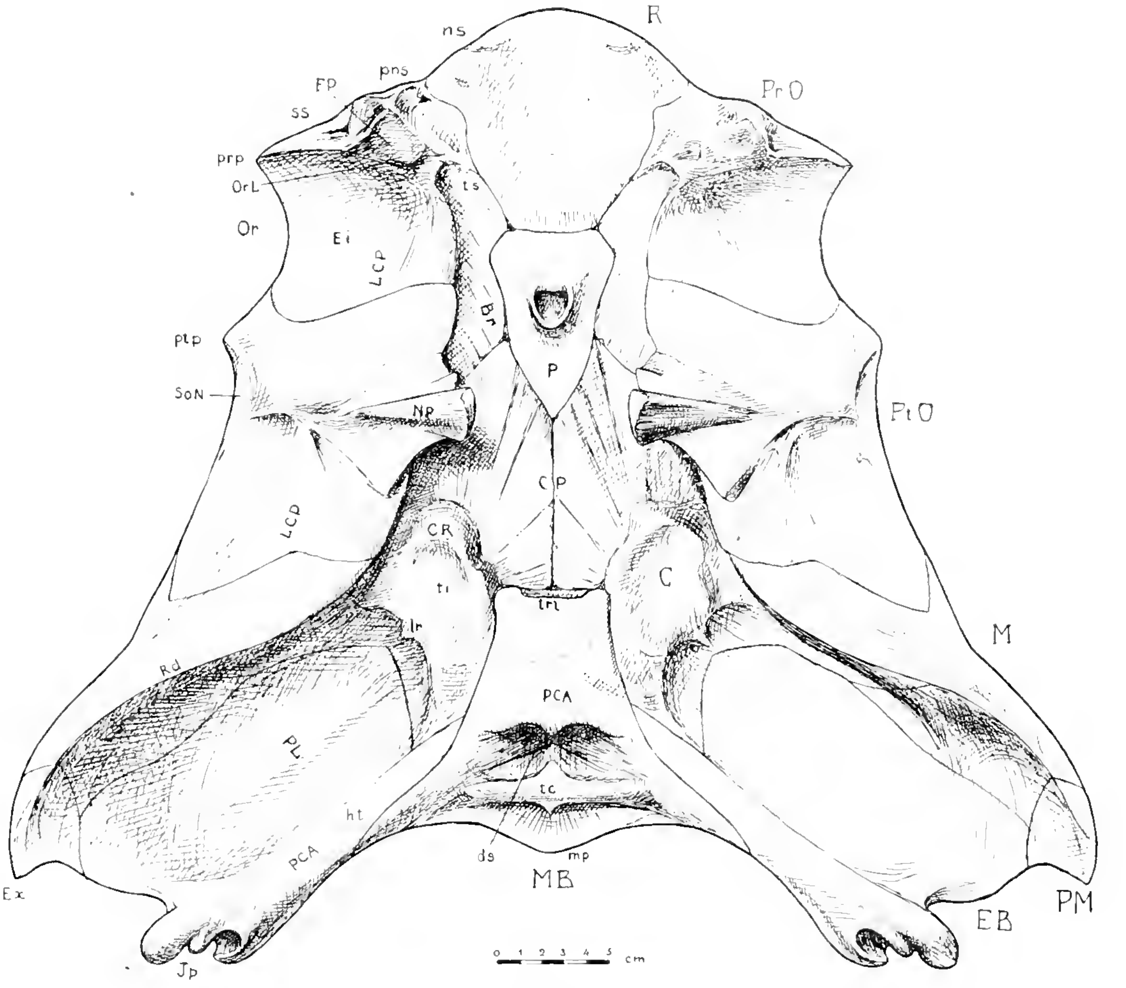
Text-figure 12.
The head roof of *Dinichthys intermedius* Nwb., outside view.

Plates: C, central; *EB*, externo-basal; *Ex*, external angle of head roof; *Jp*, joint process; *M*, marginal; *MB*, median-basal; *mp*, median point; *ns*, nostril impression; *Or*, orbit; *P*, pineal; *PM*, post-marginal; *PrO*, pre-orbital; *PtO*, post-orbital; *PrP*, pre-orbital process; *PtP*, post-orbital process; *R*, rostral.

Canals: I, pre-orbital; II-III, sub-post-orbital; IV-VI-VII, marginal; V, post-marginal; VIII, externo-basal.

the cranial roof are very strongly connected and we seldom find them isolated. Also, in adult examples the single plates have probably grown together, at all events it is often very difficult to find the limits between them.

The head roof (Text-figures 12 and 13) is a little broader than long and has an irregular trapezoidal form, narrower in front and broader in back. In front we find two feebly marked impressions for the nostrils (*ns*), and on the sides, more or less deep orbital notches (*Or*). They are marked with two angles, the pre-orbital process (*Prp*) and the post-orbital process (*Ptp*), the first more sharply pointed than the last. From the post-orbital process the shield widens gradually toward the back and attains the greatest width at the



Text-figure 13.
The head roof of *Dinichthys intermedius* Nwb., inside view.
Br, branch of central part; *C*, central; *CP*, central part; *CR*, "bridge" between lateral consolidated part and posterior consolidated arch; *ds*, double socket; *EB*, externo-basal; *Ei*, eye impression; *Ex*, external angle of head roof; *FP*, fore, thicker portion of lateral consolidated part; *ht*, hind thickening; *Jp*, joint process; *LCP*, lateral consolidated part; *lr*, ridge on posterior lateral impression; *M*, marginal; *MB*, median-basal; *mp*, median point; *Np*, neurocranial process; *ns*, nostril impression; *Or*, orbit; *OrL*, front limit of orbital impression; *P*, pineal; *PCA*, posterior consolidated arch; *PL*, postero-lateral; *PM*, post-marginal; *pns*, post-nasal sockets; *PrO*, pre-orbital; *prp*, pre-orbital process, *PtO*, post-orbital; *ptp*, post-orbital process; *R*, rostral; *Rd*, ridge on posterior part of *LCP*; *SoN*, sub-orbital notch; *ss*, sub-orbital sockets; *tc*, transverse commissure; *ti*, top impression on bridges; *trl*, transverse limit on front of *MB*; *ts*, socket behind orbital impression.

so-called external angles (*Ex*). From this point the head roof rapidly narrows into the joint process (*Jp*), the place where the head and body carapace are connected with one another in a movable manner. The hinder part of the head, between the joint processes, is strongly bent upward and only curved a little at the median point (*mp*).

From outside (Text-figure 12, Plate I), the head roof of *Dinichthys*, in contrast to nearly all the other Arthrodira, shows no sculpture.[5] The surface of the bony plates is a

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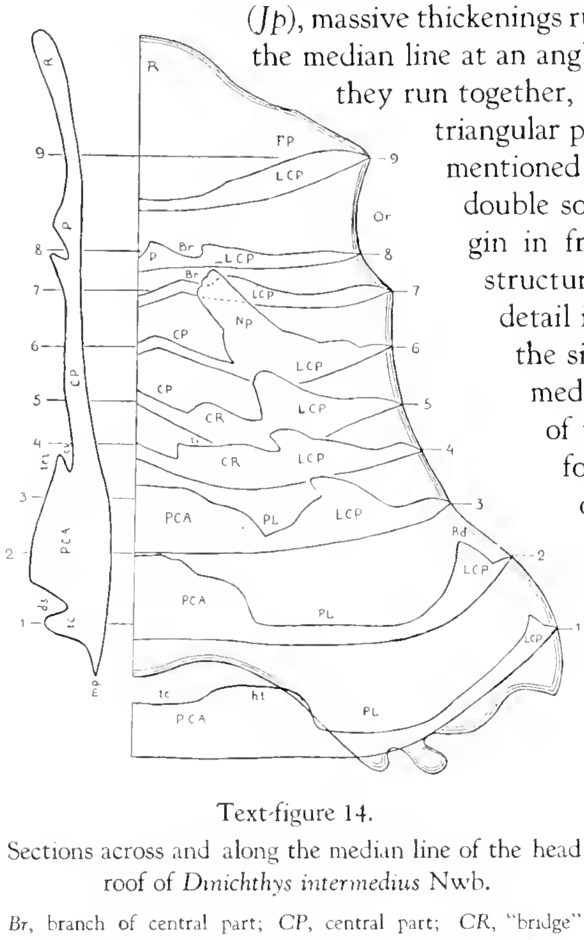
[5] The only exception is *Dinichthys pustulosus* Ea. which has a tuberculated surface.

little rough and often shows the ossification centres and the ossification rays. Very seldom can there be found a fine tuberculation in the region of the ossification center, The present writer has seen this phenomenon only twice. Moreover, the outside of the head also shows quite deep grooves for the sensory canals and the limits between the single plates. The latter are, however, often very obscure.

The whole head roof was in reality strongly curved from side to side and from back to front. But during the fossilization process it was more or less flattened, crushed and broken. Later we shall come back to this matter and see how we can reconstruct the real curving of the head roof.

The inside of the head roof shows a much more intricate picture (Text-figures 13 and 14, and Plate II). The hinder margin is strongly thickened. From both the joint processes (*Jp*), massive thickenings run along the margins, meeting one another in the median line at an angle of about 110° and connected, just before they run together, by a thick transverse commissure (*tc*). The triangular place between this commissure and the above mentioned thickenings is occupied by a very deep double socket (*ds*). The curved part of the hind margin in front of the commissure is thin (*mp*). The structure of the joint sockets will be described in detail in a later section. From the point of union the single thickening continues upward along the median line to about one-third of the whole length of the head roof. Here it suddenly stops and forms a transverse sharp limit (*trl*). The whole of this massive part of the shield composes the posterior consolidated arch (*PCA*) of the head roof.



Text-figure 14.

Sections across and along the median line of the head roof of *Dinichthys intermedius* Nwb.

Br, branch of central part; *CP*, central part; *CR*, "bridge" between lateral consolidated part and posterior consolidated arch; *cv*, cavity; *ds*, double socket; *FP*, fore, thicker portion of lateral consolidated part; *ht*, hind thickening, *LCP*, lateral consolidated part; *mp*, median point; *Np*, neurocranial process; *Or*, orbit; *PL*, postero-lateral; *PCA*, posterior consolidated arch; *R*, rostral; *Rd*, ridge on posterior part of *LCP*; *tc*, transverse commissure; *ti*, top impression on "bridge" *CR*; *trl*, transverse limit on front of *MB*.

The two other consolidated parts are placed symmetrically along the side margin of the head roof (*LCP*). They begin at the front of the head roof and at first are about one-third of its breadth, but in the hinder part they narrow quickly and run as a crest into the external angles of the roof. For the whole of this length there is a very sharp limit between them and the central thin part of the roof. This limit forms a step which increases more and more backwardly and finally becomes a high, narrow, sharp ridge (*Rd*). The side thickenings are most solid along this inner limit and become gradually thinner toward the margin (Text-figure 14). Their fore part (*FP*), placed approximately between the nostril impressions and the pre-orbital process, is strongly thickened. We find here, along the margin, the different sockets, crests and impressions (*ss*, *pns*), which serve to attach the plates of the side of the head (*PN* and *SO*) to the head roof. Between the pre- and post-orbital processes is a moderate impression for the eyeball (*E1*). It is sharply limited (*OrL*) forwards, but gradually disappears at the back. On the margin immediately behind the post-orbital process, is a shallow notch for the reception of the upper corner of the *SO* plate (*SoN*) (Claypole, 1892. 2).

The inner limit of the side thickenings not far behind the post-orbital process becomes very massive, with many small crests, ridges and impressions. From the middle of this part rises a long, thick, angular process (*Np*) which bends over the central part of the head roof. These processes extend inward from both sides and so surround a triangular room where the neurocranium lies. Therefore we will call them the neurocranial processes.

A little behind these processes the side thickenings begin to narrow, thus running nearly parallel to the inner limit of the posterior consolidated part of the head roof. In this part the side thickenings are changed to the before mentioned narrow high ridge (*Rd*) with a sharp edge. This ridge rises bow-shaped and gradually descends to the point of the external angle of the roof.

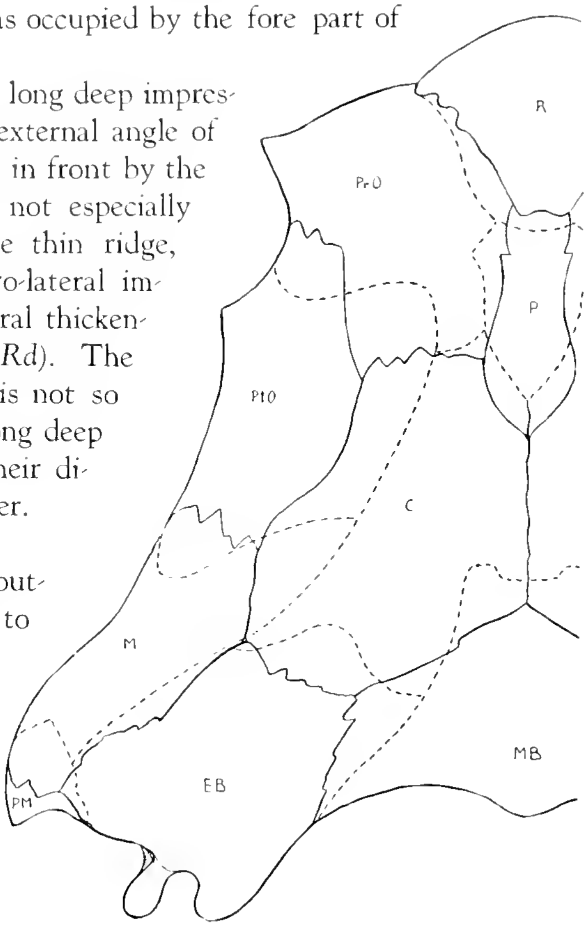
In this manner, the head roof of *Dinichthys* is consolidated with the help of several thickenings: first, the postero-median (*PCA*), then, the symmetrical antero-laterals (*LCP*). These two sets of thickenings are connected with one another with the help of two "bridges" (*CR*) which form a massive, flat thickening with an oblong impression at the top (*ti*). They go from the front of the posterior consolidated arch obliquely forward and come in contact with the side thickenings not far behind the neurocranial processes. Together with the hinder consolidated arch they form an X-shaped figure.

With the help of this system of thickenings the remaining thin part of the roof is divided into three parts: the central (*CP*) which is placed between the side thickenings, and the two postero-laterals (*PL*) placed between the hind part of the side thickenings (*Rd*) and the hind consolidated arch of the roof (*PCA*).

The central part begins at the transverse limit of the median part of the hind consolidated arch (*trl*). This limit is very sharp and steep, so that the thickened part even overhangs the thin central part, making a kind of cavity (Text-figure 14, *cv*). On the other hand, the limit between the connecting bridges (*CR*) and the thin central part (*CP*) is not so sharply marked. At both sides the central part is, as mentioned before, sharply limited by the side thickenings.

Nearly on the level of the neurocranial processes, the central part is divided into two parts by the pineal plate (*P*). This is a rather thick, oblong, triangular-shaped plate, which continues to the rostral part of the head (*R*). The thin central part, divided into two, continues upward as two branches (*Br*). They curve a little outward and end as a well marked socket behind the orbital impressions (*ts*). This central, thin part of the roof, forms a deep, well-limited cavity, which was occupied by the fore part of the cartilaginous neurocranium.

The postero-lateral part (*PL*) makes a long deep impression, which opens backward between the external angle of the roof and the joint process. It is limited in front by the connecting bridges (*CR*). This limit is not especially sharp. Nearly from its center runs a fine thin ridge, which divides the latter part of the postero-lateral impression in two (*lr*). The limit of the lateral thickenings is very high and forms a steep wall (*Rd*). The limit of the posterior consolidating arch is not so high, but is well marked. Probably this long deep fossa was occupied by strong muscles. Their direction and function will be discussed later.



Text-figure 15.
Limits between the single plates of the head roof of *Dinichthys intermedius* Nwb.: outside one in continuous lines, inside ones dotted.

C, central; *EB*, externo-basal; *M*, marginal, *MB*, median-basal; *P*, pineal; *PM*, post-marginal; *PrO*, pre-orbital; *PtO*, post-orbital; *R*, rostral.

After having described the general outline of the whole head roof, I will now try to give a description of the single plates which compose it. But it is not always easy to find the limit between the single plates, and it is therefore difficult to define clearly the overlappings between them. The best and most careful description of the single plates of *Dinichthys intermedius* Nwb. and of their relation to one another was given by Claypole in 1892. However, the results of my investigation do not always correspond with those of Claypole.

I have found in other Arthrodira (especially clearly developed in *Homostius*) that there is a law governing the manner in which the single plates overlap one another. From *MB* as center (Text-figure 9) all the posterior plates overlap the plates in front of them or at their sides. For example, *MB* overlaps *EB* and *C*, *C* overlaps *M* and *PtO*, etc. In other words, the plates are placed nearly in the same way as tiles on a roof. This principle of arrangement we also find in the building of the body carapace, and not only in Arthrodira but also (with some exceptions) in the Asterolepida. In larger forms with a thick armor, this regularity may be more or less disturbed by the very complicated structure of the sutures. Such is the case with *Dinichthys*.

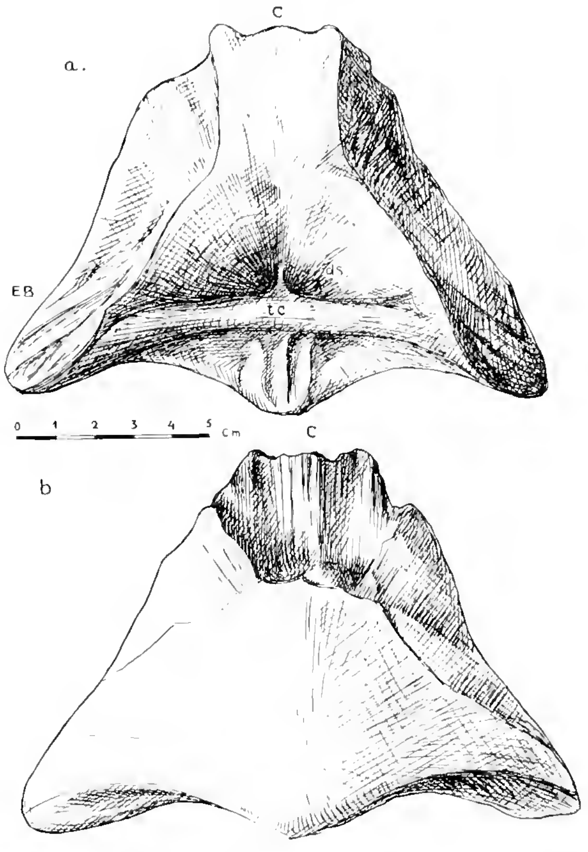
Before describing the single plates it must be noted that in the Arthrodira the individual variation in outline, size and position of the single plates is perhaps greater than in any other animals. This circumstance must be remembered in comparing this figure with the Arthrodiran fragments.

Median-Basal.—This plate (Text-figures 12, 13, 14, 15 *MB*, and 16) is the most massive one of the whole head roof. It is 9 cm. long, 15 cm. broad and 5 cm. thick;[6] and forms the central part of the posterior consolidated arch of the roof with its transverse commissure (*tc*) and double sockets (*ds*). In contradistinction to most of the other plates, *MB* can quite often be found isolated. The limits between it and its neighboring plates are well developed. At the sides *MB* overlaps *EB*. In front it is overlapped by both C plates.

Externo-Basal.—This plate (Text-figures 12, 13, 14 and 15 *EB*) forms the wings of the posterior consolidated arch. Along its posterior margin run the half-round thickenings (*ht*) on the ends of which the joint processes are placed (*Jp*). The upper, thinner part of *EB* forms the largest part of the bottom of the postero-lateral impression (*PL*). *EB* is overlapped by C, and partly overlapped by *M*. However, the limits between these three plates are difficult to see from the inside.

On the outside of *EB* we find two branches of the sensory canals (Text-figure 12) which form a V-shaped figure. The point of this goes close to the joint socket, with which it is connected by a short canal (*VII*). One of the branches extends over on the *M* (*VI*). The other goes nearly to the edge of C (*VIII*). (In some specimens this branch runs over onto C).

Marginal.—This plate (Text-figures 12, 13, 14 and 15 *M*) is a solid long one, which together with *EB* and *PM* forms the postero-lateral wing of the head roof. Nearly along its center runs the posterior high ridge of the lateral head thickening (*Rd*). It forms the side wall of the postero-lateral impression (*PL*). The *M* overlaps the *PtO* and C. On the outside are found the sensory canals. They make a three-branched figure, very



Text-figure 16.
The median-basal plate of *Dinichthys intermedius* Nwb.: a, from inside; b, from outside.
C, position of central; *ds*, double sockets; *EB*, position of externo-basal; *tc*, transversal commissure.

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[6] These measurements were made from a small example of *D. intermedius* (No. 7891) in the American Museum.

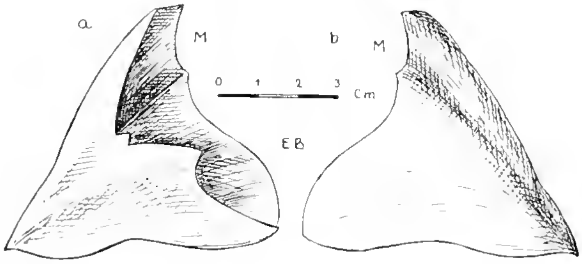
characteristic for the *M* on all Arthrodira. The center of this figure is placed in the ossification center of the plate. One branch goes up to the *PtO* (*IV*), the other (*V*) down and outward to the external angle (*Ex*) of the roof, and the third (*VI*) runs over on *EB* where it continues into the previously mentioned canal.

POST-MARGINAL. This plate (Text-figures 12, 13, 14, 15 *PM*, 17 and 18; Plate III, figure 7) is one which has never before been observed in *Dinichthys*. It is a little triangular plate that forms the extreme point of the external angle and gives to it its characteristic sharp-pointed outline. Like a little hollow cap, *PM* is fitted on to the extreme parts of *M* and *EB* and in this manner connects them firmly together. On the inside *PM* greatly overlaps *M* and *EB*; on the outside more moderately. The suture on the outside is complicated, as is seen from Text-figures 12, 17, 18 and Plate III, figure 7. *PM* is the plate of the whole head roof most loosely joined to its neighboring plates, and therefore is often found isolated. For the same reason the otherwise complete head roof often lacks *PM* only.

In other Arthrodira *PM* has been found and figured before. Thus Traquair in 1894, in describing a head of *Phlyctaenaspis acadica* Wt. from Canada, figured a new plate which formed the extreme corner of the roof and was placed behind *M* and *EB*. He called it "angular." Considering its position, relation to other plates, and the fact that we find on it a continuation of the sensory canal from *M*, this plate corresponds with our post-marginal.

Jaekel in his papers on *Pholidosteus* (1907) gives some reconstructions of this form. Here we find a small plate between *M*, *EB*, and *PSO*. This plate, considering its position and relation to other plates, must have been the same as *PM* in *Dinichthys*. Jaekel has never described it nor given it a special name. In the reconstruction of some other Arthrodira from Wildungen (1906.2) we also find some plates in the posterior part of the head which must correspond with *PM*.

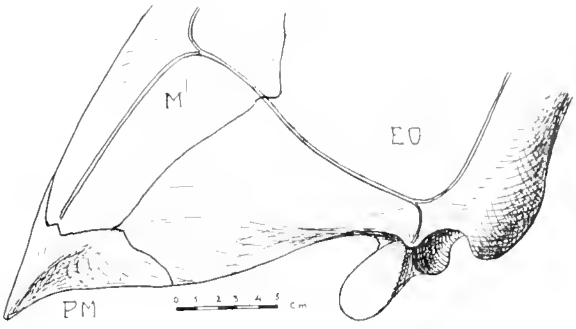
The present writer has described (1930.2) in *Heterostius* sp. a little plate placed on the extreme angle of the head roof. It was called angular, corresponding to the name given by Traquair to the same plate in *Phlyctaenaspis*. There is, however, no doubt that we have here *PM*. It is placed beside *M* and *EB*, and the sensory canal from *M* continues on it.



Text-figure 17.
The post-marginal plate of *Dinichthys intermedius* Nwb.: a, from outside; b, from inside.
M, position of marginal; *EB*, position of externo-basal.

In *Coccosteus*, *PM* has never been described. In Traquair's (1890.2) and Woodward's (1891.1) reconstructions it is absent. Jaekel's (1902) reconstruction shows a plate between the sub-orbital, post-sub-orbital and marginal. He called it "Supra-temporale." Perhaps it is a misplaced *PM*, but from its position and relation to other plates it is, rather, an entirely new element. The present writer, when studying in the Buffalo

Museum in 1930 found, among comparatively good material of *Coccosteus decipiens* Ag., a head (No. E1257) which shows a doubtful element at the extreme angle of the head (Text-figure 19). In all probability it is *PM*. However, it is not very surprising that *PM* has never been found and described in *Coccosteus*. It is very small, only a few millimetres long, and difficult to see.



Text-figure 18.

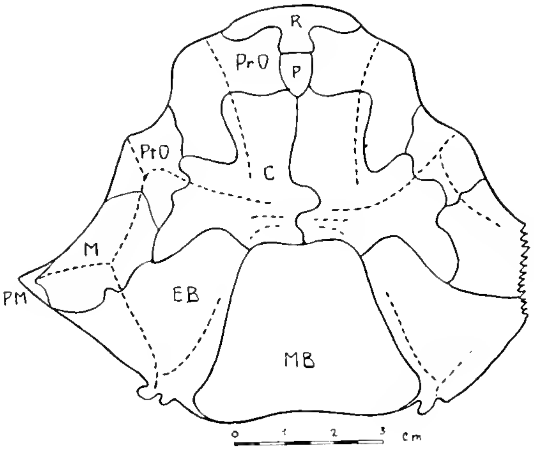
The left hind corner of the head of *Dinichthys intermedius* Nwb., showing the relative positions of *PM*, *M* and *EO*.

Even in *Dinichthys*, where *PM* is 5 to 6 cm. long, it has never been observed before. What is especially remarkable is that this plate does not occur infrequently. In the collections of the American Museum alone, it is to be found in three head roofs, in addition there are 5 or 6 isolated plates in perfect preservation. As a curiosity, it might be mentioned that one of these plates is labelled in Newberry's hand, "New genus and sp."

Only in Branson's reconstruction of *Dinichthys terrelli* Nwb. (1908.1, .2, 1911) do we find some traces of this plate. As has been mentioned, in this reconstruction (Text-figure 6) there is shown a new sensory canal, which goes nearly across to the outward branch of the *M* sensory canal (Text-figure 12 *V*). It is enough to compare Branson's figure with mine to be sure that Branson was mistaken and has taken a suture between *M* and *PM* for a sensory canal (Text-figures 9 and 12).

Central.—This plate (Text-figures 12, 13, 14 and 15 *C*) is the largest one of the whole roof, and is placed in the central part of the head. Along the median line it meets its corresponding plate from the other side. On the inside, *C* is naturally divided into two parts: one, the hind, thick; the other, the fore, thin. The posterior part is nothing other than the "connecting bridge" mentioned before. The thin part forms the bottom of the posterior part of the neurocranial impression. On this thinner part, the ossification rays are especially clearly developed. They radiate from the ossification center placed nearly in the middle of the connecting bridge (*CR*). The limit between the thin radiate and the thick smooth part of *C* is very sharp. This circumstance explains why Newberry (1889), Claypole (1892.2), and Eastman (1897.2, .3) have described *C* as two separate plates: "parietal" and "frontal."

On the outside of *C* we find some sensory canals. Their courses and lengths vary strongly, not only in different species of *Dinichthys* but also in the different individuals of the same species. Most usually there are two sensory canals which cross the upper limit of *C*—one from *PrO* (Text-figure 12 *I*), the other from *PtO* (Text-figure 12 *II*). They run downward side by side and nearly fuse in the center of the plate (ossification center). In some individuals they nearly meet, in others one of these canals is longer and continues farther down. This may in some species cross the hinder limit of *C*. and continue to *MB* (in *Dinichthys terrelli* Nwb. this is usual).



Text-figure 19.
Head roof of *Coccosteus decipiens* Ag.
(Buffalo Museum specimen No. E1257 to show the presence of *PM* in this form.)

In addition to these two canals a third is often to be found on C. It is the prolonged canal from *EB* (Text-figure 12 *VII*). From the limit between *EB* and C it continues upward and nearly unites with the two previously mentioned canals in the center of the plate. More infrequently there may be found a very short piece of canal, going nearly from the center of the plate in the direction of the limit between C and *M*. Stensiö (1925) calls this canal "the middle head line" (pit organ). It is very common in *Coccosteus*.

Thus, in some specimens, from the center of C five canals may radiate. The first runs to *PrO* (Text-figure 12 *I*), the second to *PtO* (Text-figure 12 *II*), the third (pit organ) in the direction of *M*, the fourth to *EB* (Text-figure 12 *VIII*), and the fifth to *MB*.

As we have seen all the sensory canals on C radiate from the ossification center. It is the case not only with the canals on C but also with all other sensory canals. Nearly always they either begin from the ossification center or cross it, but never cross the ossification rays. If sensory canals separate into several branches, the dividing point is always to be found in the ossification center of a plate. This phenomenon is very easily understood if one considers the manner of growth of the plates. (See Heintz 1929.1, pp. 16–19).

C overlaps all the plates which encircle it (*MB*, *EB*, *M*, *PtO* and *PrO*) except the pineal. *MB* is much overlapped, but C only touches it along their limits. Therefore, as mentioned before, we find a kind of cavity between the overlapped part of *MB* and the underside of C (Text-figure 14).

POST-ORBITAL.—This plate (Text-figures 12, 13, 14, and 15 *PtO*) together with M forms the side margin of the head roof. This is a relatively long, narrow and very massive plate. From the inside, it forms the median part of the lateral thickenings of the roof, and its inner margin coincides with the sharp inner limit of the latter. The neurocranial process rises from the median part of this limit. The anterior part of *PtO* forms the posterior half of the eye impression. *PtO* is overlapped by *M* and C and partly overlapped by *PrO*.

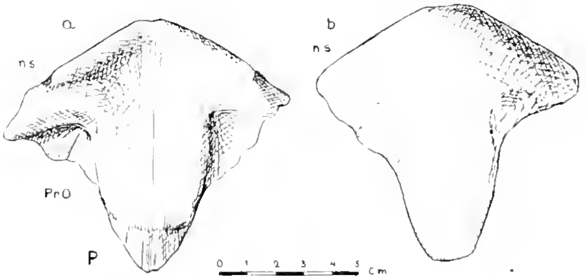
On the outside of *PtO*, the sensory canal makes a three-branched figure. This figure, like that on *M*, is very characteristic for *PtO* in all Arthrodira. The canal begins near the post-orbital processes (Text-figure 12 *III*) and runs to the ossification center. There it divides into two branches; one continues in the direction of C (*III*) and, as mentioned, goes over onto these plates; the other branch runs down to *M* (*IV*).

PRE-ORBITAL. This plate (Text-figures 12, 13, 14 and 15 *PrO*) constitutes the front angle of the head roof and defines the fore part of the eye impression. The pre-orbital process forms its most salient point. On the inside it forms the fore part of the side thickenings which are the thicker part of *PrO*. The thinner part, developed as a small border along the inner margin of *PrO*, constitutes the anterior section of the neurocranial impression. The small triangular part in the front of the eye impression is strongly thickened. Here may be found the sockets and ridges which serve to combine the head roof with the sub-orbital and post-nasal. *PrO* overlaps both the pineal and rostral plates and is itself overlapped by C.

The sensory canal on the outside of *PrO* begins in front, not far from the limit of the rostral. At first it makes an elegant curve and then continues downward along the middle of the plate to C (Text-figure 12 *I*).

PINEAL.—This is the smallest plate (Text-figures 12, 13, 14 and 15 *P*) of the whole head roof, and is placed between C, *PrO* and *R*. It is overlapped by *PrO* and itself overlaps C and *R*. It was perfectly described and figured by Dean (1891) so a detailed description is not necessary here. However, we shall only point out that the "pineal fontanelle" is not found very often. As a matter of fact, my investigations show that the deep, conical impression on the inside of the plate, often ends blindly (Woodward 1922). The openings one may find on the pineal plate are chiefly to be attributed to too energetic preparation, and are made artificially. The author could not in a single instance find in the American Museum collection a pineal plate which showed absolutely and undoubtedly the natural pineal fontanelle.

ROSTRAL.—The plate (Text-figures 12, 13, 14, 15 *R* and 20) forms the front part of the top of the head roof. Its front margin is a little thickened on the inside, with two weak impressions for the nostrils on the sides (Text-figures 12, 13 and 20 *ns*). Otherwise the rostral is rather smooth both on the outside and inside. It is overlapped by *P* and strongly overlapped by *PrO*, so that on the outside *R* often has a *T*-shaped outline.



Text-figure 20.

The rostral plate of *Dinichthys intermedius* Nwb.: a, from the outside; b, from the inside.

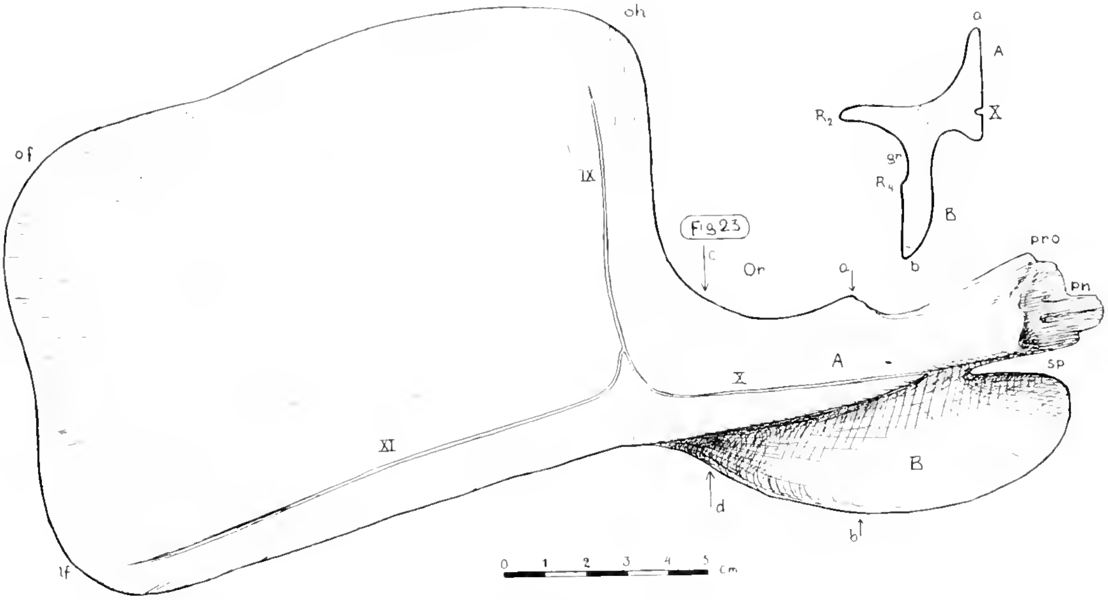
ns, nasal impression; *P* and *PrO*, positions respectively of pineal and pre-orbital plates.

We have now finished the description of all the plates in the head roof and shall pass on to describe the side plates of the head.

THE SIDE PLATES OF THE HEAD

The single plates of the side part of the head are not so often found as are the plates of the head roof. Some especially are very rare and known only in a few forms. However, it is very probable that new investigations and better material will bring to light some new plates in this part of the head. In the majority of the species these side plates are generally found isolated, only very seldom are they attached to the head roof or to one another. Some of them are small, others probably do not ossify in all species — not even in all individuals. As a result of this the arrangement and relation of the side plates is the most imperfectly known and the most disputable question in the head structure of the Arthrodira.

In this paper I shall first describe the single plates and later try to give a picture of their reciprocal positions and the relation to the head roof. At present we know only seven pairs of these plates. Five pairs belong to the upper jaw, and only two to the lower.



Text-figure 21.

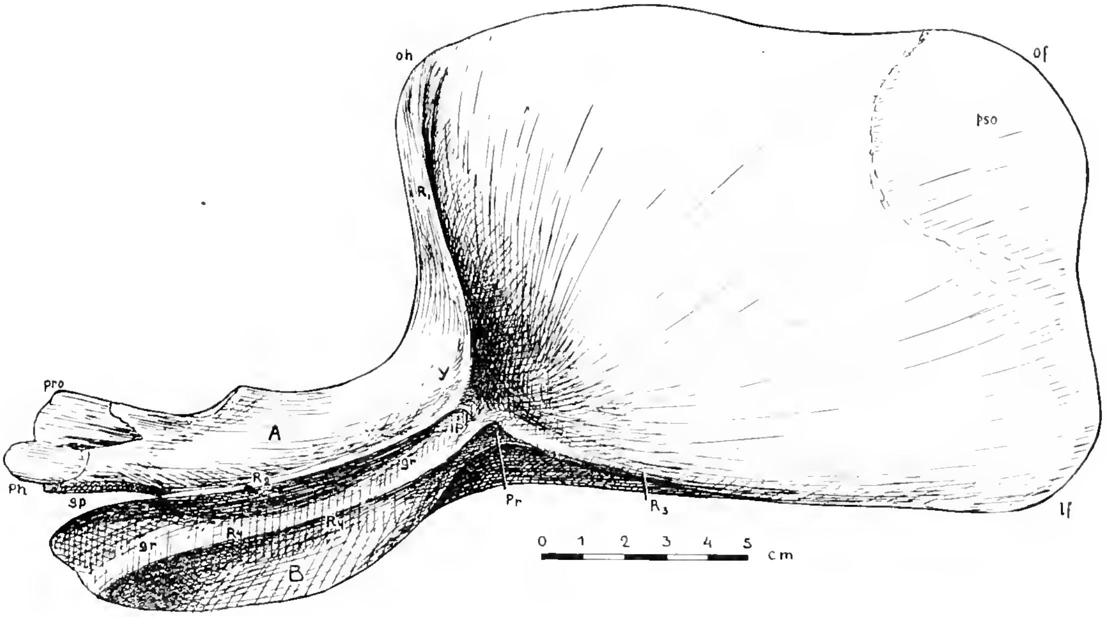
The right sub-orbital plate of *Dinichthys intermedius* Nwb. seen from the outside. The inset portrays a cross section of the "handle" in the line a–b of Text figure 23 I and II.

A, real handle; *a-b*, line of section shown in inset; *B*, tongue-shaped part of handle; *c–d*, line of section shown in inset of Text-figure 23; *gr*, groove on underside of tongue-shaped part, *lf*, lower hind corner of *SO*; *of*, upper hind corner of *SO*. *oh*, upper front corner of *SO*, *Or*, orbit; *pn*, contact point with post-nasal plate; *pro*, contact point with pre-orbital plate; R_2 and R_4, ridges on inside of *SO*, *sp*, split between real handle *A* and tongue-shaped part *B*. *IX* and *X*, sub-post-orbital canal; *XI*, gnathal canal.

The upper jaw plates are: the sub-orbital, post-nasal, post-sub-orbital, postero-supra-gnathal and antero-supra-gnathal. Those of the lower jaw are: the infra-gnathal and post-infra-gnathal.

SUB-ORBITAL. This is a large, plain plate (Text-figures 21, 22 and 23) which covers nearly the whole lateral part of the head and forms the lower margin of the orbital opening. Its outline reminds one of a cleaver, with a big, flat "blade" with the edge turned upward, and with a short "handle." The rounded incision between the blade and handle forms the margin of the orbit. The blade composes the largest part of *SO*. It is flat, oblong, four-cornered, smooth on the outside and of nearly the same breadth on the whole length. Its form on the inside will be described later.

The handle of the sub-orbital presents a more complicated picture. It is composed of two sharply differentiated parts: one, the real handle, is formed of the immediate prolongation of the blade and is composed of a long, narrow piece with nearly parallel upper and lower margins (Text-figure 21 *A*). In about the middle of the upper margin is found a well marked angle (Text-figure 21 *a*). From this point on, the handle gets narrower and its upper and front margin becomes strongly thinner (Text-figure 21 *pro* and *pn*). This part of *SO* comes in contact with *PrO* and *PN*. The other part of the handle is tongue-shaped and is placed lower down (Text-figure 21 *B*). It begins nearly at the base of the handle and runs forward in the form of an arch. The distance between this part and the real handle is greatest in the back and diminishes forward (Text-figure 23). In front these parts are divided from one another by a deep split (Text-figures 21 and 22 *sp*). The tongue-shaped part serves to attach the upper "tooth" to the suborbital.



Text-figure 22.

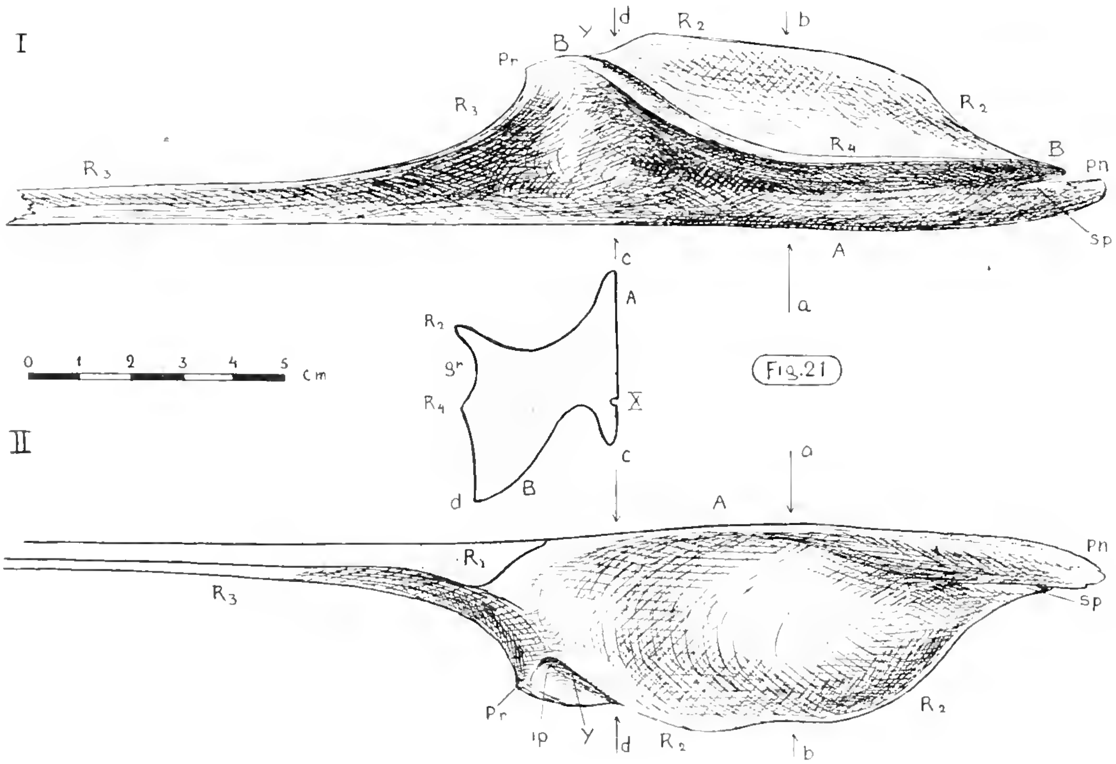
The right sub-orbital plate of *Dinichthys intermedius* Nwb. viewed from the inside.

A, real handle, *B*, tongue-shaped part of handle; *gr*, groove on under side of tongue-shaped part, *ip*, impression between curving points of ridges R_1 and R_3; *lf*, lower hind corner of *SO*, *of*, upper hind corner of *SO*, *oh*, upper front corner of *SO*. *pn*, contact point with post-nasal plate, *Pr*, high crest of R_3 ridge; *pro*, contact point with pre-orbital plate, *pso*, part overlapped by post-sub-orbital plate; R_1, R_2, R_3, R_4, ridges on the side of *SO*. *sp*, split between real handle *A* and tongue-shaped part *B*. *y*, curving point of ridge R_1.

A sensory canal (Text-figure 21 *IX*) runs from the upper front corner of the blade (Text-figure 21 *oh*) downward nearly parallel to its margin. Not far from the lower margin of *SO*, this canal curves sharply forward at an angle of nearly 90° from its original direction, and continues onto the handle (Text-figures 21 and 23 X). There it gradually approaches the lower margin and at last crosses it near the split. Another canal (Text-figure 21 *XI*) runs parallel with the lower margin of *SO*, beginning at its hinder lower corner (Text-figure 21 *lf*). A little before it meets the above mentioned canal, it curves sharply upward and fuses with the other. It is interesting to note that not in all Arthrodira do these two canals fuse. In *Homostius*, according to my investigations, they form two separate canals. According to Dean (1909), the same is true in *Titanichthys*.

On the inside, *SO* is formed in a more complicated manner. The thin hind part of the blade is smooth also on this side. It bears the trace of an overlapping margin, which is always to be found in the upper hind corner of *SO* (Text-figure 22 *pso*). This rather large and round impression evidently indicates that there is another plate behind *SO*. On the contrary, the fore part of the blade and the handle are strongly thickened.

From the upper front corner of the blade (Text-figure 22 *oh*) begins a ridge (Text-figures 22 and 23 R_1), which runs downward, at first very near the margin, later farther



Text-figure 23.

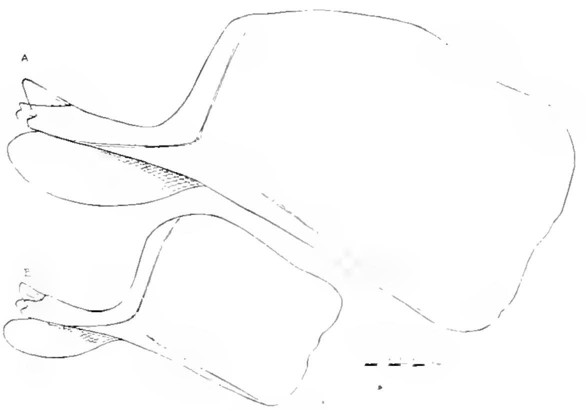
The right sub-orbital plate of *Dinichthys intermedius* Nwb. · I, from below; II, from above. The inset is a cross-section in the line a–b of Text figure 21.

A, real handle; *a–b*, line of section shown as an inset on Text-figure 21; *B*, tongue-shaped part of handle; *c–d*, section shown on inset, *gr*. groove on under side of tongue-shaped part; *ip*, impression between curving points of ridges R_1 and R_3; *pn*, contact point with post-nasal plate; *Pr*, high crest on R_3 ridge, R_1, R_2, R_3, R_4, ridges on inside of *SO*; *sp*. split between real handle (*A*) and tongue-shaped part (*B*); *y*, curving point on ridge *R*; X. sub-post-orbital canal.

away from it. It curves forward and continues onto the handle (Text-figures 22 and 23 R_2) where it runs nearly to the point of the tongue-shaped part. In the beginning this ridge is low but rises quickly and reaches its greatest height about the curving point (Text-figures 22 and 23 *y*). It keeps this height to the end. As seen from Text-figures 22 and 23, it runs in a half-circle around the orbital impression and forms its lower wall.

Another ridge begins at about the middle of the hind margin (Text-figures 22 and 23 R_3). Quickly rising, it runs forward to the curving point of the first ridge (Text-figures 22 and 23 *y*) where it makes a sharp curve, and forms a high crest (Text-figures 22 and 23 *Pr*). From this point the tongue-shaped part of the handle begins. As we know, the tongue-shaped part is placed behind the outside of *SO* and thus its inner surface is nearly on the high plane of the ridges. After a sharp curve, this ridge runs along the middle of the tongue-shaped part, but now as quite a low edge (Text-figures 22 and 23 R_4).

Between the orbital wall and this edge runs a groove (Text-figure 22 *gr*). It is deeper and narrower at its beginning, but becomes flatter and broader forward. A very clear, deep impression (Text-figures 22 and 23 *ip*), located between the curving point of both ridges, connects it with the posterior part of *SO*. As we see, the structure of *SO* is very complicated and difficult to describe. It can be better understood by studying Text-figures 21, 22 and 23. We may point out furthermore that the outline of *SO* is rather variable in different species of *Dinichthys*. Thus in *Dinichthys terrelli* Nwb. its blade is relatively long and narrow, and the handle shorter; in *Dinichthys intermedius* Nwb., on the contrary, the blade is broad and relatively short, but the handle is strong and massive (Text-figure 24).

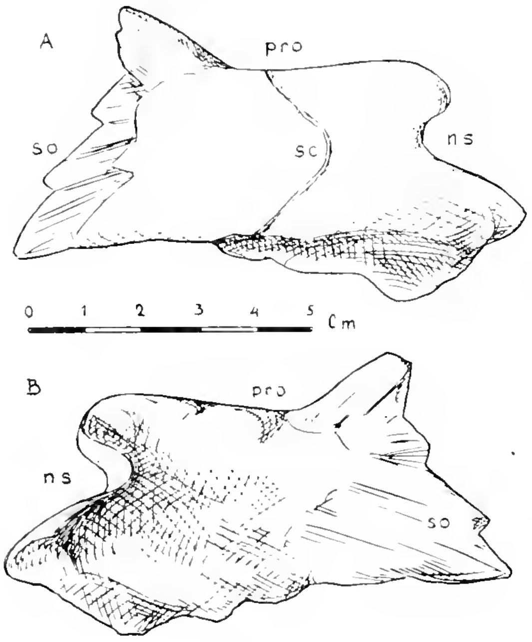


Text figure 24.
The sub-orbital plates of (A) *Dinichthys terrelli* Nwb. and (B) of *Dinichthys intermedius* Nwb. drawn to show the relative sizes of the fore and hind part of the plates.

Post-Nasal.—This plate, which is represented only by very imperfect fragments in the collection in the American Museum, has never before been described or figured in detail, but its presence in other Arthrodira is well known. Traquair (1890.4) for the first time figured it in *Coccosteus* and called it pre-maxillary (he called the *SO* the maxillary). He correctly marked the nostril openings as an impression on this plate. Woodward (1892.1, .2) described the same plate in *Phlyctaenaspis acadica* Wh., but did not find any clear trace of the nostrils.

Stensiö in 1925 based his reconstruction of *Phlyctaenaspis* on the same specimen as Woodward. He called the pre-nasal "plate L" and let "L" together with *PtO* bound the orbits on the upper side. In this manner *PrO* was surrounded by *C*, *PtO*, *PN*, *P* and *R*, and, contrary to what is found in all other Arthrodira, was excluded from bounding the orbital impression. Stensiö correctly let the sensory canal from *PrO* continue onto "L" and placed the nostril impressions between "L" and the rostral.

Jaekel mentioned this plate in many of his papers and figured it in all his reconstructions of Arthrodira from Wildungen (1902, 1906.2, 1907, 1925). According to him, the *PN* has a deep nostril impression or is even perforated by nostril openings. The sensory canal from *PrO* is continued on it. He called it in 1902 "Lacrymale", later "Post-nasale."



Text-figure 25.
The post-nasal plate of *Dinichthys ? terrelli* Nwb.: A, from outside; B, from inside.
ns, nasal impression, *pro*, contact place with *PrO*, *sc*, sensory canal connecting pre-orbital and sub-post-orbital canals; *so*, contact place with *SO*.

The first author to mention this plate in *Dinichthys* was Claypole. In his paper on *Dinichthys* in 1892 (p. 206) he described it briefly, and promised to describe it in detail in a later article, but I have not been able to find this description in any of his papers. In all probability it was never done. Here follows his brief description:

> The pre-maxillary [post-nasal], which has been hitherto unknown, is not found in the specimen here described, but its presence has been established from others. . . . For the present it must suffice to say, that it completed the outline of the fore part of the head, enclosing the nasal openings and filling up the recess observable between the nasal and pre-orbital plates.

The next author was Branson (1908.1, .2, 1911), who described the post-nasal as a fore part of the sub-orbital and was of the opinion (1908.1, p. 364) that: "The notched anterior end of it (*SO*) has not been figured or described. . . . In the interior of the notch the bone is 15 mm. thick and apparently articulated with some other bone. The anterior slime-canal seems to be continuous with the anterior slime-canal of the top of the head."

In the collections of the American Museum, *PN* is to be found as a badly preserved specimen and as a plaster cast. The cast is of a big *SO*, probably of *Dinichthys terrelli* Nwb., with the post-nasal attached to its front margin. Unfortunately no label is affixed to this cast and nobody can remember when or from what particular locality it came to the Museum. This makes it impossible to find the original, which is necessary for a detailed study. In Text-figure 25 is given a reconstruction of this plate based on the facts known from other Arthrodira, the descriptions and drawings of Claypole and Branson, and, chiefly, on the original pieces and the plaster cast in the American Museum.

The post-nasal (Text-figure 25 and Plate III, figures 3, 4 and 6) is a little, oblong, four-cornered plate with the hind margin attached to the front margin of the handle of

SO. The upper margin of *PN* comes in contact with *PrO*. There must apparently have been some process (not found on the plaster cast) which fitted into a corresponding impression on the thickened fore part of *PrO* (See description of *PrO* on page 000). In front we find an impression for the nostrils (*ns*). This part of *PN* touches the rostral, which limits the other half of the nasal opening. The under margin of *PN* is slightly curved with some doubtful processes. Perhaps this part comes in contact with the antero-supragnathal. On the inside there is nothing of special interest to see in the plaster cast.

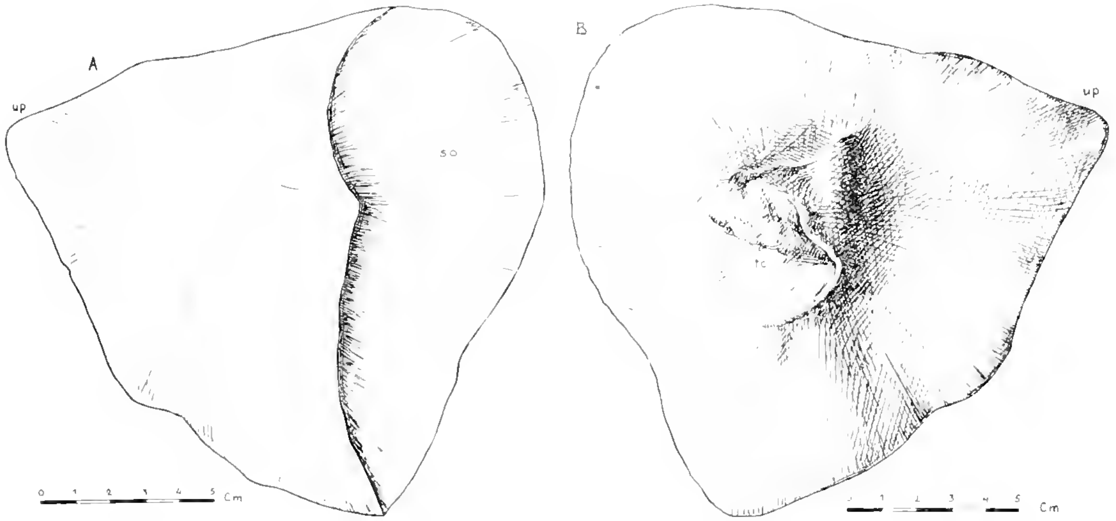
In the middle of *PN* a sensory canal (*sc*) runs in a curve from the upper to the lower margin. It forms the prolongation of the canal on *PrO* and connects it with the canal on *SO*. This position of the sensory canal on *PN* corresponds with what is known in other Arthrodira.

POST-SUB-ORBITAL.—This plate in other Arthrodira has been well known for a long time. In *Coccosteus* it was described by Traquair in 1889 under the name of jugular or post-maxillary. Woodward (1898) thought that it "occupies the position of an operculum." Jaekel in his reconstruction of *Coccosteus* in 1902 called this element "Quadratojugale," and also figured it among Wildungen Arthrodira (1906–1907). Stensiö in 1925 called this plate the *Ps* plate.

In *Dinichthys* the *PSO* has never before been found and described. But both Newberry (1889) and Claypole (1892.2) predicted its presence and we find it in Newberry's reconstruction of *Dinichthys*. However, this prediction was soon forgotten, and in the later papers on *Dinichthys* we never hear anything of this plate. The only traces of it are to be found in Branson (1908–1911). His *SO* was very large. We have seen before, that in the front it included the post-nasal. By a comparison of its posterior part with *SO* from other specimens, it is not difficult to see that it is unusually large. It looks as if another plate of triangular form were attached to the hind part of *SO*. But Branson could not find the limit between them.

Unfortunately, the material in the American Museum is also very incomplete. I have been able to find only one fragment of this plate. It must have belonged to a large specimen—perhaps to *Dinichthys terrelli* Nwb. (Plate IV, figures 8 and 9). As seen from the plate, this fragment shows the natural margin only from two sides. This makes it difficult to recognize the real form and size of *PSO* (Text-figure 26 A and B; Plate IV, figures 8 and 9). But from *Coccosteus*, which in its construction is closely related to *Dinichthys*, we know that *PSO* is of triangular form. The same is shown in Branson's specimen. We must, therefore, suppose it to be the case in *Dinichthys* also. The corner between the natural margins in our plate must then be its upper posterior corner (Text-figure 26 *up*). This supposition finds confirmation in a trace of an overlapping margin, which is located in the opposite part on the outside of the plate (Text-figure 26 *SO*). This must be the fragment of a limit between *PSO* and *SO*. (We know already that on the inside of the hind upper corner of *SO* there is found a clear overlapping impression).

When all these facts are taken into consideration, we can make a rather good picture of this plate (Text-figure 26). It is a relatively thick, triangular plate with slightly convex margins. It limits the hind margin and upper posterior corner of *SO*, and is probably to be placed so as to prolong *SO* mostly backward. Thus it fills up the space between the hind corner of *SO* and the external angle of the head roof. Its size must be quite variable in different species, all in proportion to the size of *SO*. In *Dinichthys terrelli* Nwb., where *SO* is relatively narrow and goes farther back, *PSO* is smaller in contrast to *Dinichthys intermedius* Nwb. with short and broad *SO* where it must have been much larger.



Text-figure 26.

The post-sub-orbital plate of *Dinichthys ? terrelli* Nwb.: A, from outside; B, from inside.

so, overlapping margin covered by *SO* *tc*, thickened part in center of inside serving as attachment for *PIG*, *up*, upper hind corner of *PSO*.

The most interesting point in the structure of *PSO* is a thickening placed nearly in the middle of its inner side (Text-figure 26 B *tc*; Plate IV, figure 8). It is rather large with a rough surface of horseshoe shape. If we place *PSO* as proposed before, the curving point of the horseshoe will be directed upward to the upper corner of the plate and the open part to *SO*. To this remarkable structure the lower jaw was movably attached. It has never been observed in *Coccosteus*—probably because *PSO* in this form is so small that it is difficult to study it in detail. But Jaekel in 1907 and 1925 (1925.1) in a reconstruction of *Pholidosteus* has described it as a "cartilage" placed on the underside of *PSO* (Jaekel's "Quadrato-jugale"). He supposed it was the "Quadratum."

The two other elements of the upper jaw are most commonly known under the names of the maxilla and pre-maxilla. Besides being used to designate mouth bones of the fishes, they were given to different plates in the Arthrodira themselves. Traquair called the post-nasal the pre-maxilla and the sub-orbital the maxilla. Newberry gave the same names to the "teeth" of *Dinichthys*. It is better to adopt the names proposed by Hussakof, though they are a little cumbrous.

Antero-supra-gnathal (pre-maxilla) and the postero-supra-gnathal (maxilla) are the two elements which together with the infero-gnathal (mandible) form the real chewing apparatus in the Arthrodira. In many of them were developed tooth-like tubercles, placed along the edges. The character and structure of these have been studied by many authors. The majority have come to the conclusion that these tubercles have nothing to do with teeth, but are formed of real bone substance. No traces of dentine or enamel are present. Here follow the opinions of various investigators concerning this matter in the Arthrodira.

Miller in his British Association report (1850, pp. 92–93) says "The teeth of *Coccosteus* . . . were formed of true bone." And Pander in his great work on the Placoderms (1857, pp. 68 and 87) writes thus, "Die kleinen Zähnchen scheinen mit dem Knochen innig verbunden und nur knöcherne Fortsätze desselben zu sein." While Claypole (1893.1, p. 608) notes that "This dense tissue of the mandible in no respect resembles true tooth structure. There is no trace of dentine or osteo-dentine, still less of enamel." (See also Claypole 1893.3, pp. 189–190.)

Dean (1901.1, p. 111) says "The study of the minute structures of the jaw elements in the Arthrodira shows that they correspond in all parts to the typical plates of the cranial roof." And Jaekel (1919, pp. 77 and 81) affirms that "Die Zacken [Zähne] . . . teile des Ganzen bleiben und sich nicht zu besonderen histologischen Einheiten von dem Knochengewebe absondern." (See also Jaekel, 1902, p. 107; 1911, p. 44; 1926, pt. III, Heft 3, p. 355). Likewise Goodrich (1909, p. 123) declares that "The teeth, indeed, appear to have always been continuous with the supporting bone, and possibly are merely tooth-like processes."

Hussakof (1906, p. 123) concludes that "The teeth are composed of osseous tissue which is more compact than, but not different from, that in the rest of the dermal element. No dentine is present." While Obrutschew (1927, p. 680) states that "Sections have absolutely confirmed that we are here dealing not with the real teeth from dentine, morphologically separated from the jaw, but only with the teeth-like processes of the jawplate." (Orig. in Russian). And last of all Stetson (1930, p. 37) says that "There is no trace of dentine or enamel in the jaws of *Dinichthys*."

But not all authors are of the same opinion. Agassiz in "Poissons Fossiles du Vieux Grès Rouge etc." (1844, pp. 24–26; Tab. B, fig. 2) described the minute structure of a *Coccosteus* tooth. According to him, this tooth has no pulp-cavity. Its center was occupied by a network of medullary canals, from which radiated fine dental canals. Nearly the same description was given by M'Coy in 1854 who stated (p. 602) that "The teeth have the middle occupied by a coarse network of irregular, tortuous, medullary canals, from which the fine calcigerous tubes radiate."

Claypole in his above-mentioned work (1893.1, p. 608) after describing the structure of the teeth of *Dinichthys* added that: "It is, in fact, a kind of transitional material between typical bone and typical tooth." Moodie in an article on the nature of the primitive Haversian system (1920) is of the same opinion, and thought that that the minute structure of the teeth of *Dinichthys* shows an intermediate character between the real bone and real dentine.[7]

However, the most interesting observation in the study of Arthrodiran teeth was made by Stensiö. In 1925 he described a microsection of an Arthrodiran jaw from the upper Devonian of Spitsbergen. According to him "All the teeth are ankylosed to the jaw bones with their bases and generally have the central parts occupied by a rather-large pulp cavity. . . . Basally the trabecular-dentine gradually turns into the bone of the mixicoronoid (infero-gnathal). Externally, of the dentine there is in the distal parts of the teeth a layer of bright shining enamel." It is very difficult to correlate this statement with all the others. We can only observe that the infero-gnathal described by Stensiö can not be regarded as typical for the Arthrodira. It belongs, perhaps, to one or another highly specialized Devonian family of the Arthrodira, which has a more complicated tooth structure. Further investigation on this form will show if it can be at all assigned to the Arthrodira.

Thanks to the kindness of Dr. L. Hussakof, I have had the opportunity of studying the perfect microscopical sections of the "teeth" of *Dinichthys* in the American Museum. Microphotographs of these sections are to be found in Plate V, figures 10 and 12; and Plate VI, figure 14. In Plate VI, figure 16 there is given for comparison a picture of the minute structure of a carapace plate (intero-lateral) of *Dinichthys*. As clearly seen there is no radical difference between the structure of the "tooth" and a bony plate. We find the same Haversian canals, Haversian lamellae and osteoblasts in both sections. The only difference is that the structure of the "tooth" is more compact, the Haversian canals are narrower, the lamellae more massive and dense. It is unquestionable that the "teeth" of *Dinichthys* are formed of true bone.

All three gnathal elements in *Dinichthys* are very well known and have been described in detail before by many authors. When first found, they were used as types for many species of *Dinichthys*. They are most completely described by Newberry (1875 and 1889) and Hussakof (1906). Therefore I shall only give a brief description of them here, pointing out some special characters in their position and in their relation to one another.

ANTERO-SUPRA-GNATHAL.—This plate (Text-figures 27 and 29 *ASG*) forms the big fore "tooth" of *Dinichthys*. Its outline and the relation between its single parts vary strongly in different species. But it is always easy to recognize the same elements in its structure. On the front and side this tooth is limited by two nearly plane surfaces *A* and *B* (Text-figure 27). They meet at an angle of nearly 90° and thus form a sharp and somewhat arched edge of the tooth (Text-figure 27 *eg*).

The massive sharp "pick" (Text-figure 27 *p*) of the tooth is smooth and bright, enamel-like on the outside. On the inside, a clear worn area shows the region where this tooth touches the infero-gnathal (Text-figure 29). In the section near the point, the pick of the tooth is nearly quadrangular (Text-figure 27 IV). Higher up, it becomes more flat

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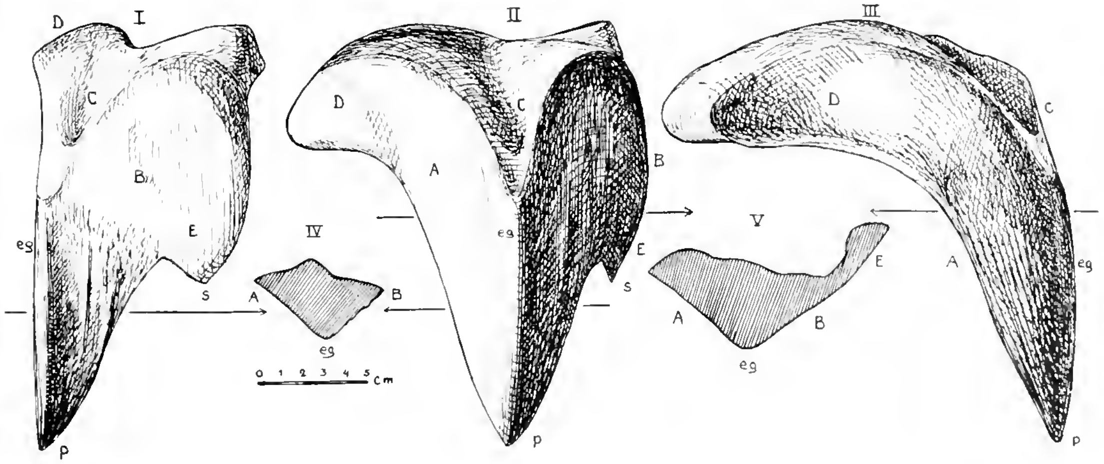
[7] Eastman in a description of the dentition of *Mylostoma* (1906 2) mentioned the presence of dentine and enamel in this form. But Stetson's investigation (1930) of Eastman's original material, shows that there is neither dentine nor enamel present.

and triangular (Text-figure 27 V). The surface *A*, which is directed sideward, continues gradually into the hind part of *ASG* (Text-figure 27 D). The surface *B*, which is directed forward, is much larger. On its lower sharp-edged margin a second smaller pick is placed (Text-figure 27 *s*). In the crevice between the two picks fits the big pick of the infero-gnathal.

In the middle of the tooth above the front edge (*eg*) is a big triangular impression (Text-figure 27 C). Farther backward it forms the upper surface of the hind part of the tooth. This hind part (Text-figure 27 *D*) serves as an attachment to other plates and forms a massive, long piece in approximate continuation of the pick of the tooth at an angle of about 90° (Text-figure 27 III). Thus, in reality, the "tooth" is a massive, curved cuspidate rod, with a thinner side part (Text-figure 27 *E*) where the secondary pick is placed. In spite of the fact that this "tooth" was made only of bone, it must have served as a very solid and effective weapon.



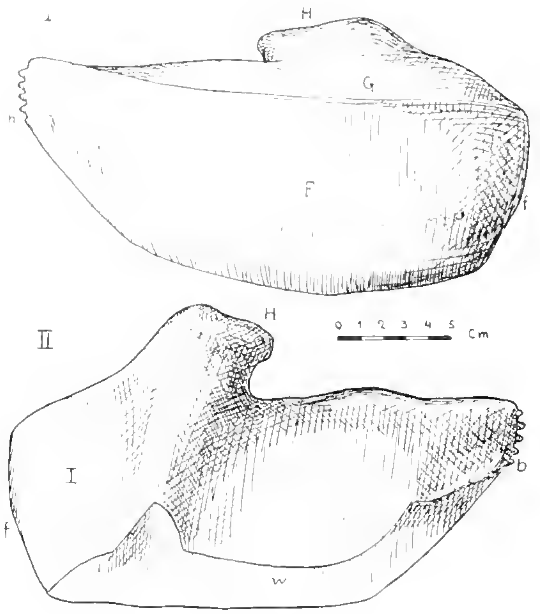
Text-figure 27.

The antero-supra-gnathal plate of *Dinichthys intermedius* Nwb.: I, from front; II, from edge; III, from side; IV and V in sections indicated by lines on the figure.

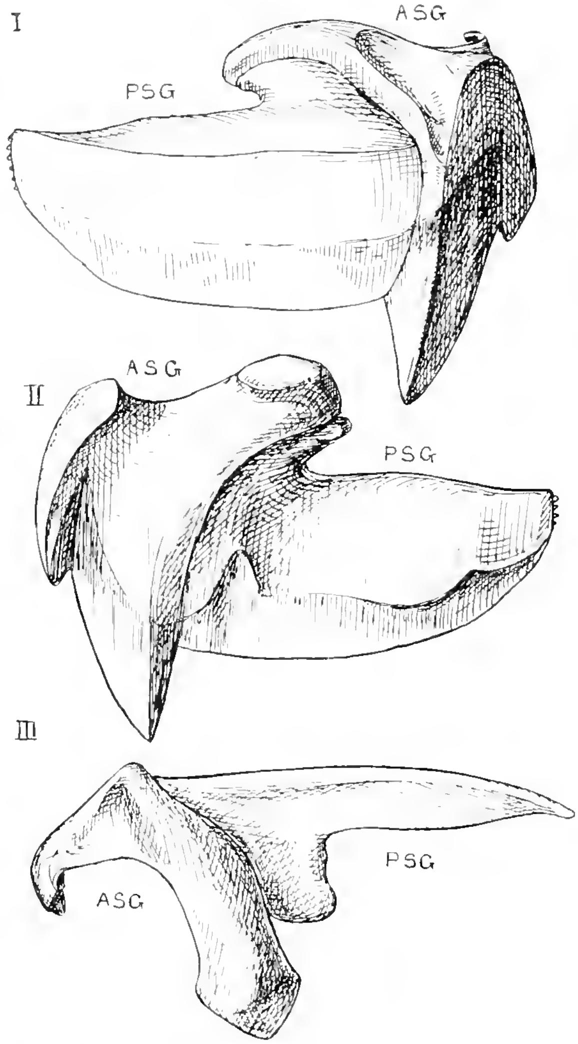
A, side surface, *B*, front surface; *C*, impression on top; *D*, hind thickened part; *E*, thin side portion on front part; *eg*, edge; *p*, chief "pick"; *s*, secondary pick.

Postero-Supra-Gnathal.—This plate (Text-figures 28 and 29 *PSG*), most commonly known under the name maxilla, is an oblong massive structure. Its hind margin forms a sharp curved edge which is smooth and bright on the outside. On the inside, a worn area also shows clearly how this tooth touches the infero-gnathal (Text-figure 28 *w*). On the outside, *PSG* is divided into two parts—the real tooth (Text-figure 28 *F*) and the attached part (Text-figure 28 G), which is connected with the former at a sharp angle. The real tooth is broadest in front (Text-figure 28 *f*) and narrower in the hind part (Text-figure 28 *h*). Along the hind margin is a row of small tubercles.

The front of the attached part continues into a long handle-like process (Text-figure 28 *H*). On the inside, this process is thickened and this thickening continues downward.



Text-figure 28.
(*Above*)
The postero-supra-gnathal plate of *Dinichthys intermedius* Nwb.: I, from outside; II, from inside.
F, lower part; *G*, attachment part; *H*, handle-like process; *I*, part overlapping *ASG*, f, front part; h, hind part with denticles; *w*, worn area.

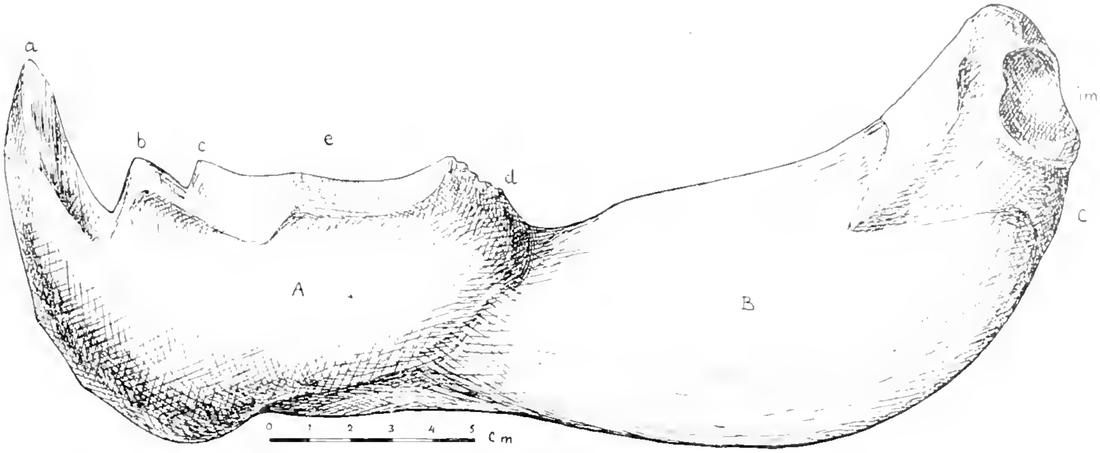


Text figure 29.
(*Right*)
Union between antero-supra-gnathal (*ASG*) and postero-supra-gnathal (*PSG*) plates of *Dinichthys intermedius*. I, from outside; II, from inside; III, from above.

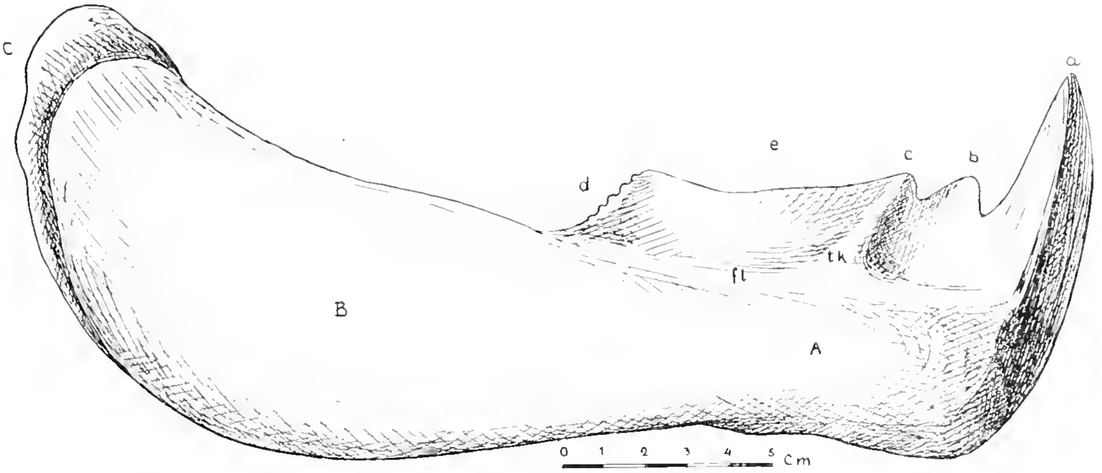
The part of *PSG*, placed in front of this thickening, comes in contact with *ASG* (Text-figure 28 I). One not infrequently finds *PSG* much broader than shown in Text-figure 28. Probably the different breadth of *PSG* comes from age the *PSG* of older examples are more worn.

As we know *PSG* comes in contact with *SO*. It touches the tongue-shaped part of the handle (Text-figure 22 *B*) on the inside so that the upper part of the real tooth is curved. The attached part thereby comes in contact with the inside of the ridge (orbital wall, Text-figure 22 R_3) which runs along the upper margin of the tongue-shaped part. With its front part, *PSG* (Text-figure 28 I) touches the surface *A* on *ASG* (Text-figure 27 *A*). The handle of *PSG* runs along the massive hind part of *ASG*. However, the attachment between these two elements can clearly be seen from Text-figure 29.

INFERO-GNATHAL. This plate (Text-figures 30, 31 and 32; Plate VII, figures 18 and 19), sometimes called the mandible or the mixicoronoid (Stensiö), is the real lower jaw. It is



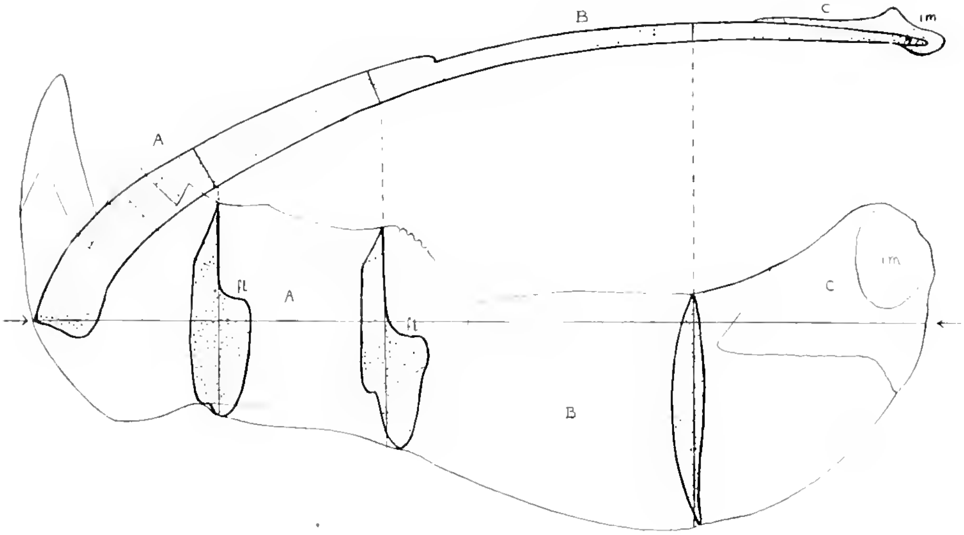
Text-figure 30.
The infero-gnathal and postero-infero-gnathal elements of *Dinichthys intermedius* Nwb., outside view.
A, functional portion; *B*, blade; *C*, *PIG*: *a*, front "tooth"; *b* and *c*, tooth-like indentations on cutting part, *b c e*, cutting part, *d*, tubercles; *im*, joint impression on *PIG*.



Text figure 31.
The infero-gnathal and postero-infero-gnathal plates of *Dinichthys intermedius* Nwb., inside view.
A, functional portion; *B*, blade; *C*, *PIG*; *a*, front "tooth"; *b* and *c*, tooth-like indentations on cutting part, *b c e*, cutting part, *d*, tubercles; *fl*, "floor" between blade and cutting part; *tk*, thickening consolidating the second indentation.

composed of a long, thin blade (Text-figures 30 and 31 *B*) and of a solid, thick functional portion (Text-figures 30 and 31 A). These two parts are very sharply divided from the outside. It looks as if the functional portion is a separate plate placed on the blade. But, as Hussakof noted in 1906, these two portions in reality form one bone with one ossification centre. This is, however, very clearly seen on the inside.

Of course, unlike *ASG* and *PSG*, the functional portion of *IG* has the worn area on the outside and is smooth on the inside. It is composed of a big front "tooth" (Text-figures 30 and 31 *a*) and a cutting part (Text-figures 30 and 31 *b*, *c*, *e*). The front "tooth,"



Text-figure 32.
The infero-gnathal and postero infero-gnathal elements of *Dinichthys intermedius* Nwb., in sections.
A, functional part, *B*, blade; *C*, *PIG*, *fl*, floor between blade and cutting part, *im*, joint impression on *PIG*.

as we know, fits in between the two "picks" on *ASG*. It is very massive and of a nearly quadrangular form in section (Text-figure 32).

With a more or less deep impression, the tooth is divided from the cutting part (Text-figures 30 and 31, *b*, *c* and *e*). On its front is to be found one or two tooth-like indentations (*b* and *c*), which are thin and sharp-edged from both sides. The front of the cutting part is consolidated by a thickening placed on the inside (Text-figure 31 *tk*). It extends to the top of the second indentation. The edge of the cutting part is long, sharp and finely polished. It works against the edge of *PSG*. On the hind part of the functional portion, from the posterior corner of the cutting edge down to the jaw blade, is placed a row of small denticles (Text-figures 30 and 31 *d*).

The blade is broad and thin on the posterior end, and gets narrower and thicker forward. On the inside (Text-figure 31) under the functional portion, it is thickest and in front fuses with the basal part of the front tooth. The inner surface of the cutting edge is placed deeper than the inner surface of the blade. Thus the upper fore surface of the blade forms a kind of floor in the recess betweenthe blade and the cutting edge (Text-figures 31 and 32 *fl*).

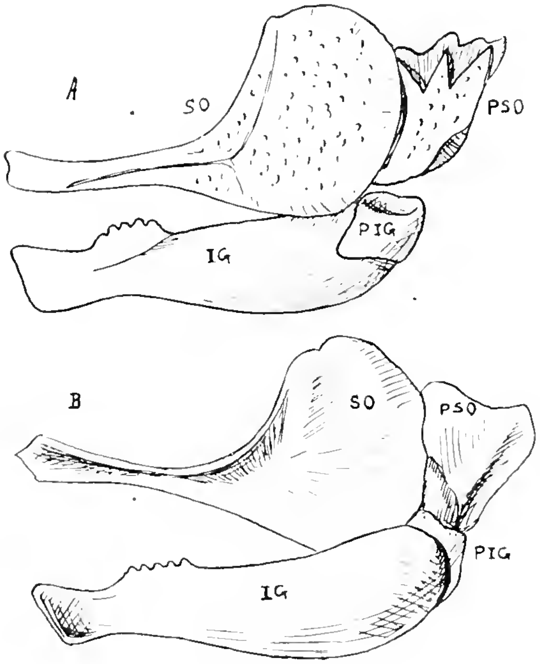
As a rule the *IG* is found more or less compressed. Often the whole bone is nearly flat. In reality it was rather strongly curved, especially the anterior or functional portion. The section drawing published by Hussakof (1906, Fig. 2) gives a very good picture of the natural curving of this plate (Text-figure 32).

Postero-Infero-Gnathal.—This structure (Text-figures 30, 31 and 32 *C*; Plate VII *PIG*) is the last plate of the head I have to describe. It has never before been described in detail in *Dinichthys*. The first author to indicate its existence in the Arthrodira was Eastman (1906.1) who described and figured it in *Dinomylostoma*, correctly indicating that it "forms a hinge [for attachment] with the suspensorial cartilage of the cranium." In 1907, Jaekel described and figured it in *Pholidosteus*. He called it "Articulare" to correspond with the similar element in higher fishes (Text-figure 33). In many later papers he mentions this plate and has also published some drawings of it (1919, 1925, 1929). In *Dinichthys* the plate was, for the first time, mentioned and schematically figured by Adams (1919) who gave only a very short description of it.

PIG is a small, triangular plate, very solidly attached to the hind rounded part of the *IG* blade. On the outside it overlaps the blade strongly and extends forward in a long, sharp tongue (Text-figure 30 C). On the inside it covers *IG* a little and forms a narrow sheath over the hind part of the blade (Text-figure 31 C). The surface of *PIG* is corrugated and rough. Its hinder part is thickened and on it is an oblong, irregular impression (Text-figures 30 and 32 *im*). *PIG* gets thinner forward and is very thin along the limit of *IG*. It is remarkable that this plate has been found only twice, attached to a pair of *IG* belonging to the same individual. It looks as if *PIG* were very strongly connected with *IG*. But, in spite of this, not even an impression or overlapping trace is to be found on the hind part of the lower jaw.

In the collection of the American Museum, among 10 to 20 specimens only two or three lower jaws were found showing a very indistinct trace of an overlapping on the hind part. In the Buffalo Museum only one example (No. E2033, described by Hussakof and Bryant, 1918, pp. 34–35, Fig. 6) showed a doubtful plate in the hind part of a jaw blade, perhaps a fragment of *PIG*. In other Arthrodira this plate, as we have seen, is only known in some forms from Wildungen (Jaekel), and in *Dinomylostoma* (Eastman). In my opinion all this indicates the possibility that *PIG* in the majority of Arthrodira has either not been ossified but was formed from cartilage, or that only its surface was ossified. This supposition also explains the rough and wrinkly surface of *PIG*.

With the help of *PIG*, *IG* was connected to *PSO*. This movable articulation corresponds with the jaw joint in all other vertebrates, as Jaekel pointed out in 1907. But we do not find here, as is usual, the well



Text-figure 33.
Jaekel's reconstruction of the jaw apparatus in *Pholidosteus*: A, from outside; B, from inside.
IG, Jaekel's "Spleniale"; *PIG*, Jaekel's "Articulare"; *PSO*, post-sub-orbital; *SO*, sub-orbital.

developed joint with a joint head on the one side and joint socket on the other. The impression of *PIG* is very flattened and quite irregular in shape. It is not placed on the upper hind margin of the jaw, as is usual, but on the side margin. The thickenings of *PSO* also bear an impression instead of a condyle. It is not placed on the lower margin of *PSG* but in the middle of its interior. In all probability *PIG* was attached to *PSG* only by ligaments, muscles and connective tissue (Adams, 1919). A real joint with condyloid articulation has not been developed here. The lower jaw was suspended to the upper, but not articulated with it.

This discovery makes it very difficult to understand in what manner the heavy and massive functional portion of the lower jaw could effectively work against the upper jaw. The thin and weak blade in itself is an unsatisfactory carrier for such a strong tooth combination.[8] Now we know that the joint also was very primitively and unsubstantially built. The functional portion of the lower jaw could not have been satisfactorily used if its movements were based on the same principle as in other vertebrates. We must wait to discuss this question further in a later section when we shall study the structure of the body carapace.

I have now described all the hitherto known side plates of the head. But in the literature descriptions of some other plates belonging to the same region can be found. Thus Claypole in 1892.1 mentioned that he had found in *Dinichthys* one pair of inter-mandibular plates and one "scalpriform tooth" between the two pre-maxillar plates, apparently working against the two inter-mandibular plates. He thinks that probably these two plates were also developed in other Arthrodira.

Hussakof (1909) described a symmetrical dental plate from a new form, *Dinognathus ferox* Huss. He thought that it either represented the fused "pre-maxillaries" or was a "pre-mandibular" placed at the symphysis. Perhaps in reality it was a median inter-maxillary plate, corresponding to that described by Claypole.

Jaekel in 1919 described three other plates placed between the *IG*, but on the underside. He thought that one pair was the ossified fore part of otherwise cartilaginous "Hyoidbogen." Together with a small median plate—copula—they were placed between the front of both "mandibles" (*IG*). Probably these three plates correspond to the plate in *Dinichthys* mentioned by Claypole. No trace of homologous elements is known from other Arthrodira.

Lastly, we shall now see how the single plates of the side part of the head are connected. In Text-figure 34 a reconstruction of this part is given from the outside (A) and from the inside (B). The drawing in itself is so clear that detailed description is not necessary. The outline and relative size of *PSO* are taken mostly from Branson's figures of the sub-orbital (1908.1). The size and form of *PN* are more or less doubtful. The front part

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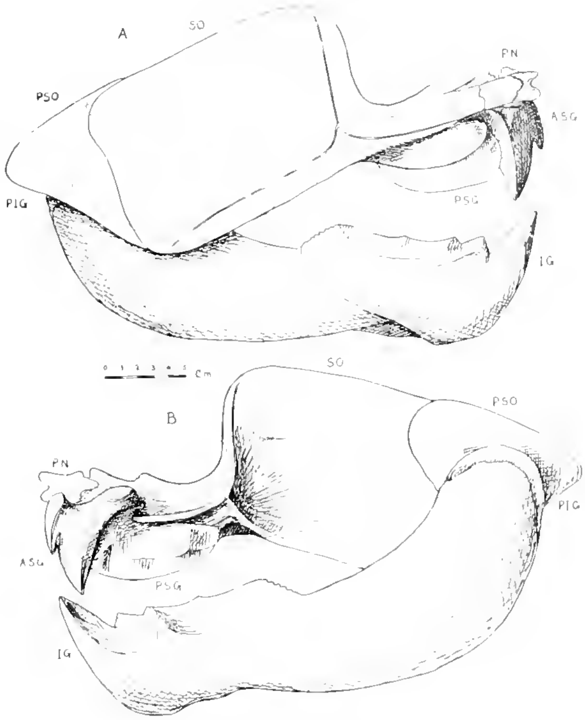
[8] Some authors (Newberry 1873; Claypole 1893.5; Hussakof 1906; Eastman 1907.2; Woodward 1922) express the opinion that the blade of *IG* was, perhaps, strengthened by cartilage. This in my opinion is improbable; the blade is convex on both sides and no trace of contact with cartilage is shown.

of *SO* and *PN* was, in reality, strongly curved inward. In the drawing they are pictured in a plane in order to show the dental elements more clearly. The same thing applies to the front part of *IG*. The position of the upper dental elements (*ASG* and *PSG*) can not be regarded as absolutely determined. They were certainly connected to *SO* with ligaments or cartilage. This makes it very difficult to fix their position. But the proposed relation is quite probable.

In another section I shall discuss the movement of the lower jaw and how the "teeth" worked against each other.



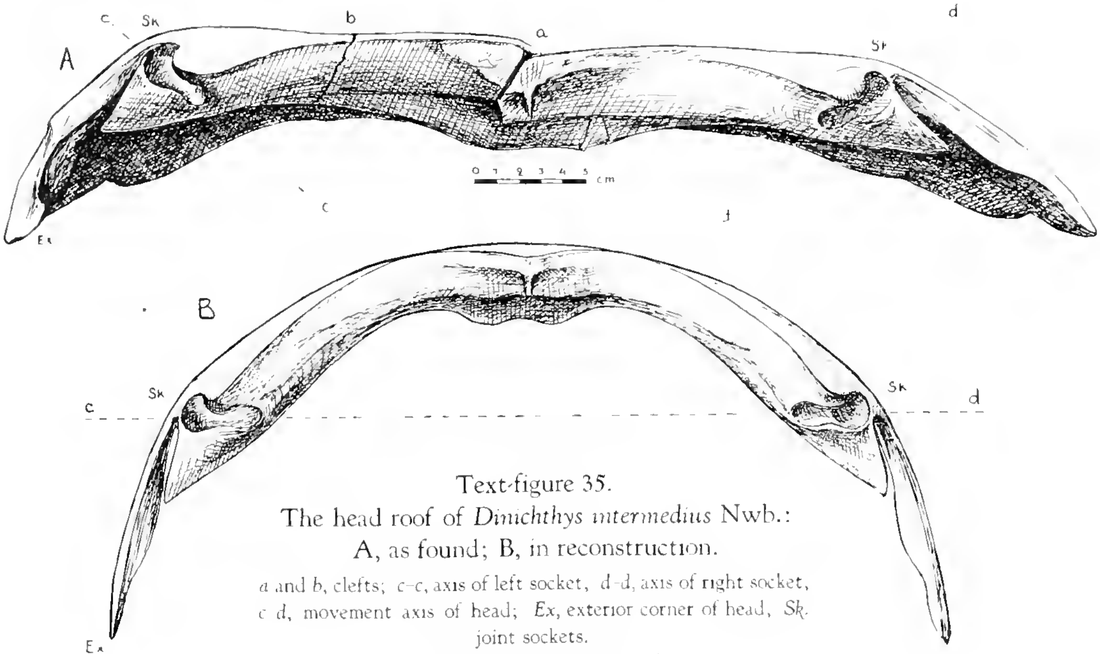
Text-figure 34.
Reconstruction of the side plates of the head of *Dinichthys*: A, from outside; B, from inside.
ASG, antero-supra-gnathal; *IG*, infero-gnathal; *PIG*, post-infero-gnathal; *PN*, post-nasal; *PSG*, post-supra-gnathal; *PSO*, post-sub-orbital; *SO*, sub-orbital.

RECONSTRUCTION OF THE HEAD SHIELD OF *DINICHTHYS*

The greatest difficulty in the reconstruction of the head roof of *Dinichthys* is to find its correct curves from side to side and from back to front. Older investigators saw clearly that the head roofs we find in the field have been without exception greatly flattened and that they were in reality much curved. Thus, the question is: How can we distinctly determine the degree of this bending? Fortunately we find some facts in the head structure which give us a very exact answer to this question.

As we know, the head roof of the Arthrodira was movably articulated with the help of a joint to the body carapace. Two oblong articulation sockets are placed on *EB*, on the hind margin of the head. Two oblong condyles are to be found on the antero-dorso-lateral plates on the body carapace. Surely the movements of the head were only possible if the long axes of both sockets (and of course also of both condyles) were placed strongly horizontally. Moreover, the axes of the right and left sockets lie in a continuous horizontal line, the motion axis of the head. If the sockets are not placed as mentioned above, their axes do not form a continuous horizontal line. The movement of the head is then absolutely impossible, one socket would hinder the movement possibility of the other. We can find an analogy in the jaw-articulation of higher vertebrates.

No attention has ever been paid to this matter, and it has been overlooked that the possibility of finding the real curve of the hind-part of the head roof is offered here. Professor Jaekel (1925.2) noted the correct position of the joints in the Arthrodira, with-



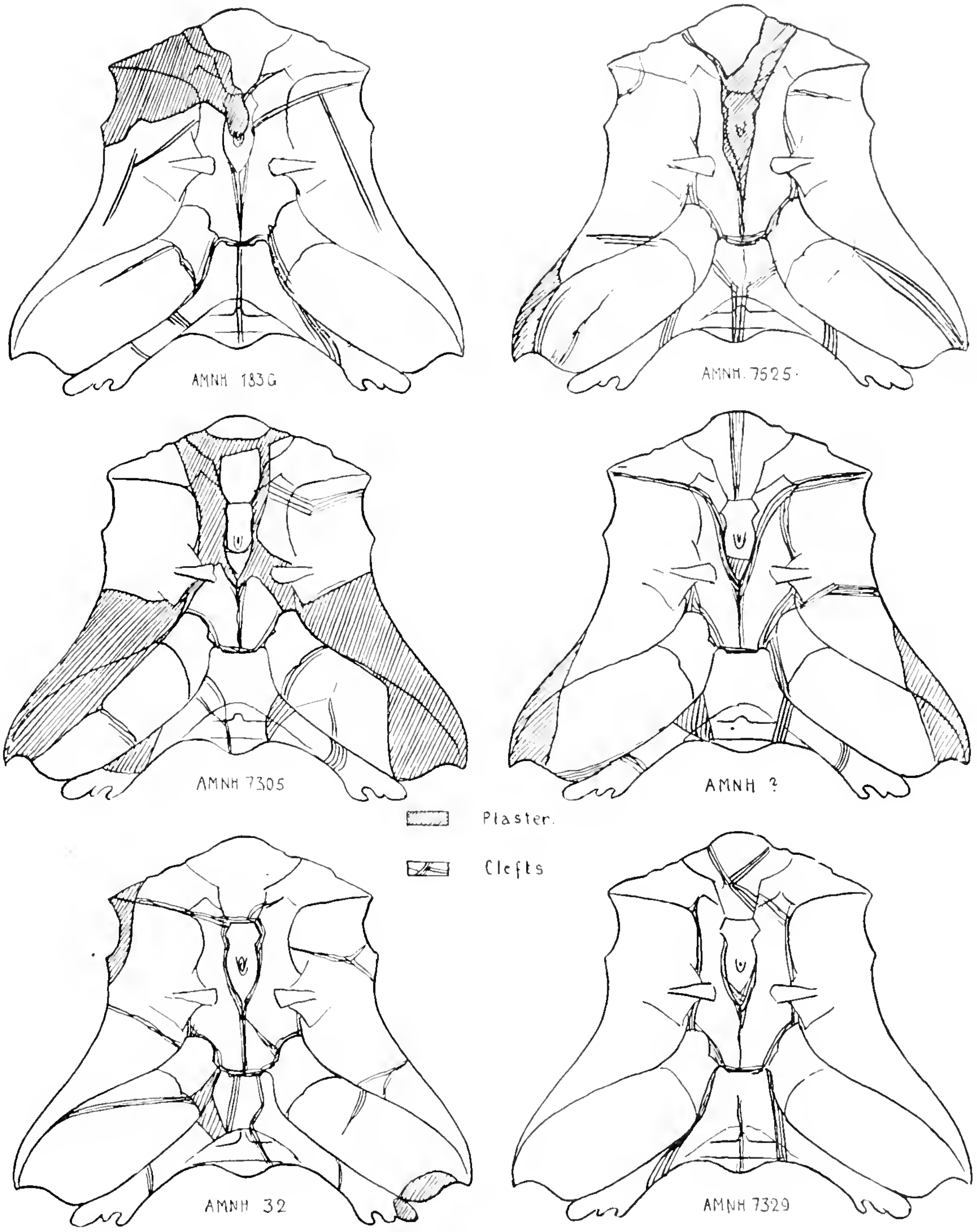
Text-figure 35.
The head roof of *Dinichthys intermedius* Nwb.:
A, as found; B, in reconstruction.
a and *b*, clefts; *c–c*, axis of left socket, *d–d*, axis of right socket, *c–d*, movement axis of head; *Ex*, exterior corner of head, *Sk*, joint sockets.
(American Museum No. 32.)

out pointing to the importance of this fact for the reconstruction of the shape of the head. The present writer in 1928 used this method in determining the curve of the head roof in *Heterostius* and *Homostius*. Stetson (1930) also mentioned this fact.

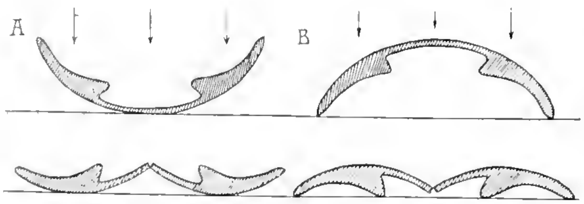
In Text-figure 35 A is shown the hind part of the head roof of *Dinichthys intermedius* Nwb. (Am. Mus. Nat. Hist. No. 32) from behind. The roof is so strongly flattened that it is nearly level above. Some large clefts (*a* and *b*) cross it and deform its outline. The joint sockets are clearly seen on each side (*Sk*). The dotted lines drawn through their long axes (*c–c* and *d–d*) meet at an angle of nearly 100°.

In reconstructing the real position of the joint sockets, we must bend the hind part of the head so strongly that the long axes of both sockets are in the same horizontal line — the movement axis of the head (Text-figures 35 B, *c–d*). Text-figure 35 B is a drawing of such a reconstruction. It shows how strongly the head roof is curved. This curving makes the head about 24 per cent narrower. The extreme side angles of the head roof (Text-figures 12 and 13), formed partly of *EB*, *PM* and *M*, are now placed nearly vertically (perhaps in reality they are still more vertical than shown on the drawing, Text-figure 35 B). We see now that the hinder consolidated arch of the head roof (Text-figure 13) was strongly bent. This explains the clefts on compressed specimens (Text-figure 36). The pressure has, of course, not only destroyed the hinder part of the head roof, but the middle and front parts are also flattened and show many clefts and chinks.

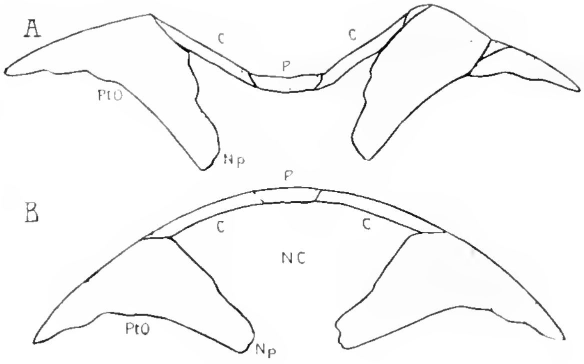
In the middle, as we know, the central part of the roof is thin (the roof of the neurocranium), while the side parts are very thick (the side thickenings of the head roof). Under pressure, the thick, curved side part was moved into a more horizontal position, without being much broken. On the contrary the thin central part was split and bent



Text-figure 36.
Sketches of some specimens of the head of *Dinichthys* from the collections of the American Museum of Natural History to show the position of the clefts.



Text-figure 37.
(Above)
Schematic drawings to show how the head of *Dinichthys* may be crushed under pressure.



Text-figure 38.
(Right)
Sections of the head roof in the region of the neurocranial process: A, crushed; B, in reconstruction.
C, central; *NC*, neurocranial cavity; *Np*, neurocranial process, *P*, pineal; *PtO*, post-orbital.

inwards. In the schematic drawing, Text-figure 37, we see that if the head roof was placed with the inside up (A) or down (B) the result of the pressure was the same. The side margins have a more horizontal position, the central part is curved inward. As a rule it broke along the median line of the head, the limit between both centrals.

This pressure phenomenon explains why we always find the head roof of *Dinichthys* with the central part bent inwards. In all the reconstructions and models of *Dinichthys* known to me this bending has not been corrected. Therefore the head has been given a flat or concave roof. The pressure also influenced the position of the neurocranial processes. In crushed specimens they are more vertically placed and the distance between their points is much larger than in reality. Besides, they are often pressed into the head roof which becomes swollen on the outside where the processes are attached. If we correct all these disturbances and reconstruct the original curve of the head and position of the processes, we shall see that the place in front of the neurocrănium is quite large and deep. Such a reconstruction is made in the half-schematic Text-figure 38. It shows the section of the head in the region where the neurocranial processes were situated.

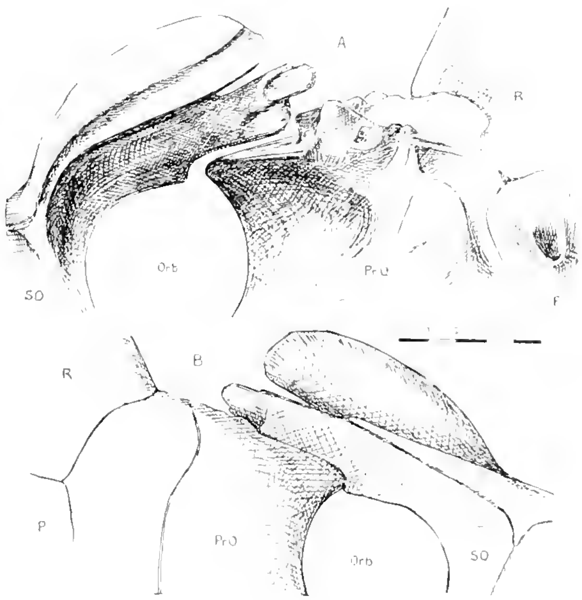
The most difficult problem is to reconstruct the original curve of the front part of the head roof. If we look at the half-schematic drawings of some *Dinichthys* head roofs given in Text-figure 36, we can easily see that all specimens are either cleft from the central part forward to the rostral region, or that more or less large portions of the front part of the head are absent. The arrangement of the clefts indicates clearly that the front part of the head was not only bent from side to side, but also from back to front. Looked at from the inside it must have formed the half of a bowl-shaped impression. Besides the clefts, the front part is also loosened along the sutures of the plates. Under pressure the single plates slid from each other along the sutures, without losing contact with one another. Such loosened sutures are often to be found between *PrO*, *P* and *R*.

The clefts and slides along the limits are, however, not enough to explain the flatness of the front part of the head in fossil specimens. To get an approximately satisfactory curving of this part, so as to fit the head roof together with the side plates, we must admit that the plates in the front region are not only crushed, cleft and slid, but flattened and deformed by pressure. We may call this kind of deformation microstructural. The plate in such a case is apparently not destroyed; it shows no clefts or breaks. But under enormous pressure it was flattened and became thinner and larger. This deformation can be perceived only by study of sections under the microscope. The whole bone becomes more or less laminated in character. The Haversian canals, placed parallel with the surface of the plate, are flattened; those placed obliquely or perpendicularly to it are enlarged. All the bone-cell cavities are also flattened. Good pictures of such a microstructurally deformed bone are to be found in Heintz 1929.1 (Pl. XXII, fig. 3; Pl. XXIV, fig. 4).

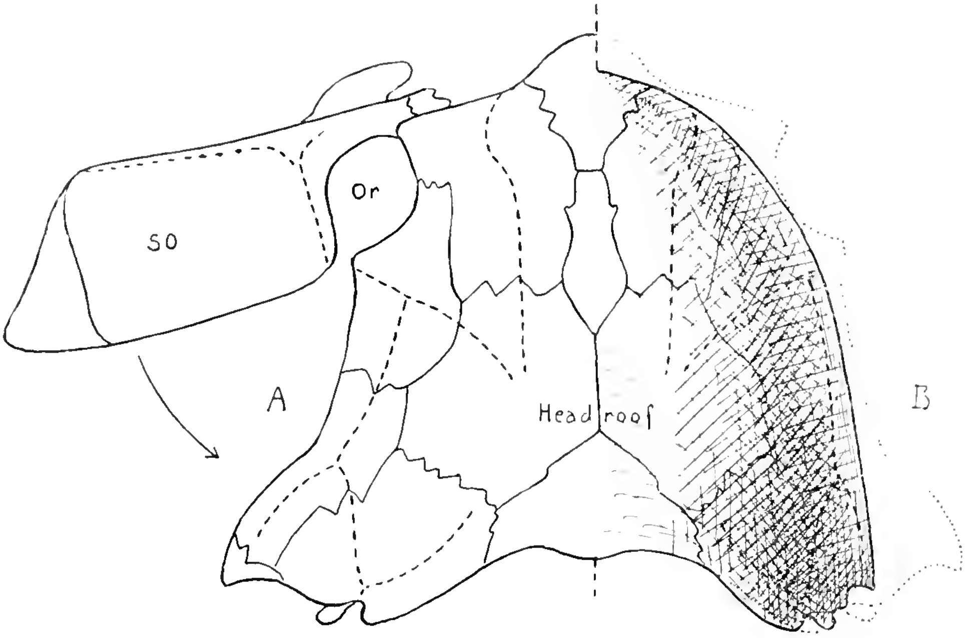
In reconstructing the curve of the front part of the head roof, the position of *SO* is of aid. As we have seen, on the front part of the handle of *SO* there were some ridges, which served to attach *SO* to the pre-orbital process of the head roof. On the latter were also developed some sockets and ridges. Text-figure 39 shows the fore part of *SO* and the pre-orbital process. It demonstrates how well the single processes and sockets were adapted to one another and how intimately these two parts were connected. But if the handle of *SO* is attached to the *PrO* of a compressed specimen, the hind part of it, the blade, stands far out from the side margin of the head roof (Text-figure 40). Meanwhile, we know that the upper fore corner of the blade should touch a notch behind the post-orbital process and the edge of the blade should run along the side margin of the head roof.

To attain such a position of *SO*, it is not enough to curve the handle, the front part of the head also must be strongly bent and shrunk. The front margin between the pre-orbital process and *R*, instead of being placed nearly perpendicularly to the median axis of the head, must be strongly curved. The point of the pre-orbital process is now not directed sideways but backwards. This gives the front margin of the head a nearly half-circular outline, instead of a nearly straight line.

The rostral in the reconstructed head roof has also greatly changed its position. Instead of extending forward,



Text-figure 39.
The contact between the head roof and the sub-orbital plate.
A, inside view—*SO* is separated from *PrO* to show clearly sockets and ridges; *B*, outside view—*SO* is in close contact with the head roof.
Orb, orbit; *P*, pineal; *PrO*, pre-orbital; *R*, rostral; *SO*, sub-orbital



Text-figure 40.
The position of the sub-orbital plate in relation to the head roof: A, in crushed specimens; B, in reconstruction.

it extends nearly downward. Its side margin touches the front part of *PN* without any strong connection. *R* and *PN* together limit the nasal openings. The post-nasal fills the recess between *SO*, *PrO* and *R*. With its hinder margin it is strongly connected to *SO*, and its upper margin comes in contact with *PrO*.

The contact between the blade of *SO* and the side margin of the head roof is not easy to reconstruct. They were only connected by means of skin, ligament, or perhaps cartilage. No sockets or crests are observable either on the edge of the blade of *SO* or on the side margin of the head roof. It is interesting to point out that, in forms from Wildungen, *SO* and *PSO* are very intimately connected with the head roof and are nearly always found together with it. But in *Dinichthys* the only certain attachment point between these two parts is a little notch behind the post-orbital process, where the upper corner of the blade of *SO* fits in. Thus the orbital openings are encircled by a very solid bony ring composed of *SO*, *PrO* and *PtO*.

SCLEROTIC RING.—This is fitted into this bony ring. It is composed, as in all other Arthrodira, of four separate bones.[9] In *Dinichthys*, as in *Coccosteus*, these elements are rarely found. In other forms from the Cleveland shale (*e.g. Solenosteus*) they are very common. Also, in all forms from Wildungen the sclerotic rings are always preserved. The sclerotic bones in *Dinichthys* (Plate III, figure 5) are relatively very broad. The opening for the eye is therefore small. Text-figure 41 gives the picture of a sclerotic

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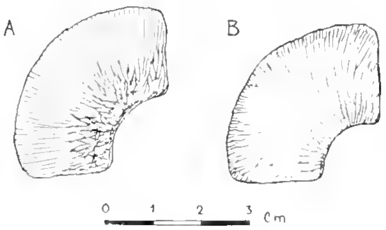
[9] Dean (1901.1) described the sclerotic ring of *Stenosteus* as composed of five plates. Probably this is a mistake.

bone from the outside (B) and inside (A). In *Dinichthys* the complete ring is seldom found. It is known from a specimen of *Dinichthys magnificus* Huss. & Br. in the Buffalo Museum. (Hussakof and Bryant, 1918; p. 41, fig. 11). Another specimen is preserved in the American Museum of Natural History. A third is figured by Newberry (1889).

Text-figures 42 and 43 show the total reconstruction of the head of *Dinichthys intermedius* Nwb. from the side and from above. From them we see that the proposed reconstructions are distinct from all that have been made heretofore. The head is much more compact and rounded in all directions; no sharp angles or processes protrude and there are no large spaces between the single plates. The head is sharply curved and thus the side and front margins of the head roof, *SO* and *PSO*, become nearly vertical. The lower jaw has at last obtained a distinct position. The nasal openings are also fixed.



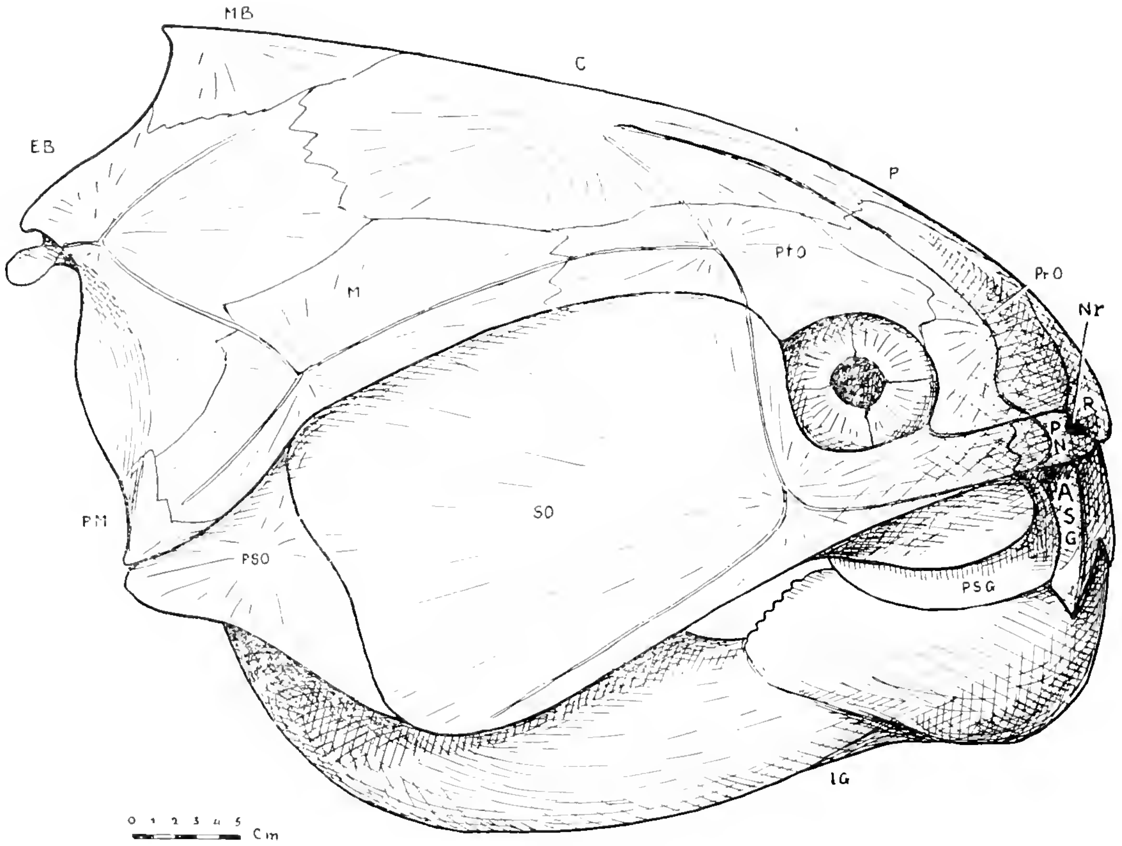
Text-figure 41.
A piece of the sclerotic ring in *Dinichthys*: A. from inside; B, from outside.

I may mention here that the well-known "eye balls," described by Newberry (1889) must, in accord with Stetson's investigation (1930), be regarded as nasal capsules. Probably they were placed behind the nasal openings, under the plate *PrO*. There is nothing to say about the sensory canals. I can only note that the short canal on *PN* unites the canal on *PrO* with that on *SO*, so that each eye opening is nearly encircled by a sensory canal.

Finally, it can be pointed out, that the division of the head of *Dinichthys* into two regions, the head roof and the side plates, is quite like the division of the head in all the fishes into the brain case and the visceral region. The head roof in *Dinichthys*, like the brain case in the fishes, serves to protect the brain, eyes, ears and olfactory organ. The side plates like the visceral skeleton form the upper and lower jaws. It is difficult to say if we have here only analogy, or also homology.

THE BODY CARAPACE

The body carapace surrounds the front part of the body as a continuous ring. It is broad in the dorsal part, becomes narrower downwards, and is narrowest where the dorsal and ventral parts meet. The latter is very large and forms a flat, long "plastron" which protects the ventral side of the fish. The whole armor is built from nineteen plates, which are more or less strongly connected. We find here, as before in the head shield, exclusively squamosal sutures. The single plates overlap each other very strongly and on each plate we find clearly limited overlapping margins. Some plates (*PL*, *Sp*) in addition to the sutures, are connected with the help of long thin spines, which go deep into the neighboring plates. In spite of these solid junctions, the carapace plates were not as strongly connected with each other as were the plates on the head roof, and almost without exception they are found isolated.



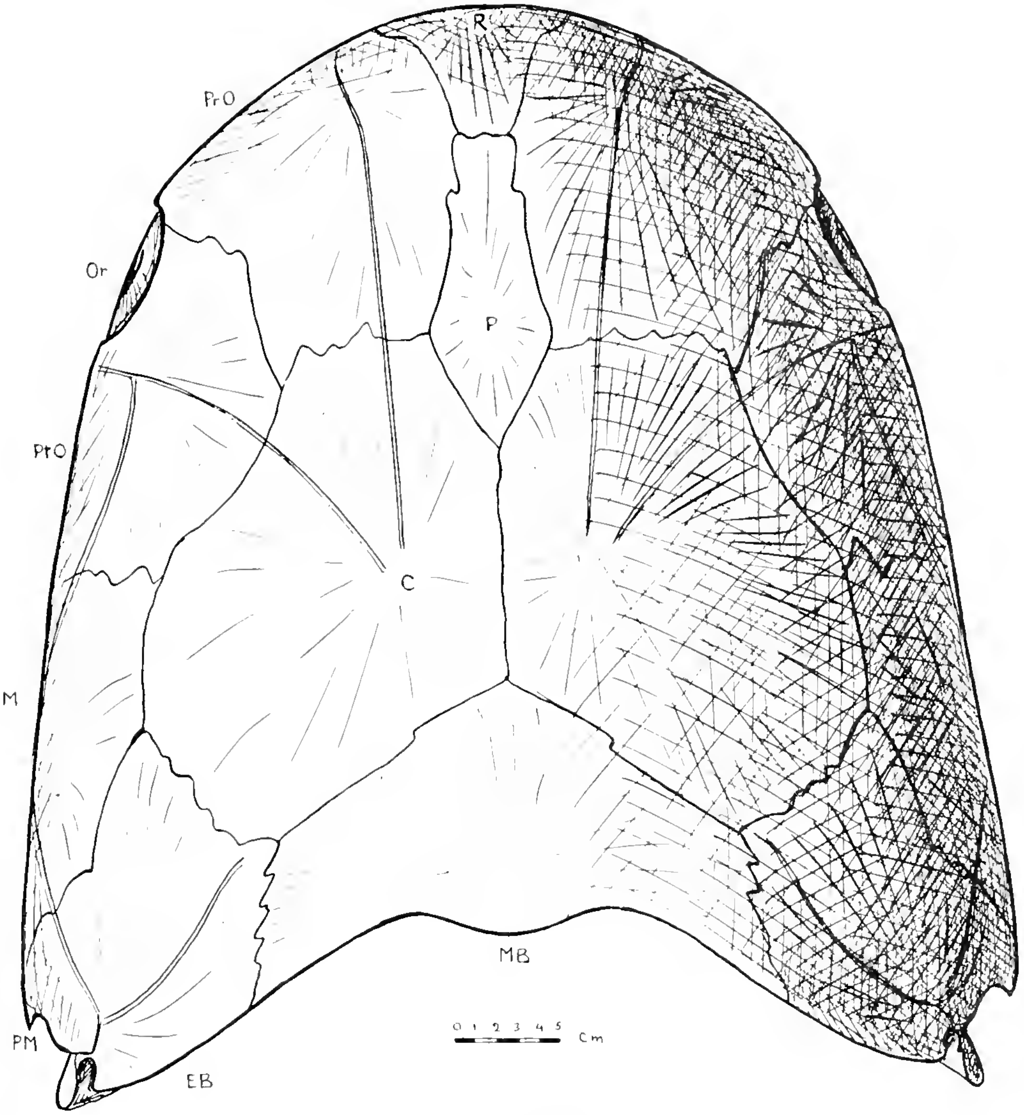
Text-figure 42.
A total reconstruction of the head of *Dinichthys* seen from the side.
ASG, antero-supra-gnathal; *EB*, externo-basal; *C*, central; *IG*, infero-gnathal; *M*, marginal; *MB*, median-basal; Nr, nostril; *P*, pineal; *PM*, post-marginal; *PN*, post-nasal; *PSG*, postero-supra-gnathal; *PrO*, pre-orbital; *PSO*, post-sub-orbital; *PtO*, post-orbital; *R*, rostral; *SO*, sub-orbital.

The whole body carapace can be divided into a dorsal shield; a ventral shield; and the plates connecting these two parts.

THE DORSAL SHIELD

The dorsal shield is composed of nine plates, namely; the single median-dorsal, the rights and lefts of the antero-dorso-lateral, of the postero-dorso-lateral, and of the antero-lateral and postero-lateral.

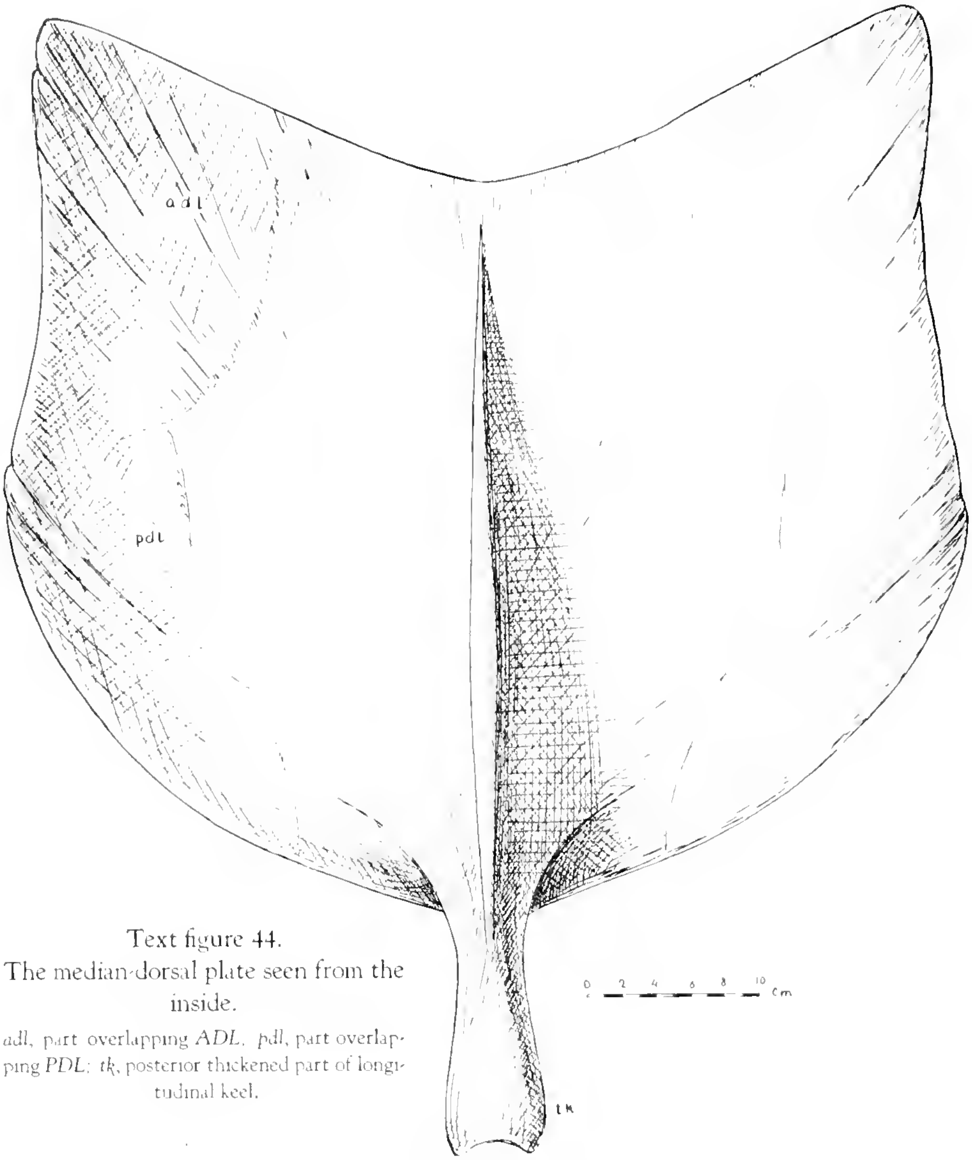
MEDIAN-DORSAL. This plate (Text-figures 44 and 45) is the largest in the whole armor of *Dinichthys*. In a large specimen of *Dinichthys terrelli* Nwb. it may measure along the median line (without the process) up to 50 cm.; across the broadest part 65 cm., and nearly 10 cm. in the thickest part. Its form and proportions are known from figures and descriptions in older works (Newberry, Claypole, Eastman, Dean, Hussakof). I shall therefore here point out only some especially significant facts.



Text-figure 43.
A total reconstruction of the head of *Dinichthys*, viewed from above.
EB, externo-basal; *C*, central; *M*, marginal; *MB*, median-basal; *Or*, orbit, *P*, pineal; *PM*, post-marginal; *PrO*, pre-orbital; *PtO*, post-orbital; *R*, rostral.

MD is always strongly flattened. Very often two clefts run from the front to the hind margin on both sides of the median line. The distance between them increases towards the back. In addition many small and large clefts cross its thinner side parts in various directions. The front angles are also often microstructurally deformed. All these circumstances make *MD* very flat. Therefore during the reconstruction it must not be forgotten that in reality it was quite strongly curved.

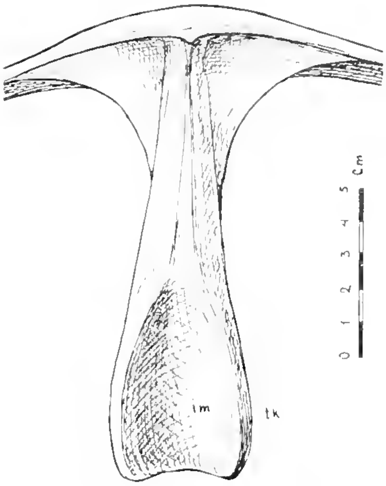
On the underside, partly along the front and partly along the side margin, is a very



Text figure 44.
The median-dorsal plate seen from the inside.
adl, part overlapping *ADL*, *pdl*, part overlapping *PDL*; *tk*, posterior thickened part of longitudinal keel.

distinct overlapping impression. This part of *MD* covers *ADL* and *PDL*. The margin overlapping *ADL* is placed on the front angle of *MD* (Text-figure 44 *adl*). It is smaller than the margin overlapping *PDL* (Text-figure 44 *pdl*) from which it is well separated. The last goes very far backwards and stops near the median line. The sharp and relatively deep grooves on the surface of the overlapping margin, demonstrate clearly how solidly these three plates were connected.

Along the median line on the underside of *MD* rises the well known longitudinal keel. It begins nearly on the front margin, and, rising gradually, runs backwards. It continues quite far back behind the hind margin of *MD*. Its posterior margin is massive and forms a rounded thickening (Text-figure 44 *tk*). This thickening is broadest at the basis, narrower in the middle and again broader at the point. Here is developed a deep sharply defined, semicircular impression (Text-figure 45 *im*). The relative form and size of this keel, as also the form and size of the whole plate, vary in different species of *Dinichthys* but all the characteristic elements are always present.



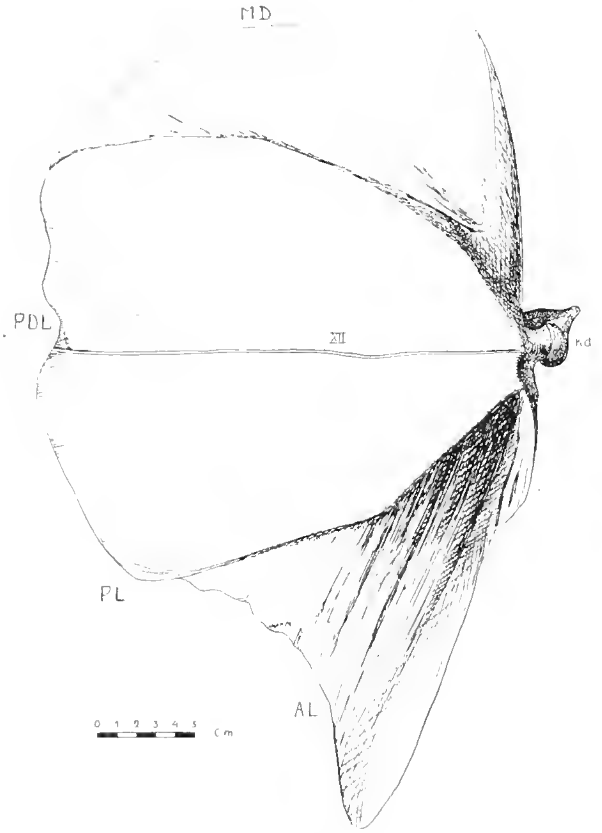
Text figure 45.
The posterior part of the median-dorsal plate seen from behind.
im, impression on thickened part of longitudinal keel, *tk*, posterior thickened part of longitudinal keel.

The significance of this keel, well known in many other Arthrodira, has been explained in various ways by authors. Pander (1857) only ascertained that it was a consolidated ridge. Woodward (1891.1) believed that it was used "evidently for connection with neural arches of the endoskeletal axis." Eastman (1906.2) thought that "the function of the posterior process was assumed to be in relation with swimming, and with its gradual development, increased locomotive facilities were acquired." Jaekel in 1902 noted that this process comes in contact with the neural arches, but in 1907 he described it as an attachment place for the muscles which move the head in relation to the body carapace. This opinion, which we also find in Adams (1919) and Stetson (1930) and which the present writer expressed (in 1929.1) must be acknowledged as absolutely correct. In a later section we shall discuss the function of the median keel in more detail.

ANTERO-DORSO-LATERAL.—This plate (Text-figures 46, 47, 48 and 55 *ADL*) is large and slightly curved. The condyle, serving as an attachment between body and head, is placed nearly in the middle of its front margin (Text-figures 46, 47, and 48 *kd*). On the outside two large impressions, the overlapping margins, are clearly developed. The first, on the upper part of the plate (Text-figures 46 and 47 *MD*), was covered by the fore angle of *MD*; the other is on the lower part of the plate. It is especially deep, and many sharply developed grooves stripe its surface (Text-figures 46 and 47 *AL*). This part was overlapped by *AL*, with which it was strongly connected.

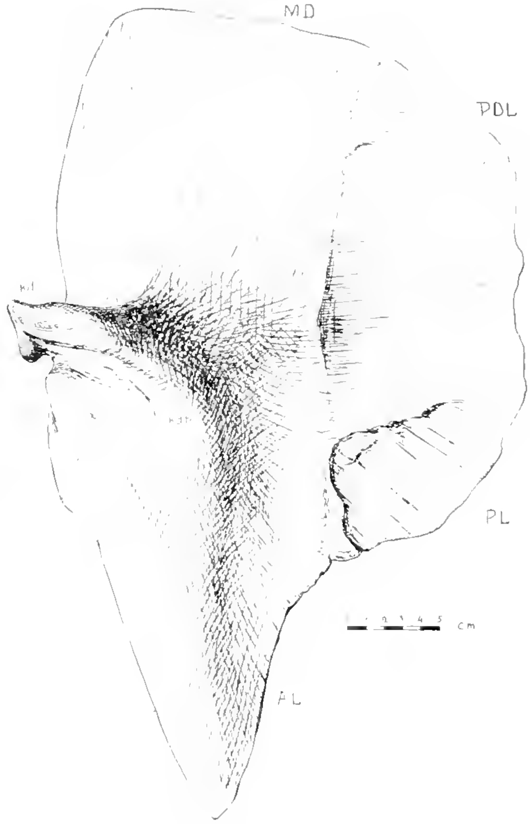
The median part of the plate, between two overlapping margins, is quite plane. A sensory canal runs from the condyle nearly horizontally to the hind margin of the plate (Text-figure 46). In some specimens the present writer has found two canals running parallel to one another across the plate. One specimen (in the Buffalo Museum) had developed three parallel canals (Text-figure 55). It must be pointed out that these secondary canals have nothing to do with the canal which in some forms (*Coccosteus*) runs obliquely downward from the condyle (Text-figure 10 *XIII*). They must be regarded only as individual variations of canal XII. Their number can change even on the right and left plate in the same individual. Thus, in the previously mentioned specimen in Buffalo, the triple canal is developed only on the right plate, on the left it is double.

On the inside we must first note the strongly developed condyle basis (Text-figure



Text-figure 46.

The antero-dorso-lateral plate figured from the outside.
kd, condyle; XII, anterior lateral canal, *AL*, position occupied by antero-lateral plate; *MD*, by median-dorsal; *PDL*, by postero-dorso-lateral; *PL*, by postero-lateral.
Similar explanations apply to succeeding figures.



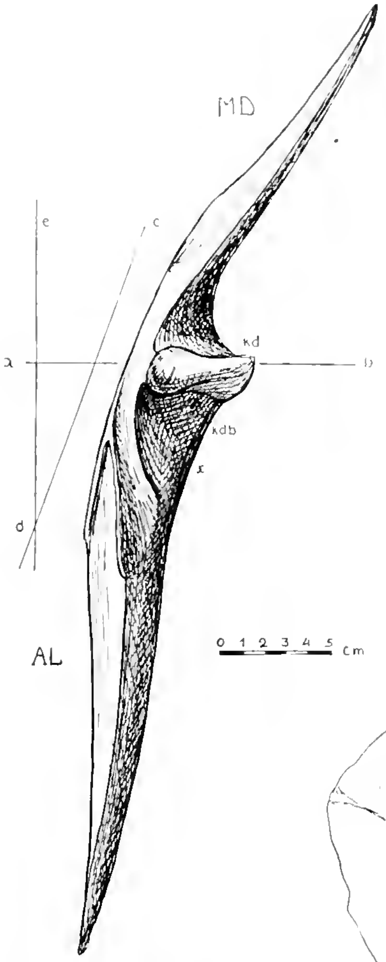
Text-figure 47.

The antero-dorso-lateral plate viewed from the inside.
kd, condyle, *kdb*, condyle basis, *rg*, ridge supporting condyle; *x*, place where process on *EB* touches *ADL*.

47 *kdb*). In the front it stands as a high, relatively narrow ridge (*rg*). Backward it becomes gradually lower and broader and at last runs over into the surface of the plate. Immediately under the condyle is a plane, well limited place (Text-figure 47 *x*). The process of the joint socket on *EB* (head roof) touches this part of *ADL*. It will be described in more detail further on.

A very distinct line, running nearly parallel to the front margin of the plate, divides the overlapping margin. Here *ADL* is thinner and its surface striped with many small grooves. To the upper part of this margin *PDL* was attached (Text-figure 47 *PDL*). The hind corner of it is again sharply divided from the upper part. It is more impressed and the grooves are much deeper and run at a sharp angle to the grooves of the upper part of the overlapping margin (Text-figure 47 *PL*). Here *PL* comes in contact with *ADL*.

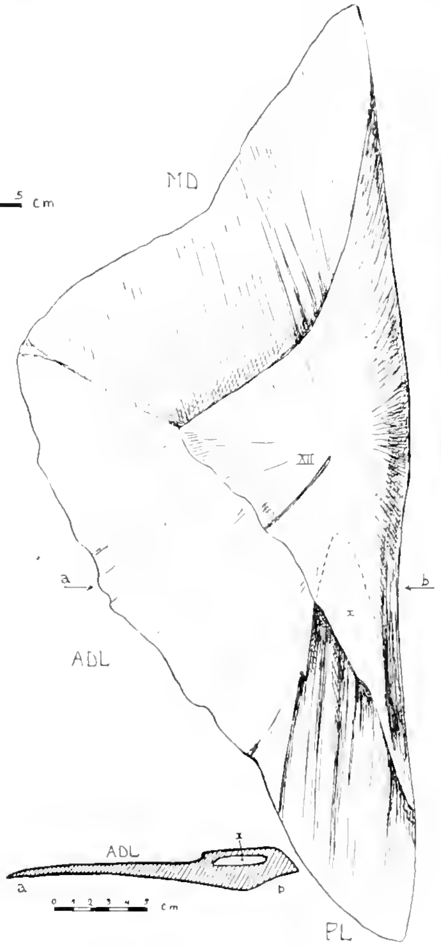
The long condyle on *ADL*, corresponding to the joint socket on *EB*, enables us to define exactly the position of *ADL* and its angle to the vertical line. In Text-figure 48



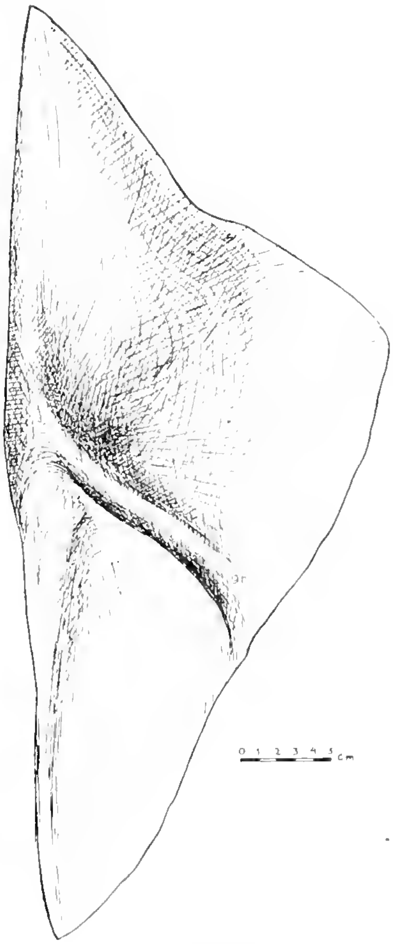
Text-figure 48.
The antero-dorso-lateral plate in front view.
a–b, axis of condyle; *c–d*, surface of plate; *e–d*, vertical line; *kd*, condyle; *kdb*, condyle basis; *x*, place where process on *EB* touches *ADL*.

the line *a–b* is the axis of the condyle. As we know, it must be placed exactly horizontally in order not to prevent the possibility of the head movement. Thus the surface of *ADL* (*c–d*) was set at an angle of nearly 20° to the vertical (*e–d*). In all the older reconstructions, it was placed at a much larger angle.

Postero-Dorso-Lateral. This (Text-figures 49, 50 and 55 *PDL*) is a large triangular plate, defining the upper part of the hind margin of the body carapace. Its hind margin is strongly thickened, but it gets thinner toward the two other margins, where it is very thin. On the outside the overlapping margins are very sharply



Text-figure 49.
The postero-dorso-lateral plate seen from the outside.
a–b, line of section shown in inset; *x*, cavity where spine-like upper angle of *PL* fits in; *XII*, anterior lateral canal.



Text figure 50.
Inside view of the postero-dorso-lateral plate, showing the groove, *gr*.

distinct from the hinder thick part which is not overlapped. The upper margin (Text-figure 49 *MD*) underlies the plate *MD*, the lower is under *ADL* and *PL* (Text-figure 49 *ADL*, *PL*). The part overlapped by *PL* is sharply defined. It is more impressed and shows deep grooves. The connection between *PDL* and *PL* becomes still more solid, as the upper spine-like angle of *PL* sticks deeply into the margin of *PDL* (Text-figure 49 *x*, section *a–b*).

On the part of *PDL* which is not overlapped runs a sensory canal (Text-figure 49 *XII*). It forms the immediate prolongation of the before described canal on *ADL*, and runs slightly upward from the boundary line between these two plates to the ossification center of *PDL*. When there are two or more parallel canals on *ADL*, we also find a corresponding number of canals on *PDL* (Text-figure 55). On the inside *PDL* shows nothing of special interest. Its surface is relatively smooth. Attention is merely called to a groove-like impression, running from the middle of the hind margin obliquely downwards to the hind side margin of the plate (Text-figure 50 *gr*).

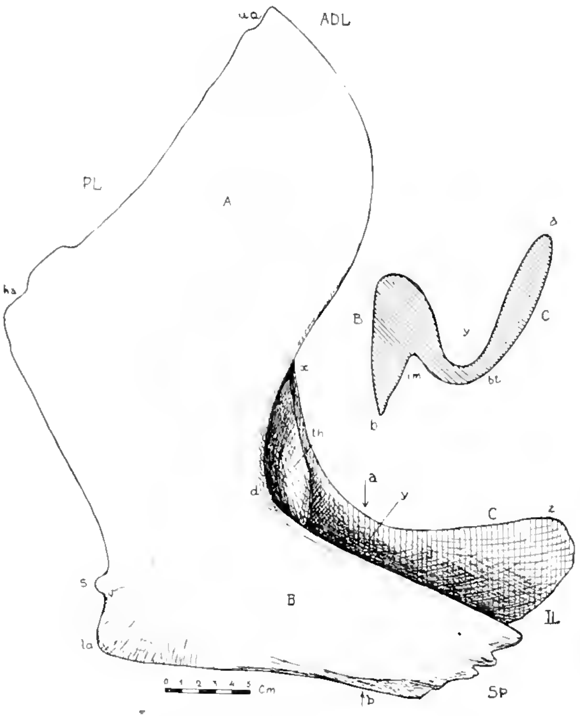
ANTERO-LATERAL.—This plate (Text-figures 51, 52, 53 and 55 *AL*) is the most complicated one in the whole body carapace. It was well known by older investigators, but its true outlines and divisions were misunderstood.

Newberry in 1889 described the first complete *AL* and called it "clavicular." This plate was in reality not only *AL*, but a complex of three different plates—namely *AL*, *Sp* and *IL*. In reconstruction they had been so strongly fastened together with plaster that it was absolutely impossible to find the boundaries between these three components. From Newberry's time on this "clavicular" was accepted as a classic and in later papers and reconstructions it was considered a single plate. It is interesting to point out that as early as 1893 Claypole (1893.1) had described and figured a clavicular plate from *Dinichthys* or from *Titanichthys* which shows very clearly a border dividing a short part of the "clavicular" from the hind part. The front part is *Sp*; the hind, the real *AL*. But this observation remained unnoticed.

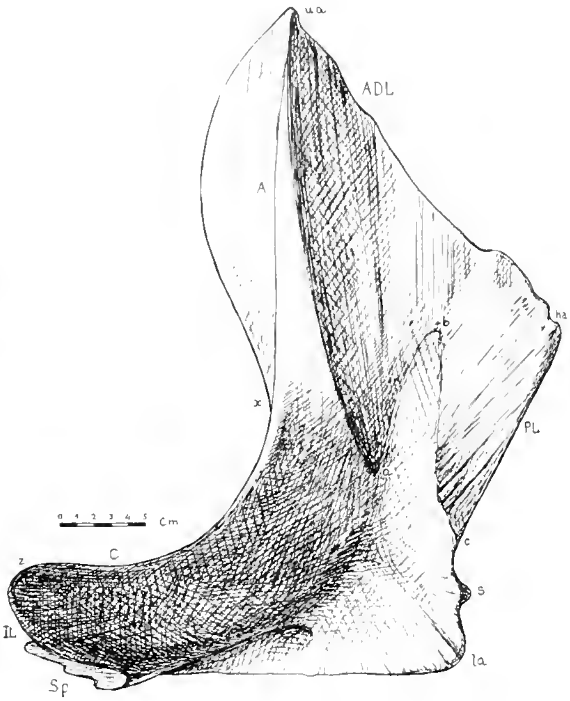
Later, various authors came to the opinion expressed by Eastman (1907) that ". . . in *Dinichthys* the inter-lateral does not occur as a distinct plate, but may be represented by the fork-like prolongation of the so-called clavicular, the broad upper portion of which corresponds of course to *AL*." However, Newberry's "clavicular" is not only composed of three separate bones, but is also strongly deformed by pressure. Newberry did not correct this mistake, but only filled up the clefts with plaster. As a result his "clavicular" becomes too flat and its inner wing runs nearly parallel with the outer. This fault misled Dean in his reconstruction of *Dinichthys* (1909). Instead of combining the inner wing of the clavicular with the ventral shield, he made it a supporter of the infero-gnathal. We also find the same mistake made by Bryant (1918).

In reality, the antero-lateral (Text-figures 51, 52 and 53) is a big plate with a large upper part (*A*), a relatively small lower part (*B*), and an inner wing (*C*) which extends obliquely inward. On the outside the plate is nearly plane and smooth. In its overlapping relations *AL* shows an exception to the usual rule. It is not overlapped by the plates placed on top of it (*ADL*, *PL*) but overlaps them itself. The only overlapping margins on the outside are on the point of the lower part (Text-figures 51, 52 and 53 *Sp*) and the outside of the inner wing.

The front margin of *AL*, from the upper angle of the plate (*ua*) runs downward in the form of an arch. Then it makes a very sharp curve forward (*d*) and here defines the lower part of the plate in a nearly straight line. The hind margin is much more angular.

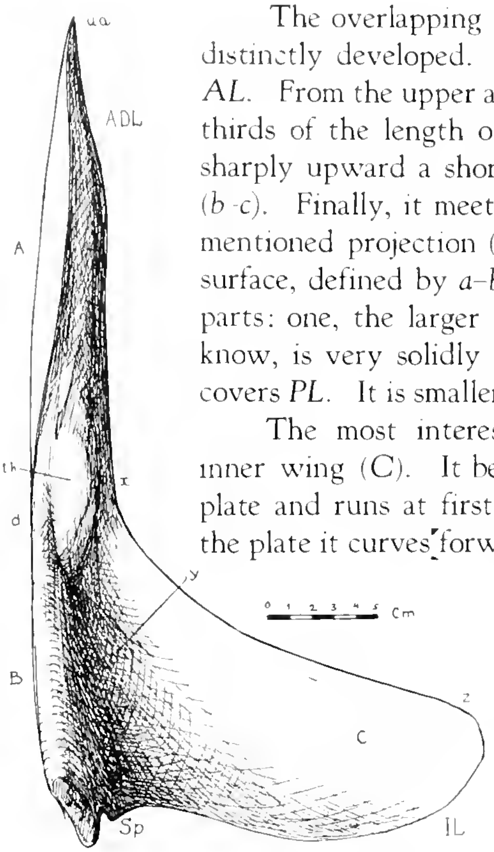


Text-figure 51.
The antero-lateral plate seen from the outside.
A, upper part, *a-b*, line of section seen in inset, *B*, lower part, *bt*, bottom of groove between *B* and *C*; *C*, hind wing, *d*, curving point of front margin; *ha*, hind angle; *im*, impression between *B* and *C*. *la*, lower angle; *s*, projection of unknown significance; *th*, thickening between *A*, *B* and *C*; *ua*, upper angle, *x*, curving point of hind ridge; *y*, groove between *A*, *B* and *C*. *z*, front part of *C*.



Text-figure 52.
The antero-lateral plate viewed from the inside.
A, upper part; *a*, *b*, and *c*, curving points on limits between *ADL*, *AL* and *PDL*. *C*, hind wing; *ha*, hind angle; *la*, lower angle; *s*, projection of unknown use; *ua*, upper angle; *x*, curving point of hind ridge; *z*, front part of *C*.

From the upper point it runs obliquely downwards in an uneven line to the hind angle (*ha*) of the plate, from this point down to the lower angle (*la*), and on forward, forming the lower margin of the lower part of *AL*. The part around the lower angle and along the lower margin is relatively thin and shows a rough surface with many small impressions. It is probable that some ligaments or muscles have been attached to these parts. Immediately above the lower angle a little projection (*s*) of unknown significance is generally found.



Text-figure 53.

The antero-lateral plate in front view.

A, upper part, *B*, lower part, *C*, hind wing, *d*, curving point of front margin; *th*, thickening between *A*, *B* and C, *ua*, upper angle; *x*, curving point of hind ridge, *y*, groove between *A*, *B* and C, *z*, front part of C.

The overlapping margins on the inside of *AL* (Text-figure 52) are distinctly developed. They occupy the hind portion of the upper part of *AL*. From the upper angle (*ua*) their edge extends downward nearly two-thirds of the length of the whole plate (*a*). From here it curves very sharply upward a short distance (*a–b*), and then again turns downward (*b–c*). Finally, it meets the hind margin of the plate a little below the mentioned projection (*s*). The long cuneate part of the not overlapped surface, defined by *a–b–c* divides the overlapping margins on *AL* in two parts: one, the larger (Text-figure 52 *ADL*), overlaps *ADL* and, as we know, is very solidly connected with it; the other overlapping margin covers *PL*. It is smaller and less ridged (Text-figure 52 *PL*).

The most interesting thing in *AL* is the previously mentioned inner wing (C). It begins as a thickened ridge at the upper angle of the plate and runs at first nearly vertically downward. Near the middle of the plate it curves forward and downward (Text-figures 51, 52 and 53 *x*). Between it and the other part of the plate a groove is formed, which becomes larger and larger as it extends forward (y). The upper part of this groove is occupied by a roundish thickening (*th*), which gradually disappears upward, but is sharply defined downward (Text-figure 53). In the lower part, the wing itself is quite broad and thin, its upper margin running nearly parallel to that of the lower part of *AL*. It ends in a rounded point (*z*) far behind the surface of *AL*. Its lower margin arches to the front point of the lower part of *AL*.

If we look at the section through the lower part of *AL* and the wing (Text-figure 51 *a–b*), we notice that the bottom of the groove between them is quite thin (*bt*). Thus there is formed from beneath a deep impression (*im*) between the inner surface of the lower part and the bottom of the wing. This whole division is S-shaped in section, and not especially solidly built. It is, therefore, comprehensible that it is nearly always strongly compressed in fossil examples and as a rule the wing is pressed against the underside of the lower part, and the connection totally destroyed. But in some specimens this part is well preserved and in others it can easily be rebuilt. For example, the clavicular of *Dinichthys magnificus* Huss. & Bry., figured and described by Hussakof and Bryant (1918, p. 42; Pl. 7, fig. 2), shows the grooves between the wing and the lower part of *AL* very distinctly.

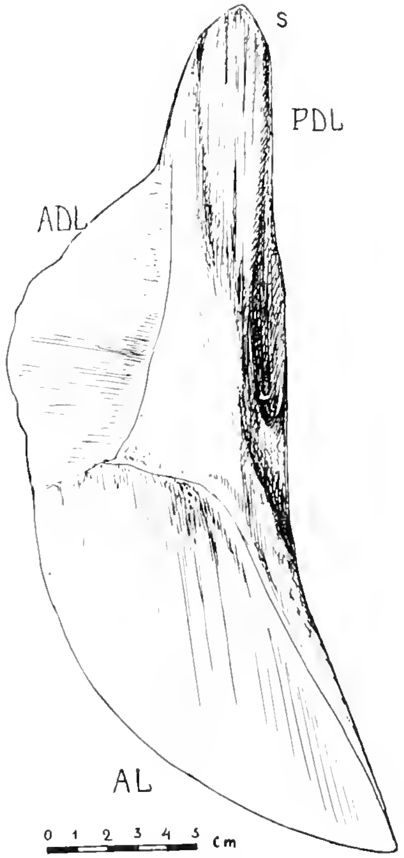
Thus (erroneously) the structure of *AL* in *Dinichthys* seems unusual. The structure of this part of the Arthrodiran carapace is difficult to study. Very often, especially in small forms, the limits and outlines of the intero-lateral and spinal are indistinct, and it is therefore difficult to determine the boundaries of *AL*. However, in *Coccosteus decipiens*

Ag., for example, the wing on *AL* is always clearly shown. Traquair (1890.4) described it as part of *IL*. This part is developed especially concisely in *Coccosteus canadensis* Wd. which I had the privilege of studying in the Buffalo Museum. In some of the Wildungen Arthrodira also, *AL* shows the same structure. In Acanthaspida it is also quite easy to see traces of the same structure (Heintz, 1929.1; Figs. 8, 9, 12, 13, and 14). The wing of *AL* is described as part of *IL*. Finally, in *Homostius* (Heintz, 1928) the structure of *AL*, in spite of a very high degree of specialization, shows traces of the same characteristic outlines.

Postero-Lateral.—This plate (Text-figures 54 and 55 *PL*) has never before been described in *Dinichthys*, In the majority of reconstructions it is absent (Newberry, Eastman, Dean, Hussakof, Branson, Bryant, Stetson). Only in the reconstruction exhibited in the American Museum of Natural History do we find *PL* (made of plaster) as a relatively large, broad plate. In Dean's description and photographs of this reconstruction of *Dinichthys* (1909) this plate was not included.

The present writer has been successful in finding, first one quite good example of this plate in the collection of the American Museum (Bungart coll., 1914; field No. 13), and later two perfectly preserved plates in the Buffalo Museum (Nos. 15613/E3808 and 15616/E2811). Text-figure 54 is a drawing of this plate based on these three specimens.

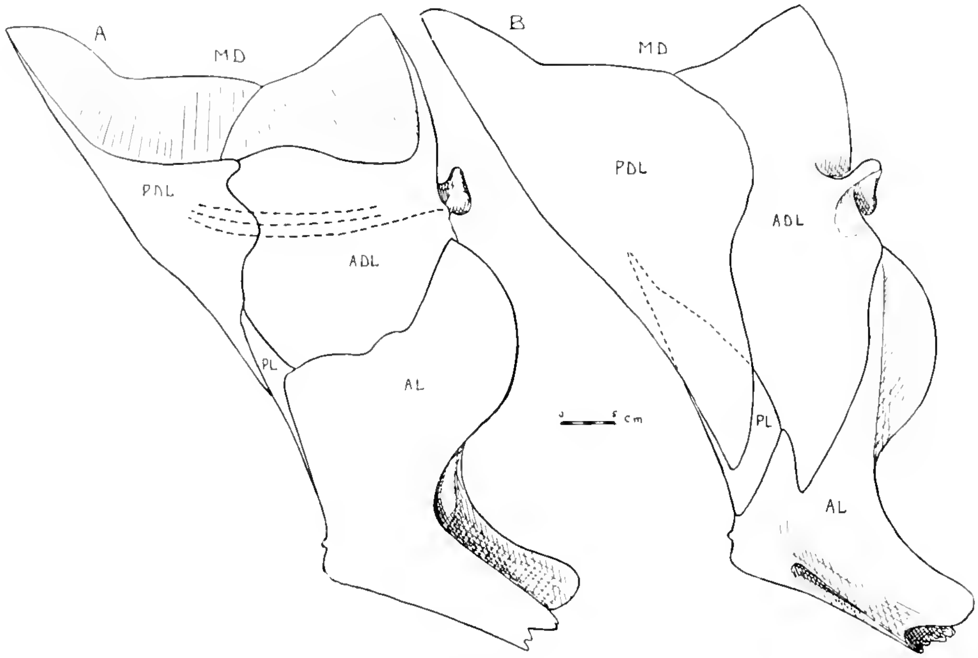
This is a relatively small, triangular plate, much smaller than the one we find in the reconstruction in the American Museum. It combines all three elements of the body carapace and is strongly connected with them. On the outside, nearly the whole plate is covered by the neighboring plates. Their overlapping margins form the largest part of it. The not-overlapped part consists only of its thickened hind margin. As we know, its spine-like upper corner extends into the lower margin of *PDL* (Text-figure 54 *PDL*). Its side margin (Text-figure 54 *ADL*) comes in contact with the previously mentioned impression on the overlapping margin on *ADL*. Lastly, the lower margin of *PL* occupies the hind overlapping margin on *AL*. On the inside, nearly the whole *PL* is covered by the lower part of *AL*.



Text-figure 54.
The postero-lateral plate seen from the outside.
s, spine-like upper angle which fits into cavity on *PDL*.

To understand the structure of the dorsal shield of *Dinichthys* better, there is given in Text-figure 55 a contour drawing of the four side plates of *Dinichthys* (?) *intermedius* Nwb. connected together (from outside—

A; from inside—B). This drawing is based on material in the Buffalo Museum. All the plates belong to one specimen so one cannot doubt that their relation, position and size are correct. *MD* is not shown on the figure; only its overlapping margins on *ADL* and *PDL* are seen. The upper part of the last two plates was in reality curved backwards. To make it clearer it has been flattened in the drawing. The previously mentioned triple sensory canal on *ADL* and *PDL* is shown by dotted lines in Figure A. The complete outline of the plate *PL* is not visible either from the outside or from the inside. Therefore its contour is dotted in figure B.



Text-figure 55.
The relative positions of the side plates in the body carapace of *Dinichthys:* A, from outside: B, from inside.
Figure based on material from the Buffalo Museum

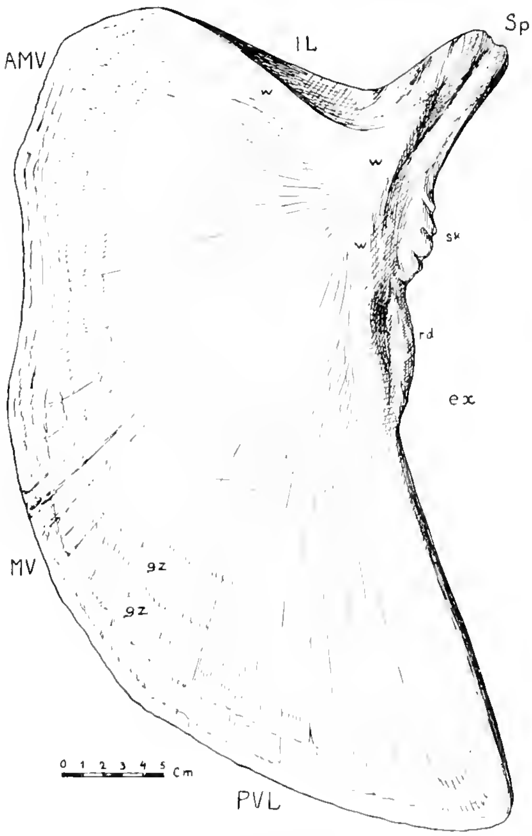
These two drawings show how strongly the single plates of the dorsal shield were connected. They formed a very solid and massive girdle, which served not only as a protecting armor, but also as the place where the strong body muscles were attached.

THE VENTRAL SHIELD

The ventral shield or "plastron" was well known in former times. As early as 1875 Newberry gave a fairly good figure of it, and in 1894 Wright published an absolutely correct reconstruction. Later Eastman, Dean, Hussakof, and Smith described and figured it several times.

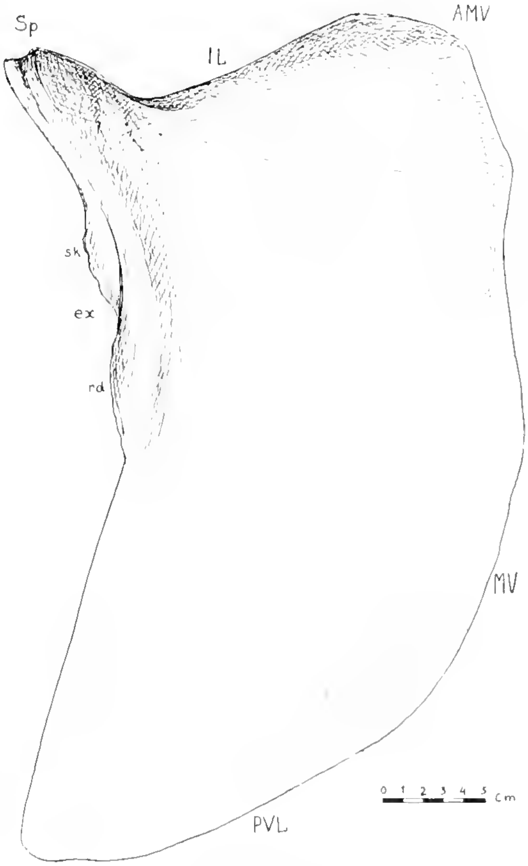
But the connection between the dorsal and ventral shields has never been studied and described. Therefore all the previously mentioned investigators have not noticed that the ventral shield makes it possible for us to determine the exact breadth of the fish. In reality, the distance between the two extreme corners of both the antero-ventro-lateral plates (Text-figure 61), to which the extreme corner of *AL* was attached, gives us the maximum breadth of the ventral side of *Dinichthys*. This measurement is of very great value as it is the only exact measure of the breadth of the fish we know. It helps very much in reconstructing the outline of *Dinichthys*.

All the plates in the ventral shield are quite flat and relatively thin. But we have no reason to suppose that they have been strongly deformed and flattened by pressure. It is probable that they were in reality flat. No distinct clefts of other traces of marked deformation, like those in some plates in the dorsal carapace or the head, are to be found here. It is also doubtful whether the ventral shield was strongly curved, as the curving would shorten the distance between its two extreme angles, and thus make the whole carapace narrower, which is very improbable.



Text-figure 56.
The antero-ventro-lateral plate shown from the inside.

ex, exterior margin; *gz*, grooved zone; *rd*, ridges; *sk*, sockets; *w*, wall around front and side margins.



Text figure 57.
The antero-ventro lateral plate figured from the outside.

ex, exterior margin; *rd*, ridges; *sk*, sockets.

The whole ventral shield (Text-figure 61) is composed of six single plates: two (right and left) antero-ventro-laterals; two (right and left) postero-ventro-laterals; one median-ventral, and one antero-median-ventral.

ANTERO-VENTRO-LATERAL.—This plate (Text-figures 56, 57 and 61 *AVL*) is large, oblong and flat. It is thickened along the front (*IL*) and external margins (*ex*); elsewhere it is relatively thin. The most characteristic point in *AVL* is a quite long, thick process, forming the extreme angle of its front margin (*Sp*). Both the front (*IL*) and the external margins (*ex*) are concave, the internal (*AMV*, *MV*, *PVL*) on the contrary forms a strongly arched convex line.

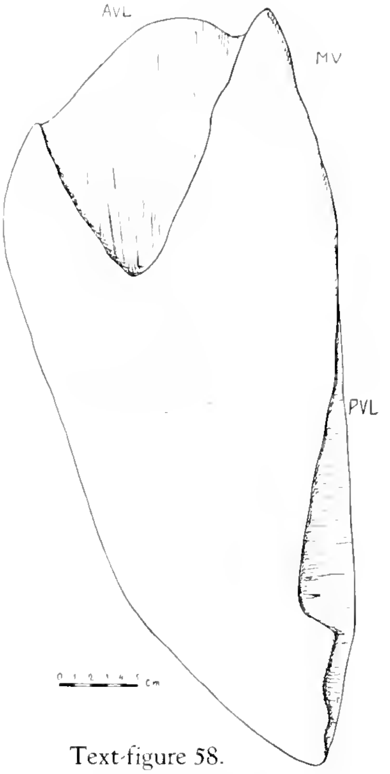
On the inside (Text-figure 56) the thickened part forms a wall (*w*) along the front and forepart of the external margin and strengthens the external process (*Sp*). This wall goes gradually inward into the inner surface of the plate. On this wall are developed some ridges (*rd*) and sockets (*sk*). They are especially clear and deep on the external process. Probably they have served as attachments for ligaments and connecting tissues. The other part of the inner surface of *AVL* is quite smooth and plane. The overlapping margins are not sharply developed and are difficult to recognize. On the contrary the ossification rays are especially clear. At the same time the growth zone, in the form of concentrically arranged lines, is very remarkable along the inner margin of the plate (Text-figure 56 *gz*).

From the outside the plate is still more plane and smooth. It only curves quite steeply downward along the front margin (*IL*, *AMV*) and the fore part of the external margin, where some ridges are developed (*rd*).

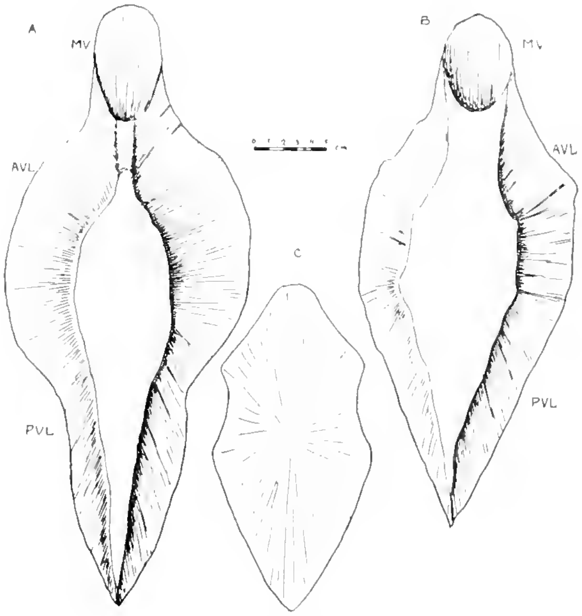
POSTERO-VENTRO-LATERAL.—This plate (Text-figures 58 and 61 *PVL*) is the other large plate of the ventral carapace. It is slightly concave and shows no special thickened parts. The only thing clearly noticeable from the outside is the deep overlapping impression on its upper corner (Text-figure 58 *AVL*) where the hind corner of *AVL* fits in. On the left plate (looking from underneath) another overlapping margin is to be found. It is situated along the inner margin and was covered by the corresponding right plate (Text-figure 58 *PVL*). On the inside, this plate is plane and smooth and no clearly overlapping margins are developed.

MEDIAN-VENTRAL.—This (Text-figures 59 and 61 *MV*) is a relatively small plate which occupies the central part of the ventral shield and touches all its other five components. Its outline varies strongly in different species of *Dinichthys*, ranging from narrow and long to relatively broad and short. In Text-figure 59 are shown three different *MV* plates from: (A) *Dinichthys terrelli* Nwb. (Amer. Mus. No. 7309); (B) *Dinichthys (?) intermedius* (Buffalo Mus. No. 15608, E2803); and (C) *Dinichthys (?) curtus* (Amer. Mus. No. 7062).

As we see, this plate is overlapped on every side by the margins of adjacent plates. The part not overlapped forms the inner, thicker division. The upper point of *MV* is covered by the lower point of *AMV*; the upper parts of the side margins by the right and left *AVL*; the lower part of the side margins by the right and left *PVL*. On the inside, *MV* is smooth and level, and shows the ossification rays very distinctly.



Text-figure 58.
The postero-ventro-lateral plate shown from the outside.



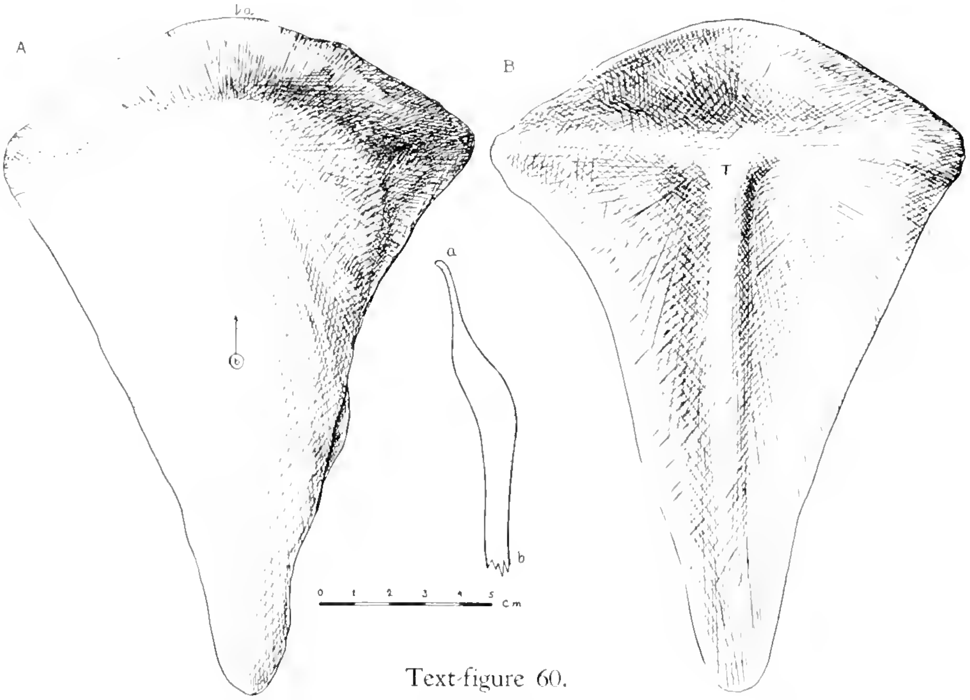
Text-figure 59.
Three different median-ventral plates.
A, *Dinichthys terrelli* Nwb. (American Museum No. 7304) shown from outside; B, *Dinichthys* (?) *intermedius* Nwb. (Buffalo Museum No. 15608-E2803) from outside. C, *Dinichthys* (?) *curtus* Nwb. (American Museum No. 7062) from inside.

ANTERO–MEDIAN–VENTRAL. —This plate (Text-figures 60 and 61 *AMV*) fills up the cleft between the two antero-ventro-laterals and forms the median strongly curved part of the ventral shield's front margin. It is a small plate with an arched front margin and concave side margins. Broadest in front, it becomes narrow backward, where the side margins run together in a roundish point. On the inside, its fore part is quite deeply impressed; thus the front margin forms a semicircular wall. A T-shaped thickening consolidates the fore part and the median line of the plate (Text-figure 60B *t*).

On the outside *AMV* is smooth. Its front margin is curved downward, corresponding to the front margin of *AVL*. *AMV* is slightly overlapped by *AVL* along the side margin, and its posterior point strongly overlaps the anterior part of *MV*.

In a paper published in 1896, Dean described a ventral shield of *Dinichthys terrelli* Nwb., noting that in this form the *MV* and *AMV* instead of forming two plates, formed only one. In that same year, Eastman pointed out the improbability of this fact. He noted that in all other known forms of *Dinichthys*, as in all other Arthrodira, these plates are developed as two isolated plates. Later Wright (1897) and Hussakof (1906) mentioned this question. Hussakof conjectured that in primitive forms of *Dinichthys AMV* and *MV* were isolated, but that in the more specialized forms these two plates fused.

My opinion is that these two plates are always represented as two independent elements. I have never found them fused, either in specimens in the American Museum collection, the collection in the Buffalo Museum, or that in the Museum of Comparative Zoology at Harvard. On the contrary, the isolated plates were frequently found with very clearly overlapping margins. If these plates really could fuse, such was probably only the case in aged individuals. This contact would then have been of a secondary character. These two plates in all cases have preserved separate ossification centers and independent series of ossification rays, and cannot, therefore, be regarded as a single plate.



Text-figure 60.

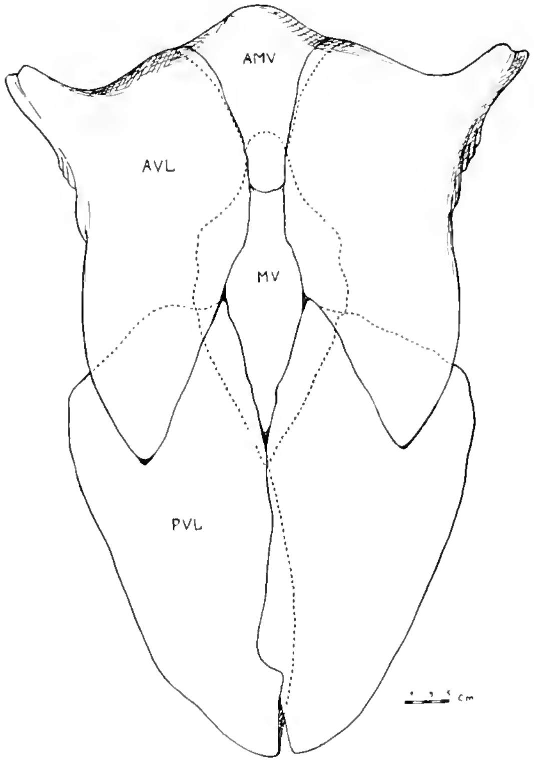
The antero-median-ventral plate: A, from outside; B, from inside.
a b, longitudinal section of front part of plate in line *a b* of *A*. *T*, the T-shaped thickening.

THE CONNECTING PLATES BETWEEN THE DORSAL AND THE VENTRAL SHIELDS

As in all other Arthrodira, the dorsal and ventral shields in *Dinichthys* are connected. Without a connection—as, for example, in Dean's reconstruction—the whole structure of the body carapace becomes too unsolid, weak and unsatisfactory as an attachment for the strong body muscles. The dorsal and ventral shields are connected by the help of two plates, the spinal and the intero-lateral. Thus in this character also *Dinichthys* corresponds with all the other Arthrodira. As we know, since Newberry's time these two plates have been counted as portions of the clavicular. Nobody has determined and described any of them before, in spite of the fact that Claypole as early as 1893 pointed out the limit between *Sp* and *AL*, and that the collection of the American Museum contains well preserved specimens of both plates.

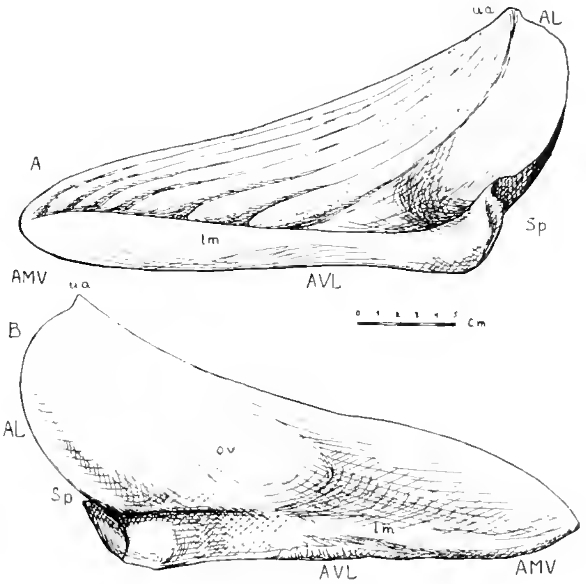
INTERO-LATERAL.—This plate (Text-figure 62; Plate VIII, figures 20 and 21) forms the front part of the hind wing of Newberry's "clavicular," as Eastman, Hussakof and Smith have correctly pointed out. The only description of this (and it a short one) was given by Smith (1909 and 1910) in papers on the ventral shield of *Dinichthys holmodeus* Cl. According to Smith it resembles the *IL* in Coccosteus.

In other Arthrodira it has long been known. Pander (1857) figured it in *Coccosteus*; Traquair described it in the same form (1890.4), and later in *Phlyctaenaspis* (1893); and also Jaekel in 1903.2 described *IL* correctly in *Coccosteus*, calling it the "Jugulare." In 1907, in describing *Pholidosteus*, he mentioned *IL* in this form as belonging to the lower jaw, and called it "Angulare." He believed that: "Die Angulare dem Bauchpanzer entnommen, erst sekundär in den Verband des Unterkiefers gezogen ist." In reality, as Dean pointed out in 1908, Jaekel here made a mistake. His "Angulare" is *IL*, which in some crushed specimens was displaced and moved near the blade of the lower jaw (Text-figure 63). But in many other specimens, as the present writer was able to discover in examinations of Jaekel's collection in 1927, this plate was in contact with *AVL*. It fits so perfectly into the front margin of *AVL* that without doubt it was attached to *AVL* and had no connection with the lower jaw. This is clearly seen in Text-figures 63 and 64, which represent the sketch made by the present author from Jaekel's original material. Heintz mentioned *IL* in a description of *Acanthaspis* (1929.1, .2).



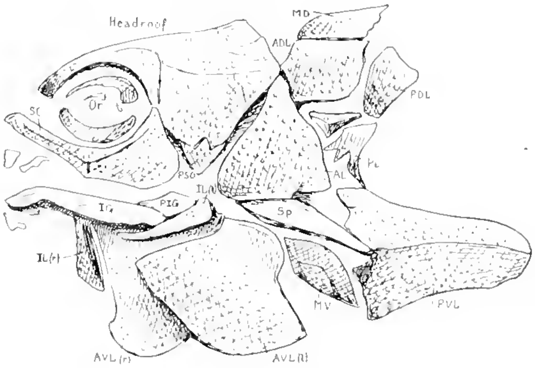
Text-figure 61.
The ventral shield of *Dinichthys intermedius* Nwb., outside view.

In Text figure 62 it is seen that *IL* in



Text figure 62.
The intero-lateral plate: A, from outside; B, from inside.
lm, lower margin; *ov*, overlapping margin; *ua*, upper angle.

Dinichthys is a nearly triangular plate with the hind lower part strongly curved upward (*Sp*). It is thickened along the lower margin and thin elsewhere. On the outside, the lower margin (*lm*) is sharply separated from the upper part. In the hind part it is strongly curved forward and upward. The upper part is clearly divided in two, with a border running from the upper angle of *IL* (*ua*) in an arch-shaped curve downward nearly to the middle of the lower margin. The part between this edge and the upper margin of *IL* is striped with some fine impressions, all beginning from the upper angle, running in an arch shape downward to the lower margin, and dividing the surface of the plate into long narrow strips. The most remarkable feature is that this part is ornamented by fine, very dense, small tubercles. It is the only part of the whole armor of *Dinichthys*, where such ornamentation is found. In Plate VIII, figure 22, a part of *IL* is reproduced three times enlarged to show the ornamentation more clearly. We shall come back to this remarkable structure later.



Text-figure 63.
Crushed head and body carapace of *Pholidosteus* sp. Jk.
(Sketch made by the author in 1927 from Jaekel's original material.)
(*l*), left, (*r*), right *AVL* and *IL*.

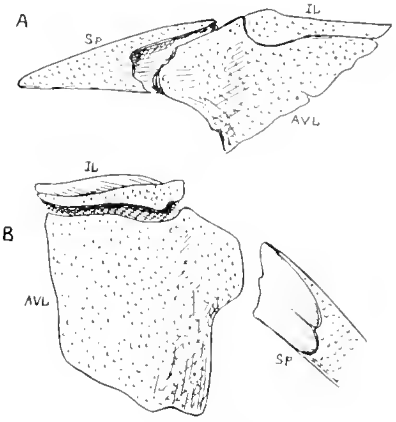
The other part is very thin and smooth. It is, following the curved lower margin of the plate, strongly curved itself in the hind lower portion. Its margin, between the upper angle (*ua*) and the lower thickened portion (*lm*), is very thin and nearly always broken, which makes it difficult to determine its outline precisely. On the inside, *IL* is smoother. The thick lower margin is a little concave and its surface is rough. The upper part shows a distinctly overlapping margin (*ov*) on its hind corner. This part of *IL* covers the fore part of the hind wing of *AL*.

SPINAL.—This plate is the second which aids in the union of the ventral and dorsal shields. Claypole early indicated its presence in *Dinichthys* (1893.1). In recent times Abel (1919) has pointed out that in *Dinichthys* "kurze Rudimente der Spinale ist vorhanden." But its real form and attachment to the other body plates have never been described.

In other Arthrodira it was mentioned for the first time by Newberry, as the spine in his new genus *Acanthaspis* (1870, 1875) which he placed in Cephalaspida. Von Koenen in a series of papers on the placoderms from the north German Upper Devonian (1876, 1880, 1883, 1886, 1890.1, .2 and 1895) described a new *Coccosteus*—*Coccosteus birkensis* v. K.—with a long spine. He regards this spine as homologous with the movable appendix in Asterolepida known under the name "Ruderorgan." From von Koenen's drawing it is clear that, as a matter of fact, his "Ruderorgan" corresponds to our spinal. In a discussion with von Koenen, Traquair (1890.5) asserted that in *Coccosteus decipiens* Ag. the spinal was not developed as an isolated element, but in the same year he himself figured the spinal in this form as a part of the intero-lateral (1890.4). Three years later he also noted *Sp* in *Phlyctaenaspis* (1893).

Woodward (1891.2) wrote on this element in *Acanthaspis* from Spitsbergen, which he, however, did not regard as an Arthrodire but as an Antiarch. In 1902 and 1903, Jaekel described this element as an isolated plate in *Coccosteus decipiens* Ag. under the name "Ruderorgan." In 1906 and 1907, he spoke of the same plate in some new forms from Wildungen, proposing to name it spinal. Obrutschew (1927) also mentioned *Sp* in describing a new Arthrodire from Siberia (*Angarichthys*). It is, however, doubtful whether the element he figures is really a spinal. Finally, Heintz (1929.1, .2) described it in Acanthaspida from Spitsbergen, and Broili (1929, 1930) in Acanthaspida from Germany.

In all the previously mentioned forms, this element is actually developed as a more or less long spine. It is attached between *AL* and *AVL*, which overlaps its basis from the upper and under side (*Acanthaspis*, *Phlyctaenaspis*, *Pholidosteus*. In *Coccosteus* the relation is not yet clear). In *Dinichthys*, on the contrary, the spinal in no way resembles a spine. It is a small, strongly-bent plate (Text-figure 64; Plate IX, figures 23, 24, 25, and 26) which forms the lower, curved part of Newberry's "clavicular." It is represented by four well preserved specimens in the collection of the American Museum (one attached to *AL*), and by two good pieces in the Buffalo Museum.



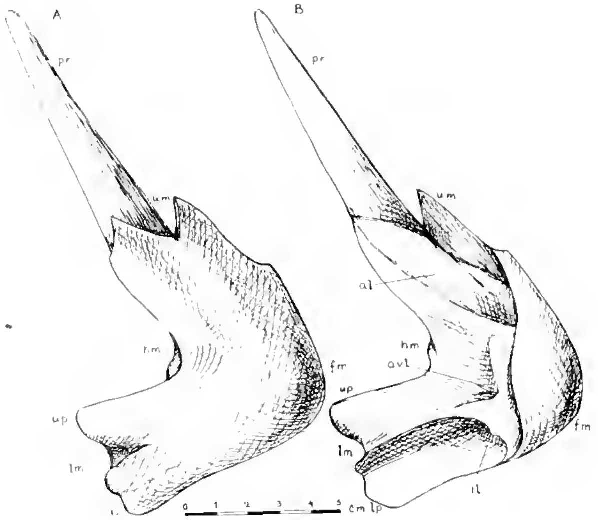
Text-figure 64.
AVL, *IL* and *Sp* in contact with each other in two different species of *Pholidosteus* sp. Jk.
(Sketches made by the author in 1927 from Jaekel's original material.)

Here the present writer wishes to express his gratitude to the Buffalo Museum of Natural Science for its kind permission to describe this plate, and for the fine photographs of it given him by the Museum (Plate IX, figures 23, 24, and 25,).

At first glance, the long upwardly-directed, spine-like process (*pr*) catches the eye. This process serves to consolidate the contact with the hinder front part of *AL*. It fits into a deep, narrow socket on *AL* and thus joins these two plates very strongly. A corresponding arrangement is to be found between *PDL* and *PL* It is difficult to say whether this spine is always so strongly developed. The writer has only found it in two examples in Buffalo (belonging to the same specimen). None of the specimens in the American Museum show this remarkable spine. Of course, it may be broken, but it may also be possible that the strong development of the *SP* in the examples in Buffalo is an individual variation only.

The upper margin (*um*) of *Sp* (Text-figure 65) is more or less zigzag in form, where it comes in contact with *AL*. The well-rounded front margin (*fm*) is sharply bent. The lower margin (*lm*) is clearly divided in two parts. The lower (*lp*) touches *IL*. The upper (*up*), which forms a small process, must probably be regarded as the last fragment of the real spine which we find in other Arthrodira. The hind margin of *Sp* (*hm*), corresponding with the strongly convex front margin, is strongly concave.

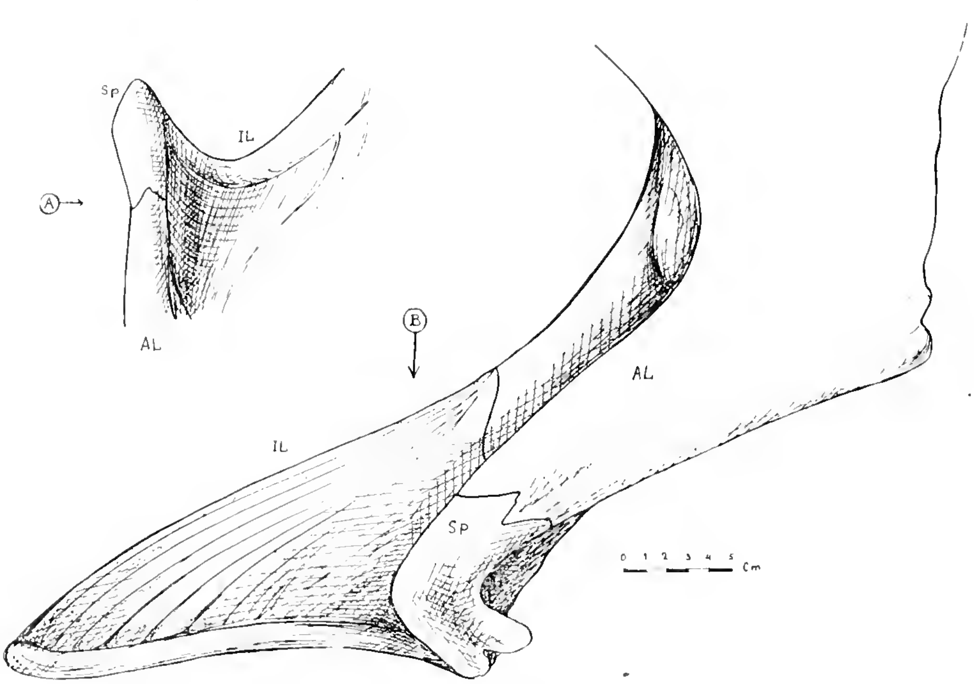
On the inside, nearly the whole plate is occupied by overlapping margins. Only its front part, divided from the hind part by an almost vertical line, is rounded and smooth (*fm*). The upper corner was overlapped by *AL* (*al*). *IL* with its thickened hind margin comes in contact with the lower process (*il*) on the lower margin. Lastly, *AVL* with its long side process touches the spinal from the inside, fitting into the impression on its concave hind margin (*avl*). Thus the spinal in *Dinichthys* serves to connect *AL*, *IL* and *AVL*.



Text-figure 65.

The spinal plate of *Dinichthys* drawn: A, from the outside: B, from the inside.

al, part overlapped by *AL*. *avl*, part overlapped by *AVL*. *fm*, front convex margin, *hm*, hind concave margin; *il*, part overlapped by *IL*, *lm*, lower margin, *lp*, lower process; *pr*, spine-like process which fits into *AL*. *um*, upper sigzag margin; *up*, upper process corresponding to the spine in other Arthrodira.

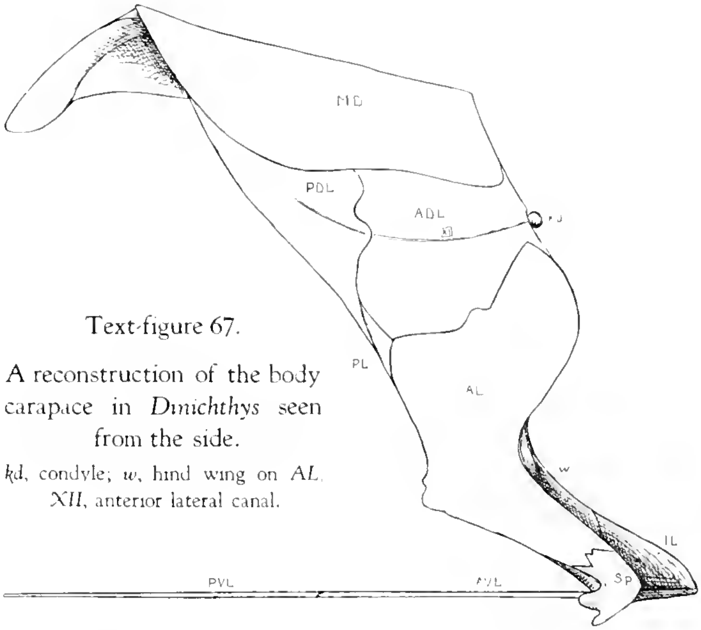


Text-figure 66.

A reconstruction of the relative position between *AL*, *IL* and *Sp* seen: A, from the side; B, from above.

In Text-figure 66A is given a picture of the lower part of *AL* with the attached *Sp* and *IL*. Here it is not difficult to recognize Newberry's clavicular. Text-figure 66B gives the clavicular from above showing where the single plates were connected. By the help of *IL* and *Sp*, the dorsal shield was joined to the ventral shield. The lower thick margin of *IL* was joined to the front margin of *AVL*. Its curved, hind part fits into the curved part on the side of the front margin of *AVL*. The side process on *AVL* touches the hind margin of *Sp*. As in many other Arthrodira, *AL* itself does not come in contact with *AVL*.

It only remains to take a look at the complete reconstruction of the *Dinichthys* body carapace, shown in Text-figure 67 in side view, and on Text-figure 68 from the front. Here it is seen that the *Dinichthys* body carapace forms a relatively narrow ring, especially narrow in the contact points between the ventral and dorsal shields, where it is consolidated with the hind wing (Text-figures 67 and 68 *w*) of *AL*. All the plates fit together very well, and as a whole the carapace makes a very solid structure, serving not only as armor to protect the body, but also, in no less degree, as an attachment for the strong head and body muscles.



Text-figure 67.

A reconstruction of the body carapace in *Dinichthys* seen from the side.

kd, condyle; *w*, hind wing on *AL*. *XII*, anterior lateral canal.

The front view (Text-figure 68) shows us that *Dinichthys* was in reality narrower and higher than formerly supposed. It is interesting to note how much, seen from this view, the carapace of *Dinichthys* is like that of *Acanthaspida* from Spitsbergen (Heintz, 1929.1, .2), one of the oldest known Arthrodira. The position of *IL* and its contact with *AL* and *AVL* is identical. On the other hand, the long, strongly developed spine of *Acanthaspida* (Text-figure 69) is reduced in *Dinichthys* to only a short plate.

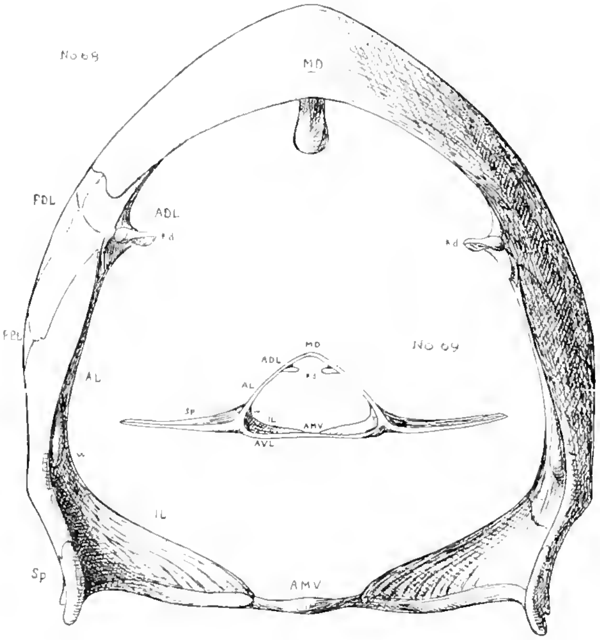
THE CONNECTION BETWEEN THE HEAD AND THE BODY CARAPACE

It is now necessary to describe how the head and body carapace are joined. This is one of the most crucial matters in our study of *Dinichthys*, and calls for careful consideration.

THE JOINT BETWEEN THE HEAD AND THE BODY

From the earlier investigations we know that the head shield and the body carapace of the Arthrodira were connected by means of a movable joint. The first worker to describe this structure was Assmuss (1856). However, he misunderstood this structure of the

Arthrodire carapace and thought that this joint was placed between two parts of the body carapace. The next year (1857) Pander gave a relatively detailed description of it in *Coccosteus*, *Heterostius* and *Homostius*, with many drawings.



Text figure 68 (large).
A reconstruction of the body carapace in *Dinichthys* seen from the front.

kd, condyle, *Sp*., the short spinal; *w*, hind wing of *AL*.

Text figure 69 (small).
The body carapace of an *Acanthaspida* from Spitsbergen (Heintz) in front view.

Sp., the much elongated spinal plate.

In later papers of well-known investigators of the Arthrodira (Traquair, Woodward, von Koenen, Newberry, Dean, Eastman, Hussakof), surprisingly little attention has been given to the structure of this part of the Arthrodiran carapace. This is especially notable when we remember that the name "Arthrodira," proposed by Woodward (1891.1), was based on this character. Not until 1919 was a detailed description of this joint published. This was by Jaekel who pointed out its great importance in an understanding of the structure of the Arthrodira. In the same year (1919) Adams also called attention to this unusual structure, and lastly Abel (1928) described it in detail in *Heterostius* from Esthonia.

In *Dinichthys*, the joint between the head and body has never been carefully studied.[10] All authors have been content to state the fact that the joint socket is to be found on *EB*, and that the condyle is developed on *ADL*, without describing their structure or trying to explain how they work. As a matter of fact, this structure is the most characteristic one in the Arthrodira, and, except in the Antiarcha (Asterolepida), is unknown in any other vertebrate. Its strong development in all Arthrodira shows clearly its great importance to the animal and gives us at least a possibility of understanding this mechanism. I shall now attempt to give an accurate description of the connection between the head and body carapace.

As we know, on the hind margin of *EB* is a deep, long joint socket (Text-figure 70 A, B, C; *fg*). After Jaekel (1919), we call it the "fossa glenoidalis." In section it is semicircular (B C); broader in front, it narrows insignificantly backward. The upper margin of *EB* runs in a solid, slightly curved process, bordering the joint socket from above. We will call it the upper joint process (*ujp*). On the underside, the fossa glenoidalis is

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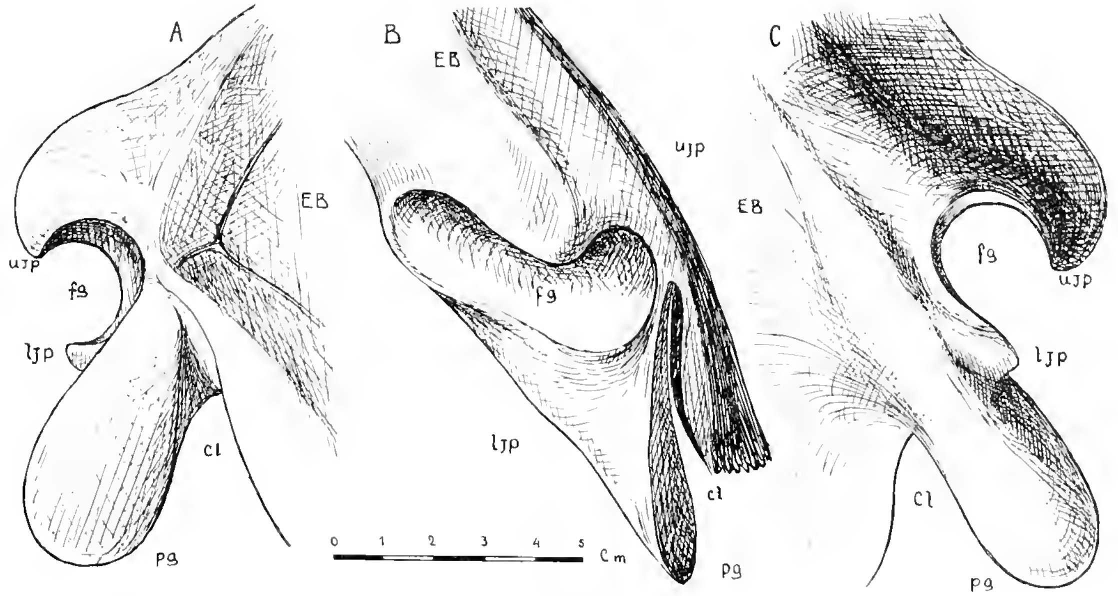
[10] The most complete description was made by Kemna (1904).

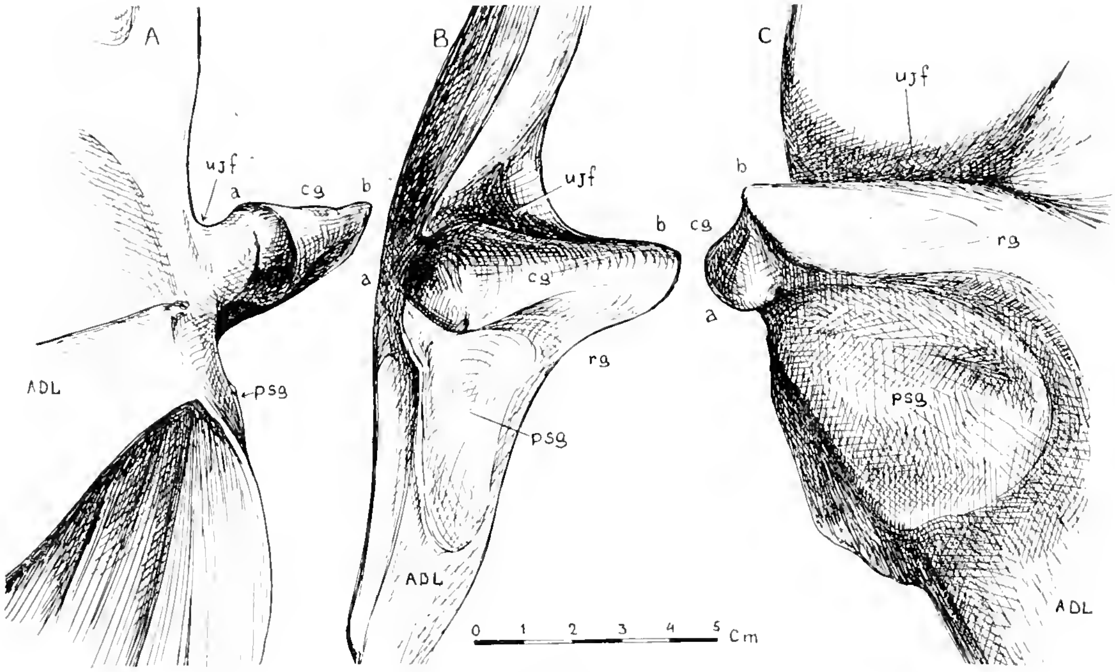
limited by a very large and heavy process, "processus glenoidalis" (*pg*), which forms the immediate prolongation of the lower consolidated arch of the head (Text-figure 12). Its front is roundish, and oblong in form, with a plane surface (Text-figure 70B). On the underside it is semicircular in section and is gradually attenuated towards the point (Text-figure 70B and C). On its inner side we find a small process, the lower joint process (*ljp*), placed nearly opposite the upper joint process. The lower margin of *EB* is divided from the processus glenoidalis by a deep cleft (*cl*). The whole arrangement is very strong and massive.

Corresponding with the fossa glenoidalis on *EB*, is the strongly developed "condylus glenoidalis" (Jaekel) on *ADL* (Text-figures 71A, B, C; and 72A, B). It is composed of the real condylus (*cg*) and a broad strong and massive ridge (*rg*), serving as a support. The condyle is long, roundish in the front part (*a*), posteriorly it takes on a more conical outline and its hind corner (*b*) is relatively narrow. The supporting massive ridge (*rg*) has a broad hinder part which gradually goes over into the surface of *ADL* (Text-figures 71B; 72A and B). Toward the condyle it rises and becomes thinner. On both sides of the condyle it is relatively very thin, thus forming two well-marked impressions (see section—Text-figure 73). The impression on the upper side of the condyle is especially strongly developed and forms a real fossa. We shall call it the upper joint fossa (*ujf*). On the inner surface of *ADL* immediately under the condyle ridge, is a well marked, roundish place (*psg*). Corresponding with what is found in other Arthrodira,



Text-figure 70.
The joint socket on the hind margin of the externo-basal plate: A, from outside; B, from behind; C, from inside.

cl, cleft between processus glenoidalis and hind margin on *EB*; *fg*, fossa glenoidalis; *ljp*, lower joint process; *pg*, processus glenoidalis; *ujp*, upper joint process.

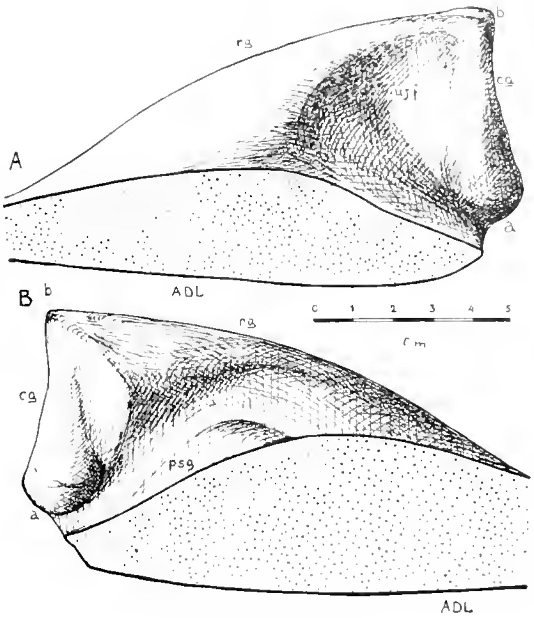


Text-figure 71.
The joint process on the front margin on the antero-dorso-lateral plate: A, from outside; B, from front; C, from inside.
a b, axis of condyle, *cg*, condyle, *psg*, processus sub-glenoidalis; *rg*, supporting ridge for condyle; *ujf*, upper joint fossa.

where this part is developed as a process, we may call this "processus sub-glenoidalis" (Jaekel).

The condylus glenoidalis fits perfectly into the fossa glenoidalis, so that the plate *EB* (and also the whole head) can easily be moved around the long axis of the condyle (*a–b*). The previously mentioned processes round the fossa glenoidalis (Text-figure 73) serve to reduce this movement to a relatively small degree only. The upper joint process (*ujp*), when the head is moved upward, fits into the upper joint fossa (*ujf*) and thus limits the possibility of the upward movement. The processus glenoidalis (*pg*) with its plane inner surface comes in contact with the surface of the processus sub-glenoidalis (*psg*). When the head is moved, the processus glenoidalis slides on the surface of the processus sub-glenoidalis. In a downward movement the processus glenoidalis comes in contact with the underside of the condyle ridge, which thus limits the possibility of the movement. This is also reduced by another factor. The upper, rounded part of *AL* overlaps the margin of *EB* and partly that of *PM*. On both these plates we find distinct rounded impressions (see Text-figures 12, 18 and 42). In case the head was moved downwards *AL* fitted into this impression, and thus stopped the movement. In spite of these arrangements, which strongly reduced the mobility of the head, its movement was comparatively large—in *Dinichthys* between 25 and 35 degrees.

Evidently in living fishes the fossa of the condyle and the surface of the processes were covered with articular cartilage. The whole joint was also safely protected and bound together by ligaments. We can very clearly see a trace of ligament-attachment on both *ADL* and *EB*. Especially on *ADL* it is easily found. Beginning on the extreme margin of the processus sub-glenoidalis, it runs along the edge of the supporting ridge to its point, thence back again on the other side of the ridge and around the upper joint fossa to the margin of *ADL*. It continues along the margin making a very sharp line on the front part of the condyle, and at last comes back to the margin of the processus sub-glenoidalis. On *EB* the ligament was attached around the fossa and along the edge of the processus glenoidalis and the upper joint process (Text-figure 74).

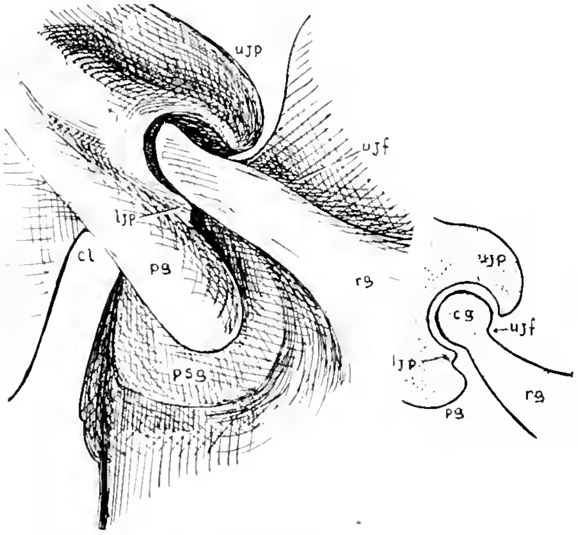


Text-figure 72.

The joint process on the front margin of the antero dorso-lateral plate: A, from above: B, from below.

a–b, axis of condyle; *cg*, condyle; *psg*, processus sub-glenoidalis; *rg*, supporting ridge for condyle; *ujf*, upper joint fossa.

It is obvious that such a complicated and solidly built joint must have been of a vital importance to the fish. It allowed the movement of the head in relation to the body and thus is analogous [11] with the occipital joint between the cranium and spine in other vertebrates.



Text-figure 73.

The neck joint in *Dinichthys* shown in surface view and in section.

cg, condyle; *cl*, cleft between processus glenoidalis and hind margin of *EB*. *ljp*, lower joint process; *pg*, processus glenoidalis; *psg*, processus sub-glenoidalis; *rg*, supporting ridge for condyle; *ujf*, upper joint fossa, *ujp*, upper joint process.

THE RELATION BETWEEN THE GNATHAL ELEMENTS

Before we can describe the mechanism of the movement of the head and jaws in *Dinichthys* and the importance of this to the animal, it is necessary to describe in detail the relative position of the gnathal elements and to give the different theories about the jaw mechanism in the Arthrodira.

The jaw elements in the Arthrodira are the most unsatisfactorily known and

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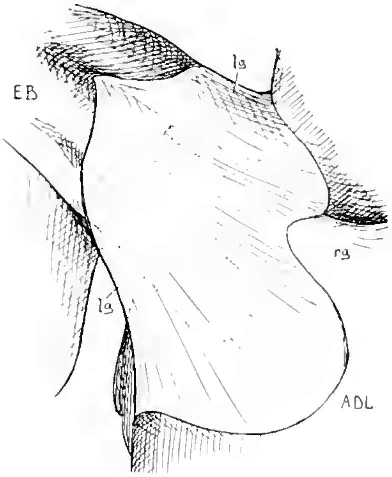
[11] It is obvious that this joint can not be regarded as homologous with the occipital joint. It is placed on the side of the head roof, far from the occipital region of the head and from the spine.

most enigmatic parts of the whole fish. From the earliest times investigators have wondered about this remarkable jaw structure, which is without any analogy in other animals. Miller, in "Old Red Sandstone" (1841) described the small teeth placed in the symphysial part of the lower jaw. This discovery, later confirmed by other investigators (Pander, Traquair, Woodward, Newberry, Dean, Hussakof), leads one to suppose that the lower jaw halves in the Arthrodira were not connected in front. When explaining this character so unusual for vertebrates, the different authors proposed diverse theories. Miller considered that the mouth in *Coccosteus*, like that of the Arthropoda, was vertically, not horizontally, placed. In his opinion the symphysial teeth worked against each other. Nearly the same opinion was expressed by Patten (1912). He said that: "The mandibles were capable of very complex movements. Both ends were free and could be either rotated, or moved in a transverse and longitudinal direction."

A very careful investigation of the movement of the jaws in the Arthrodira—especially in *Dinichthys*—was made by Hussakof (1906). In his opinion, the lower jaw was not connected in symphysis. In opening the mouth the lower jaw not only moved downwards but also sideways. Hussakof thought to find a confirmation to this fact in marks of wear on the "teeth" and in bite marks, which can sometimes be found on the armor plates of *Dinichthys*.



Text-figure 74.
A reconstruction of the ligament attachment of *EB* and *ADL* in the neck joint of *Dinichthys*.
(Compare with Text-figure 73).
lg, ligament, rg, ridge supporting condyle.

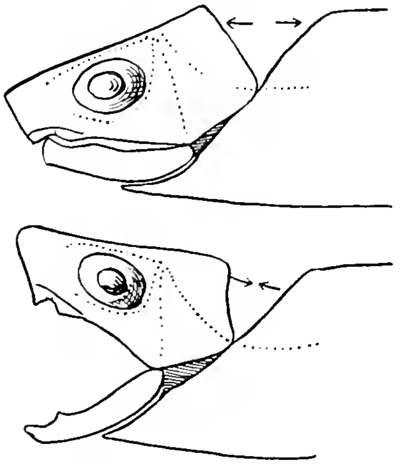
Contrary to the opinions of these three authors, who considered the Arthrodire mouth built in a way unusual to other vertebrates, other investigators have held that the Arthrodire lower jaw was formed and that it functioned on the same principle as the jaws of other fishes. Newberry was the first to compare the jaws of *Dinichthys* with the mouth apparatus of the Dipnoi. According to him the rami of the lower jaw were connected in symphysis and attached to the cranium by the help of cartilage. Traquair (1900), Jaekel (in a paper before 1907), more recently Woodward (1922), and Stensiö (1925) supposed the mouth construction in the Arthrodira to be of the usual fish type.

Opposing these opinions stands the theory of Jaekel and of Adams. As early as 1907, in describing the morphology of *Pholidosteus*, Jaekel mentioned that in opening the mouth the upper jaw (head) in the Arthrodira moved more than the lower jaw. In 1919 he gave a more detailed description of the jaw mechanism in the Arthrodira (Text-figure 75). According to him the hind corner of the lower jaw was by the aid of a special plate ("Articulare" = *PIG*) attached to the post-sub-orbital plate ("Quadrato-jugale"). In opening the mouth, the head roof by the contraction of the strongly developed muscles running from *MB* to *MD* was lifted up around the joint between the head and body. The hind corner of the lower jaw was thus also elevated, the symphysial part moved down, and the mouth opened. In shutting the mouth, no strong muscles were necessary; the dorsal muscles merely slackened and the heavy head fell down on the lower jaw ("Fallbiss"). Unfortunately Jaekel incorrectly included in the structure of the lower jaw a part of the ventral carapace—the intero-lateral (his "Angulare"). According to him this plate was placed on the underside of the hind part of the "Spleniale" and when the mouth was opened, it slid along the front margin of *AVL*. This arrangement is perfectly impossible. When the mouth was opened, the lower jaw—as also the "Angulare"—moved up and down in a plane almost parallel to the long axis of the body. The front margin of *AVL* on the contrary is placed nearly perpendicularly to this plane, which excludes any possibility that the "Angulare" could slide along *AVL* (Text-figure 75).

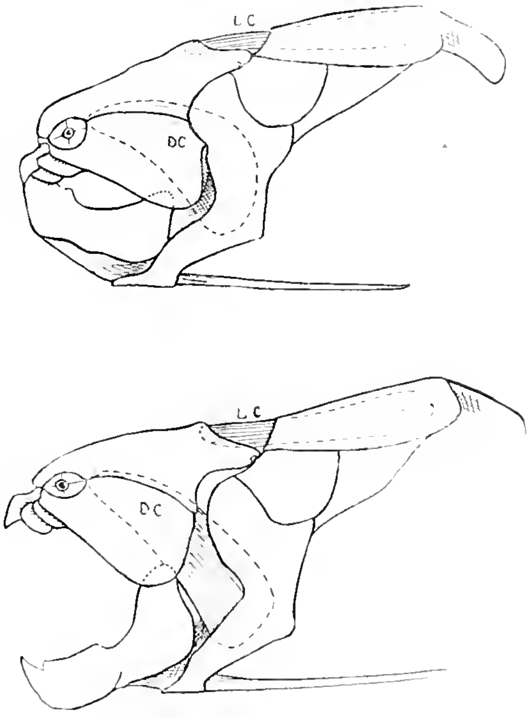
During the same year, Adams, independently of Jaekel, arrived at almost the same conclusion in studying the jaws of *Dinichthys* (Text-figure 76). In his opinion the "mandible" was attached to the hind lower corner of *SO*. Otherwise he explained the mouth mechanism somewhat in the same way as Jaekel. The only difference is that he also suggested a pair of muscles for shutting the mouth. They were attached on one side to the side margin of the head, on the other side to the lower part of the "clavicular."

This Jaekel-Adams theory was not generally accepted. Especially in Germany, Jaekel's new theory was received with great scepticism. Later I shall try to demonstrate its correctness. First, however, the relative position of the jaw elements must be studied.

On all the gnathal elements in *Dinichthys* we find a strongly marked, polished cutting

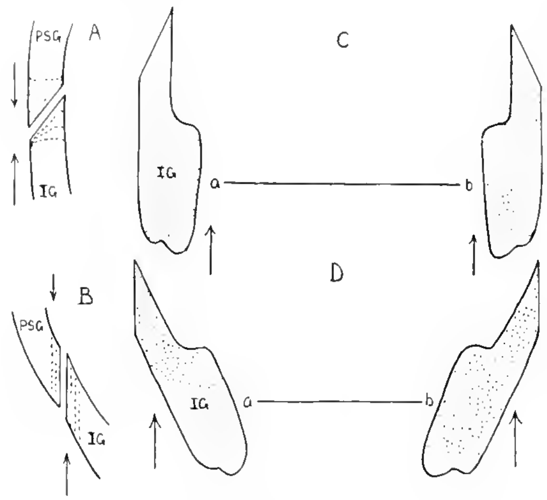


Text-figure 75.
Jaekel's reconstruction of the jaw mechanism in the Arthrodira (1919).

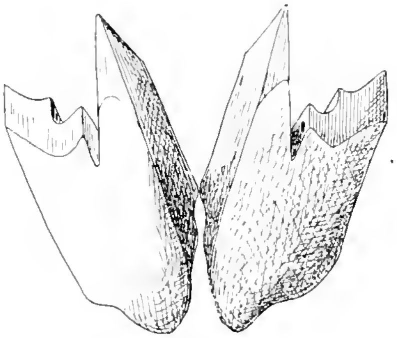


Text-figure 76.
(*Right*)
Adam's reconstruction of the jaw mechanism in *Dinichthys* (1919).
DC, musculus depressor capitis, *LC*, musculus levator capitis.

edge where the "tooth" works against the corresponding part of the opposite "tooth." These cutting edges are placed on the inside in the upper jaw elements; in the inferognathal, on the outside (Text-figures 27, 28, 29, 30, 31, 32 and 78). If we examine them it is easily seen that they are remarkably plane. When the specimens are not crushed or bent, this plane surface is maintained for the whole length of both *IG*, *ASG* and *PSG*.



Text-figure 77.
The position of the gnathal elements *PSG* and *IG* in *Dinichthys* A and C, according to older reconstructions; B and D, in the author's opinion.
a–b, movement axis of the head.



Text-figure 78.
The position of the infero-gnathal plates seen from the front, according to the author's idea.

It is very usual to compare the working of the gnathal elements in *Dinichthys* with a pair of scissors. This comparison is very adequate. The cutting edges of the jaws are thus like the inner surface of the scissors. The inner surface of each half of a pair of scissors is placed in the same plane, perpendicular to the movement axis of the scissors. When the jaws of *Dinichthys* work like scissors their cutting edges also must be placed perpendicularly to the axis of the head movement and parallel to each other (Text-figure 77B and D). As we know, the axis of the head movement is strongly horizontal. Thus the cutting edges of the "teeth" have to be strongly vertical. This arrangement of jaw elements in *Dinichthys* has never before been proposed. Always, in all mounted specimens or reconstructions the surfaces of the cutting edges are placed at a smaller or larger angle to the vertical line (Text-figure 77A and C). But such a position of the jaws excludes the possibility of preserving their plane and sharp cutting edges. As seen in Text-figure 77A, in use their edges are constantly worn and in time they would come to look more like the crushing teeth of *Mylostoma*. On the other hand, if the cutting edges are placed vertically (Text-figure 77B), they wear evenly along their whole inner surfaces and preserve their sharp edges.

Usually in reconstructions of *Dinichthys*, we find the outer surfaces of the gnathal elements in a vertical position (Text-figure 77A and C). As we now know that this was not the case, we can place them more correctly. The new position has only a slight influence on the upper jaw it becomes somewhat more curved. The position of the lower jaw, however, is more changed. Its outer surface becomes strongly bent inward. This makes the lower front corners of the left and right *IG*, come closer together (Text-figure 78). They were probably connected by a hitherto unknown bone, or by cartilage and ligaments. (It may be pointed out that the inner surface of the front part of *IG* is rough which indicates the presence of cartilage). At the same time the points of the big "front teeth" are extended quite far apart from each other (Text-figure 78). This explains very satisfactorily the presence of the symphysial teeth. Only the lower front corners of both *IG* plates were connected. The upper parts, where the symphysial teeth were placed, have never touched each other.

Surely all these facts indicate that the lower jaws of the Arthrodira were connected in symphysis and in an extremely unusual manner. The drawing in Text-figure 78 shows the lower "jaw" of *Dinichthys* from the front. The new arrangement of *IG* makes the whole jaw structure much more solid and compact.

THE MECHANISM OF THE MOUTH MOVEMENT

Among the theories mentioned in the last section, those of Miller, Hussakof, and Patten must be excluded as incompatible with the newly known facts. The opinion of these three authors was that *IG* in the Arthrodira was not articulated to the cranium and not fused in the symphysis. But we know that the lower jaw was connected to *PSO*, and, in all probability, also fused in symphysis.

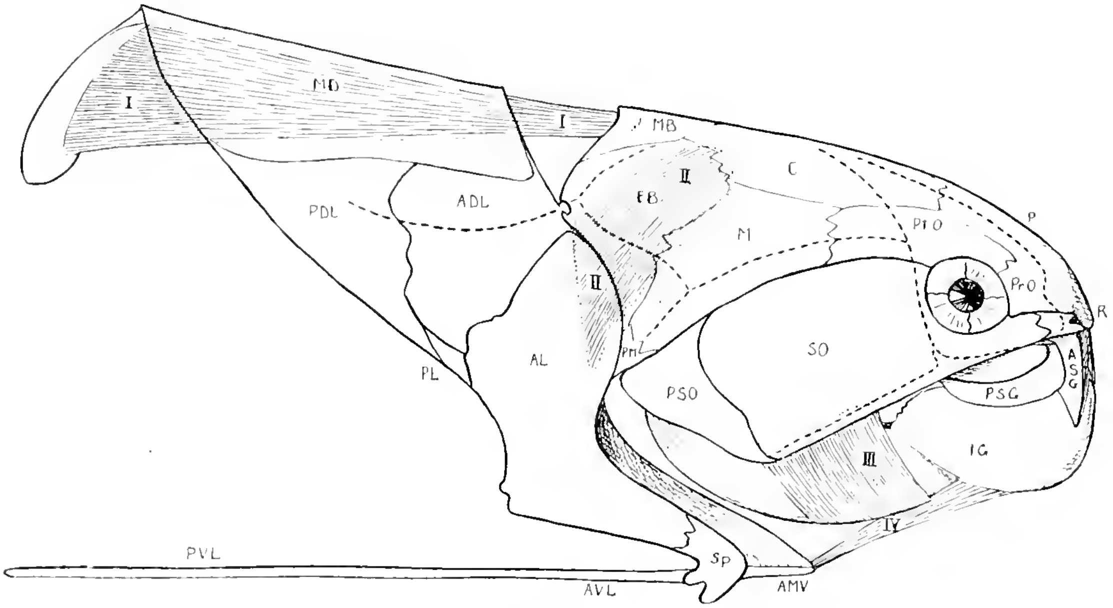
The theory, that in the Arthrodira the mouth was built on the same principle as that of other fishes (Traquair, Newberry, Woodward, Eastman, Stensiö), is also more or less unacceptable. The joint between the head and lower jaw in the Arthrodira, as we have seen in a previous section is very unsatisfactorily developed. In fact, it is not a joint, merely an attachment point. In a fish like *Dinichthys*, with very strong, heavy teeth, such a weak joint would exclude the possibility of effectively working jaws. Also, the thin blade of the lower jaw is not solid enough to serve as an attachment for the strong muscles necessary for moving the jaws up and down.

The theory proposed by Jaekel and by Adams is the only one giving a logical and satisfactory explanation of all the remarkable facts in the structure of the Arthrodira and a complete picture of the mechanism of the jaws—an unexpected mechanism, never before observed in any other animal living or fossil.

The following facts may confirm the correctness of this Jaekel-Adams theory, and the more we study the structure of *Dinichthys* in detail, the more probable this theory becomes. These facts are:

1. The presence of a joint between the head and body allows the head to move up and down. This joint, very strongly developed in all Arthrodira and Antiarcha, must be of vital significance for these animals. Nearly all living and fossil fishes have the head practically immovably connected to the body. It is difficult to understand why it was so necessary for the Arthrodira to move the head up and down. Whereas in typical benthonic forms, such as the Acanthaspida, Homosteida or Antiarcha, this arrangement is intelligible

(we find a kind of analogy in the occipital double sockets pointed out in *Gemundina* by Broili in 1930 and found in recent rays); it is incomprehensible in forms like *Coccosteus* or *Dinichthys*, which, in all probability, could swim relatively very well. This is especially true when we observe that in typical benthonic forms the neck joint was somewhat weak (Heintz 1929.1, .2), but in forms like *Dinichthys* and *Coccosteus* very strong.



Text-figure 79.
The author's reconstruction of the armor of *Dinichthys* to show the mouth mechanism—the mouth shut.
I, musculus levator capitis; *II*, musculus depressor capitis; *III*, musculus levator gnathalis; *IV*, musculus depressor gnathalis.

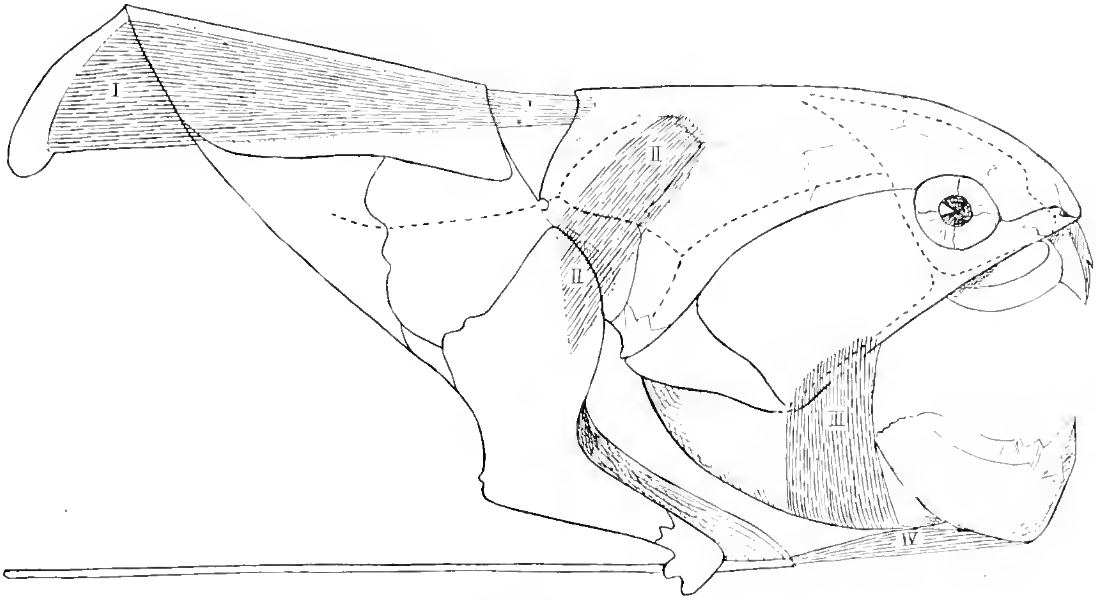
2. The enormous keel on *MD* serves as an attachment for the muscles, which were fastened by their fore part to the hind margin of *MB*. These muscles moved the head up and down. Such strong muscles must have performed a movement of special importance to the animal.

3. The hinder part of the lower jaw, as mentioned before, is weakly built. It is thin and narrow, without ridges or sockets for attachment of strong muscles. There is no reason to suppose that it was consolidated with cartilage.

4. The joint between the upper and lower jaws is very primitively built and, in fact, can not be called a well developed joint. It has no condyle or fossa condyli.

5. The front part of the lower jaw, on the contrary, is very strong. It is thick, heavy and carries large teeth with distinct working marks. The hind part of the jaw and the joint are too weakly built to give the heavy front part the necessary power to work.

The whole mechanism functioned with the help of four pairs of muscles (Text-figures 79–81). Two pairs were attached to the head roof (*I* and *II*); two pairs to the lower jaw (*III* and *IV*). The first strong pair, which we, like Adams (Text-figure 76) can call the "musculi levatores capitis" (Text-figures 76, *LC*; 79–81, 83 and 84 *I*) were attached on one side to *MB* on the head roof, on the other side to the keel on *MD*. The strongly thickened hind part of the head roof (*MB*) (Text-figures 13 and 16*b*), with its rough surface and with deep impressions and ridges, shows clearly that the musculi levatores capitis were very strong. The deep double impression (*ds*) on *MB* serves as a more solid attachment for these muscles. The other ends of the musculi levatores capitis were attached to the underside of *MD* and especially to its strongly developed keel. Doubtless, the thickened hind edges of the keel served as the chief attachment place for muscle ligaments.



Text-figure 80.
The author's reconstruction of the armor of *Dinichthys* to show the mouth mechanism—the mouth open.
I, musculus levator capitis; *II*, musculus depressor capitis; *III*, musculus levator gnathalis; *IV*, musculus depressor gnathalis.

Adams fastened the hind ends of these muscles not far from the hind margin of *MD*. In my opinion this is wrong. This part of *MD* shows no traces of muscle attachments, and such a heavy muscle as the levator capitis would leave a distinct trace on the surface of the bone.

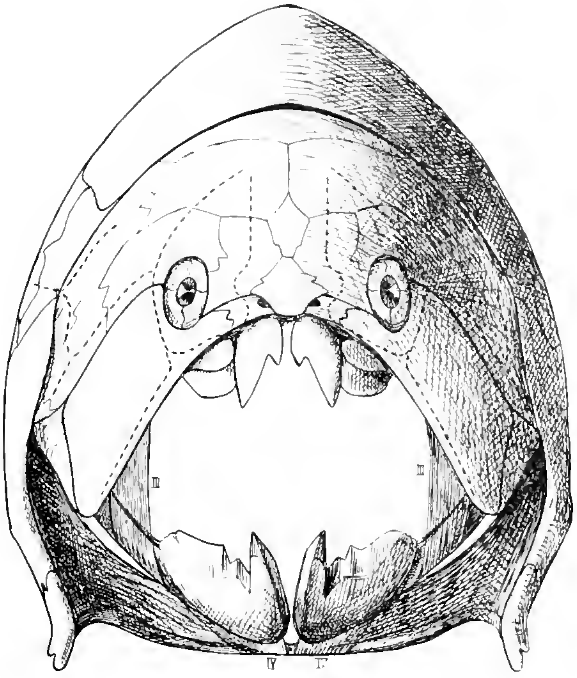
The development of more or less strong keels on different parts of the skeleton, as attachments for muscles, is a commonly known fact. Here, we shall only point out two examples which remind us of the arrangement in *Dinichthys*. In all carinate birds the strongly developed keel (carina) on the sternum is very like the keel in *Dinichthys*. Also it is here that the well developed and very important flying muscles are attached. Another example shows closer analogy with *Dinichthys*. If we study the head structure of the fossil saber-toothed tiger, *Smilodon*, we can easily see traces of the attachment of very strong muscles at the back of the head. On the second or axis vertebra, we find an unusually long, highly compressed neural spine, which in its form resembles the keel on the *MD* of *Dinichthys*. To this spine were attached the muscles going from the back of the head. They served to lift the head. When using the saber-teeth not only the mouth opened, but also the whole head was lifted up with the help of the previously mentioned muscles. Without doubt, the same happened in *Dinichthys*, the sharply pointed *ASG* was used as a very effective weapon comparable with the saber-tooth of *Smilodon*. The greatest difference in the arrangement of the muscles and their attachment in these two cases is that in *Dinichthys* they were attached to the dermal skeleton (head roof and *MD*), in *Smilodon* to the inner skeleton. Thus, in the first, the keel extended from the surface into the body; in the second, from the axial skeleton out to the surface. But the function in both cases was the same.

The second strong pair of muscles, which can be called "depressores capitis" (*DC*, Adams: Text-figures 76 *DC*, 79–81, 83 and 84 II) serve to move the head downwards and are, of course, antagonistic to the levatores capitis. Jaekel held that no muscles were necessary to move the head downward, that the heavy head would fall down on the lower jaw by itself ("Fallbiss"; Jaekel, 1919). This theory is quite improbable. Though in *Dinichthys*, perhaps, the head was heavy enough to fall down with relatively great power, in all smaller forms (*Coccosteus*) this would not happen. The resistance of tissue and of water, would make the "fall down" without help of muscles too slow and powerless.

Adams attached these muscles with one end to the side margin of the head (along the marginal) where there is a long ridge (Text-figure 13, *LCP*, *Rd*), and with the other end to the middle part of *AL*. This position of the muscles is, however, hardly acceptable. *SO* is in contact with the ridge along the marginal and there is no place to attach any muscles here. At the same time, thus attached the depressor capitis on each side would cover the opening between *PSO* and *AL*. Here, as we shall see later, were the gill openings.

In my opinion, the musculi depressores capitis were fastened higher up than proposed by Adams. In the head roof they occupied the deep impression (Text-figures 13 *PL*, 79, 80, 83 and 84 *II*) on both sides of the median-basal and were attached to its bottom and steep walls. In the body carapace they were attached to the upper part of the high ridge running on the underside of *AL* (Text-figures 51, 79 and 80). Each muscle was comparatively short but broad, and was very strong. It performed the same work as the musculus adductor mandibuli (Adams) in other fishes. Like the last it was a bite and chew muscle, but it worked in the opposite direction to the adductor mandibuli, which moved the lower jaw up, while the depressor capitis moved the upper jaw down. Being very strong, this muscle with its position so near the joint gave the upper jaw a special power. The teeth of the upper jaw, placed far from the joint, were moved downwards with a horrible power. Since Newberry's time marks of teeth have been known on some body plates of other specimens. Some plates with undoubted marks are preserved in the American Museum. One described by Hussakof (1906) is especially interesting since it has deep round cuts like that from a pair of teeth. Hussakof thought that these cuts were made by the front "pick" of the lower jaw. I think differently. In the first place, the lower jaw was not so strongly muscled, and in the second, the marks are on the *MD* plate. It is difficult to imagine that the lower jaw could make impressions on a dorsal plate, since in this case one of the fishes, must have been ventral side up. It is more likely that the marks were made with the upper "teeth."

The two other pairs of muscles are more difficult to determine. They moved the lower jaw up and down. As we know, in raising the head, the front part of the lower jaw automatically went down, as its hind corner attached to *PSO* was lifted up. The muscles now to be described merely acted as a support in making this mechanism more effective.



Text-figure 81.
Front view of the reconstructed head armor of *Dinichthys*—with the mouth open.
III, musculus levator gnathalis; *IV*, musculus depressor gnathalis.

The muscles of the first pair, which we shall call "musculi levatores gnathalis" were probably attached to the lower margin of *IG* with one end, and to the ridge on the lower margin of *SO* with the other (Text-figures 79, 80 and 81 *III*). Of course, no especially marked traces of muscle attachment are found either on *IG* or on *SO*. We must suppose that such a muscle covered *IG* from the outside. The function of these muscles was to stop *IG* in its downward movement, and in closing the mouth to move *IG* up to meet the upper jaw pressed down by the depressores capitis. The muscles antagonistic to the levatores gnathalis were the depressores gnathalis (Text-figures 79, 80, 81 and 89 *IV*). Attached at one end to the underside of the front part of *IG*, where we find distinct traces of muscles, they probably ran downward to *AMV* on the ventral shield.

Stetson in his last paper, in discussing jaw muscles in *Dinichthys*, states that perhaps one of the lower jaw muscles was attached to a process in the fork formed by two arms of *AL* (Text-figures 50 and 52 *th*). I think it improbable, since muscles thus placed would cover the gill openings. It is likely also that the muscles of the gill apparatus were partly attached to the underside of *IG*.

The musculi levatores capitis and depressores gnathalis worked together to open the mouth. In contrast, by the contraction of the musculi depressores capitis and levatores gnathalis the mouth was closed. These four pairs of muscles were of the greatest importance in the mechanism of the mouth. Surely many others, smaller and weaker, were attached to different parts of the upper and lower jaws, and helped in their work.

But to reconstruct their position and function is a hopeless task, in our present stage of knowledge.

THE COMPLETE RECONSTRUCTION OF THE HEAD AND BODY CARAPACE OF *DINICHTHYS*

After the detailed description given of the head and body plates in *Dinichthys*, it is not necessary to spend much time in describing the complete armor. This has already been done in the preceding sections. I shall here only summarize the new points in my reconstruction (Text-figures 79, 80 and 81) as follows:

1. The head is strongly curved from side to side and from back to front.
2. The fossa condyli has a horizontal position.
3. Four new plates are found in the head: (a) post-nasal, limiting the nasal openings; (b) post-marginal; (c) post-sub-orbital, serving as an attachment for the post-infero-gnathal; (d) post-infero-gnathal, which comes in contact with post-sub-orbital.
4. The gnathal elements are arranged so that the position of the cutting edges is strongly vertical.
5. This causes the lower front corners of right and left *IG* to come nearer together.
6. The body carapace is narrower and higher than proposed before.
7. The dorsal and ventral shields are connected.
8. We can assert the presence of the following plates: (a) postero-lateral; (b) spinal; (c) antero-lateral.
9. The two last plates serve to connect the dorsal and ventral shields.
10. The median plate in the ventral carapace is not single but double (*AMV* and *MV*).

OTHER STRUCTURES AND ORGANS OF *DINICHTHYS*

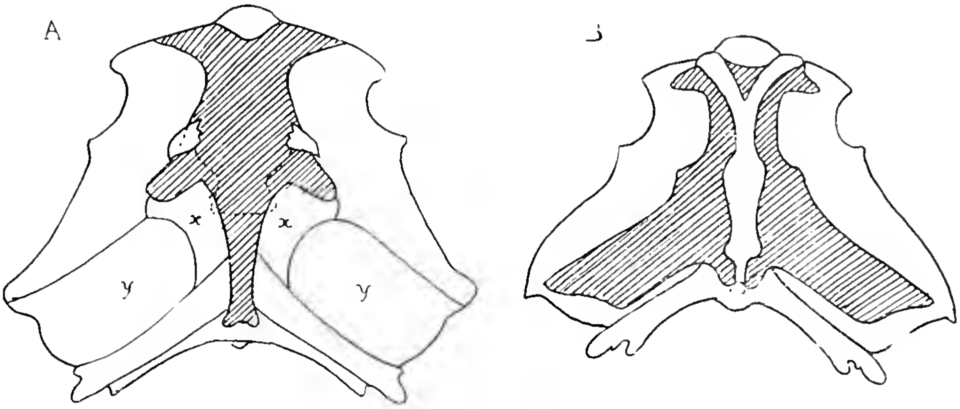
About the inner skeleton of *Dinichthys* we know very little. Practically nothing of this is preserved in the fossils. Some conclusions can be drawn from impressions on the armor, from homology with other animals and from logical necessity. Of course, all these arguments are of a more or less subjective character and can, in no case, give exact results.

THE PRIMORDIAL NEUROCRANIUM

In the Arthrodira the primordial neurocranium was built of cartilage, and no traces of it have ever been found. The only things left to direct us are the impressions and processes on the under side of the head roof. These characters give no positive facts, and the significance of the different impressions can be explained in various ways.

The first author to mention the position and shape of the neurocranium in the Arthrodira was Woodward in describing *Homostius* (1891.3) and *Dinichthys* (1922). According to him: "The bony cranial shield extends backwards beyond the brain, and there can be no doubt that in all Arthrodira it covers the branchial chambers behind the occiput." In *Dinichthys* the thickened part of the central plate (Text-figures 13 *CR*) is the "ossified cartilages on the posterior end of the brain-case." The ridges of the lateral consolidated part (Text-figure 13 *LCP*) are the "ossified upper part of the lateral walls of the brain-case . . . firmly united with the cranial roof." The thickenings on the front part of *PrO* (Text-figure 13 *FP*) "may be regarded as the lateral ethmoid" (or ectethmoid). Finally he called the deep paired impressions on the hind part of the head roof (Text-figure 13 *PL*) "the branchial chambers."

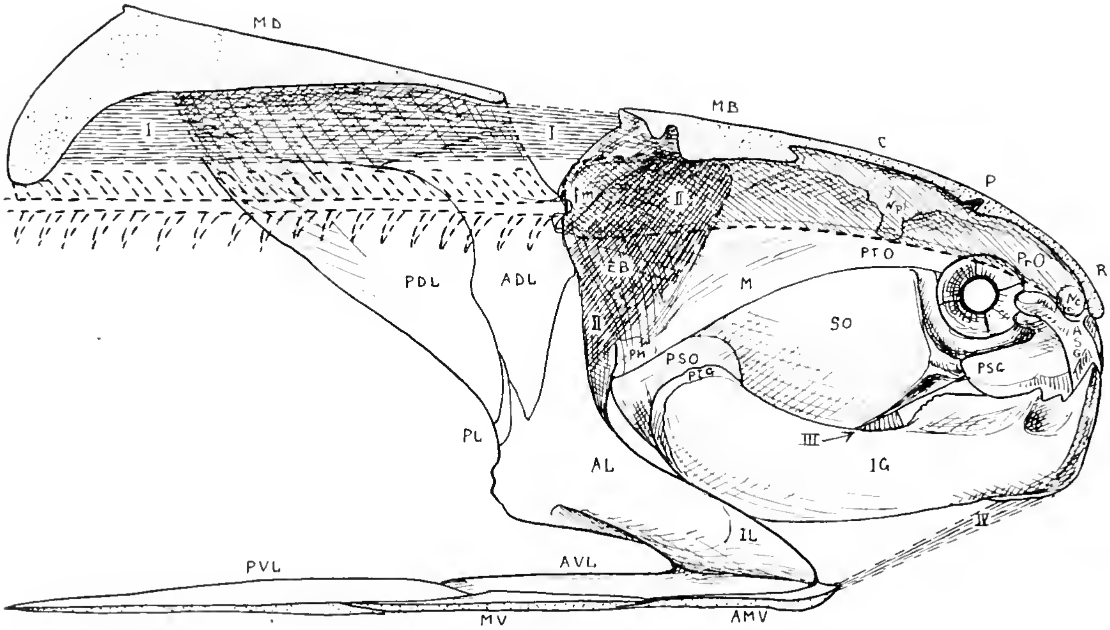
We have learned that no "ossified cartilage" or "ossified walls of the brain-case" are to be found in *Dinichthys*. All these parts named by Woodward are, in reality, only thickenings on the plates composing the head roof and not parts of the neurocranium. The impressions for branchial chambers, as we have seen before, are each really occupied by a musculus depressor capitis. They are, in all cases placed too high up to be occupied by gill apparatus.



Text-figure 82.
A reconstruction of the neurocranium of *Dinichthys*:
A, according to Stetson; *x-x*, plates bounding posterior wall of anterior division of occipital region, y-y, branchial chambers.
B, according to Stensiö (the contour of the head is added by the present writer).

The next to describe the neurocranium of *Dinichthys* was Stensiö (1925). On the basis of his detailed investigation of the neurocranium in *Macropetalichthys*, Stensiö tried to reconstruct the neurocranium in the Arthrodira (Text-figure 82B). It must here be pointed out that in the present writer's opinion *Macropetalichthys* is not related to the Arthrodira, and, therefore, the structure of the brain-case in this form can not give us any evidence about the brain-case in the Arthrodira. (A discussion on the relationships of the Arthrodira is to be found in the last section of this paper.) The sketch of the neurocranium given by Stensiö, is based on the figures of the head roof of *Dinichthys* given by Newberry and by Woodward. From drawings it is very difficult to get the correct picture of the inner surface of the head of *Dinichthys*. Therefore Stensiö's reconstruction in some directions does not correspond with the real facts we find in *Dinichthys*. The preorbital processes shown by him could hardly fit into the impressions on the under side of the head. The same is true of the large side processes occupying Woodward's "branchial chambers." In fact, these chambers are divided from the central impressed part of the head roof by a solid wall (Text-figure 13 *CR*). Thus the neurocranium could hardly continue into them.

A careful study of the head roof of *Dinichthys* led Stetson (1930) to give another picture of its neurocranium (Text-figure 82A). He conjectured that the neurocranium occupied the central thinner part of the head roof and was clearly limited by the lateral head thickening *(LCP)*. Like Woodward, Stetson thought that the thickened central part of *C* is a separate plate, but one not limiting the hind part of the brain-case (Text-figure 82A *x–x*). The hind part of the neurocranium was narrow and was placed along the median line of *MB*. Into the deep bilobed impression on the hind part of *MB* (Text-figure 13 *ds*) fitted the "cranio-spinal process," which was developed in *Dinichthys* as in *Macropetalichthys*. Stetson states that the impressions for the "musculi depressores capitis" were probably "cavities for branchial apparatus" (Text-figure 82A *y–y*). As mentioned before, I cannot accept the relationship between *Macropetalichthys* and the Arthrodira, and therefore believe that the Arthrodira never possessed the "cranio-spinal process." The bilobed depression on *MB* is the attachment place for the musculi levatores capitis.

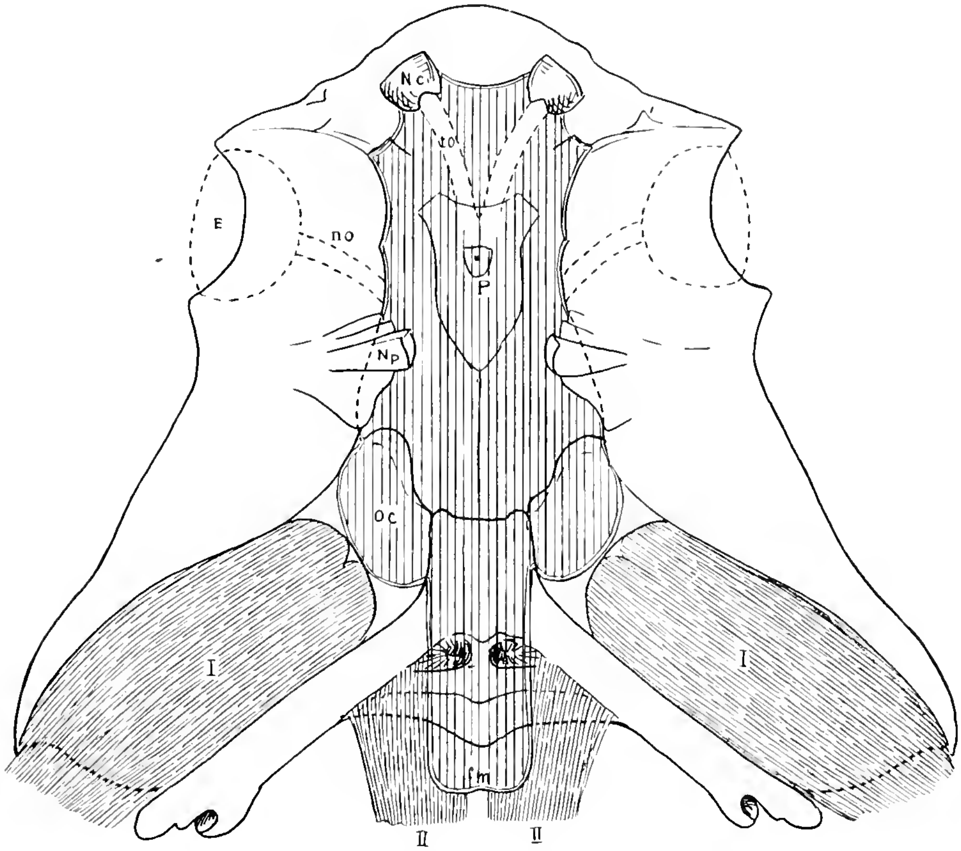


Text-figure 83.

Longitudinal section of the head and body armor in *Dinichthys* showing the position of the neurocranium (lined and cross-hatched) and of the gnathal muscles (lined and numbered).

Nc, nasal capsule, *Np*, neurocranial process; *fm*, foramen magnum, *I*, *II*, *III*, *IV*, gnathal muscles. Outline of spinal column schematic.

When trying to reconstruct the position and size of the neurocranium in *Dinichthys*, we must first find some definite points, which, for certain, have been in contact with the neurocranium. Beginning at the front, we find the first clear traces of the neurocranium in the olfactory capsules. These structures, which Newberry described (1889) as eye capsules, can, according to the investigations of Stetson (1930), only be regarded as nasal capsules. Their structure reminds us very much of the nasal capsules of modern Elasmobranchs. We can say, with certainty, that they were placed not far back of the nasal openings (Text-figures 83 and 84 *NC*). These nasal capsules formed the front part of the neurocranium.



Text-figure 84.
A schematic drawing of the head of *Dinichthys* from below, showing the neurocranium (shaded in parallel lines) and the gnathal muscles (lined and numbered).

E, eyeball; *fm*, foramen magnum; *Nc*, nasal capsule; *no*, nervus opticus; *Np*, neurocranial process; *oc*, otic capsule (?); *P*, pineal organ; *to*, tractus olfactorius; *I* and *II*, gnathal muscles.

The next parts which without doubt bordered the neurocranium were the neurocranial processes (Text-figures 13, 83 and 84 *Np*). A section through this part of the head roof (Text-figure 38 B) shows clearly a well defined cavity, broadest at the top, narrower at the bottom. These two processes have usually been regarded as muscle attachments (Adams 1919, Woodward, 1922, Stetson 1930). Claypole (1892.2) described them as supports for a new problematic plate, which "corresponds in position and function to the vomer or the presphenoid of a recent fish."

No traces or remains of such a plate have been known hitherto. Possibly a bony plate or cartilage served to connect these two processes and formed the roof of the mouth. The high walls running forward and backward from these processes form the natural boundaries of the neurocranium on both sides. Woodward (1922), Stensiö (1925), and Stetson (1930) have also pointed out that these ridges are the limits of the neurocranium.

To reconstruct the hinder part of the neurocranium is a most difficult problem. Only the position of the foramen magnum, a more or less fixed point, can be of any help. In a form like *Dinichthys* with a relatively very movable head, it is most natural to suppose that the foramen magnum was placed on the movement axis of the head, (that is in the middle of the horizontal line connecting the fossa condyli, Text-figure 35). If not, the occipital joint could not exist at all. Instead, we would have to find a joint on the spine — a very unusual formation. On the other side is the occipital joint, placed below or above the neck-joint axis, so that in moving the head such a spine would be either compressed or stretched and thus counteract the movement of the head.

The facts make it very probable, that the foramen magnum was placed on the axis of the neck-joint (Text-figures 83 and 84 *fm*). The whole neurocranium thus had an outline as shown on Text-figures 83 and 84. It was a flat box, placed in the median depression of the head roof and supported by the lateral consolidated parts of the head roof, especially by the neurocranial processes. Somewhat behind the neurocranial process, the neurocranium, following the limits of the "bridges" (Text-figure 13 *CR*) becomes narrower, and in the hind part runs along the median part of *MB*. In the hind part of *MB*, where the musculi levatores capitis are attached, the neurocranium loses connection with the head roof, and continues backward along the under side of these muscles. Thus, as seen on Text-figures 83 and 84, the neurocranium extends farther back than the head roof. Possibly the impression on the thickened part of plate *MC* (Text-figure 13 *CR*, *ti*) was occupied by the otic capsules (Text-figure 84 *oc*).

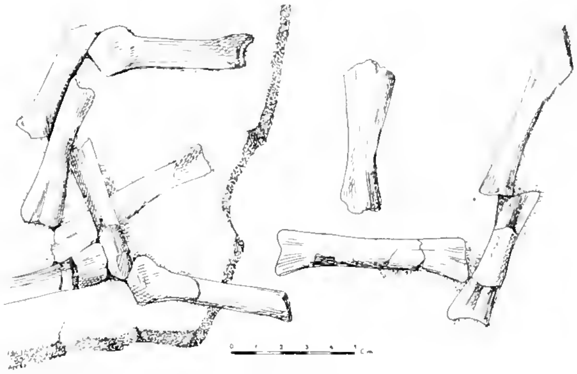
Naturally a reconstruction of the brain cavity or the brain itself is a very difficult problem, as our knowledge of the neurocranium is too scanty. We only know the position of the nasal capsules, the tractus olfactorius (Text-figure 84 *to*), the pineal organ (*D*) and eyes (*E*). The position of the labyrinth organ of the ear is not certain. No traces of other nerve canals are known.

THE SPINAL COLUMN AND FINS

Our knowledge of the axial skeleton is very modest. The only specimen (an imperfectly preserved one) showing traces of notochord and of vertebral arches was described by Dean (1896). As in *Coccosteus*, so also in *Dinichthys* no traces of vertebral centra have been found. Only the neural and haemal arches can be seen. They look like those of *Coccosteus*, but are shorter and more uniform.

We know somewhat more about the fins of *Dinichthys*. Not infrequently there are found long narrow crushed bones, which Newberry had already determined as "fin rays"

(1889). Newberry's specimen shows 7–8 "rays" in the natural position lying close together. In the previously mentioned specimen described by Dean, the rest of the fin structure also is well preserved. A small specimen of *Dinichthys curtus* in the American Museum also has some rays in situ. In Text-figure 85 are pictured some fragments of rays from the Buffalo Museum of Sciences (No. 15611/E2806). They enable one to see clearly the structure of the single bones. As Newberry has already mentioned, the rays are only calcified on the surface. Their inner parts were probably filled with cartilage. Therefore they are always more or less strongly flattened and crushed. They are thicker and rounder at both ends and narrower in the middle part. They were joined together by the thicker parts. The longer and more even spines described by Newberry may have belonged to the dorsal fins; the smaller, shorter, from Buffalo, to the paired fins.



Text-figure 85.
Fragments of the fin rays of *Dinichthys*.
(Buffalo Museum specimen No. 15611/E2806).

The presence of a dorsal fin is distinctly indicated on Dean's specimen. It is in nearly the same place as in *Coccosteus*. Also, fragments of the pelvic fins and pelvic girdle [12] of the same specimen make it evident that *Dinichthys*, like *Coccosteus*, had these fins. Apparently the previously described rays from Buffalo descend from these fins.

It is much more difficult to decide whether *Dinichthys*, or rather all Arthrodira, had pectoral fins. As we know, on this point the opinion of scientists is sharply divided. The older investigators, such as Miller, von Koenen, Trautschold and Newberry supposed that the Arthrodira had pectoral fins just like other fishes. But the majority of later scientists have come to the conclusion that the Arthrodira had the pectoral fins either very strongly reduced, or not developed at all (Traquair, Woodward, Dean and others). This opinion is, however, based exclusively on a negative character. In not a single one of the thousands of specimens of *Coccosteus* or other Arthrodira hitherto known, have there ever been found marks which could be explained as traces of pectoral fins. Even specimens with well preserved spinal columns and pelvic girdles carry no fragments of the pectoral fins.

Jaekel, contrary to all the other investigators, in all his papers on the Arthrodira since 1902 has advocated the opinion that the Arthrodira had pectoral fins. He had no actual facts to confirm this theory, but only judged that the strongly developed pelvic girdle made it very improbable that the pectoral fins were reduced. (Analogous cases in

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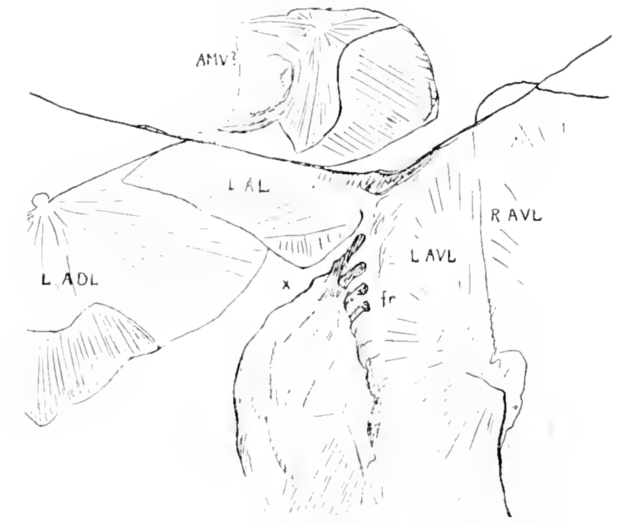
[12] A short description of a new find in the Bull. Cleveland Mus. Nat. Hist. no. 33, 1926, confirms the presence of a back-bone in *Dinichthys*.

other fishes are unknown). On the other hand, the deep impression between the dorsal and ventral armor can also be explained as the place for pectoral fins.

In reality, the deep narrow cleft between the dorsal and ventral carapace in *Dinichthys* (Text-figure 79) is very remarkable, and hard to explain if we do not accept the presence of fins. A concretion in the American Museum, containing strongly crushed fragments of an Arthrodire (not a *Dinichthys*), carries on the side of the plate *AVL* some traces of fin rays, arranged in a parallel fashion (Text-figure 86). This specimen, however, is too badly preserved to make certain that we have here real pectoral fins. The absence of traces of pectoral fins in *Coccosteus* can not be used as a sure proof for the absence of fins in the other Arthrodira. We must remember that it is a usual occurrence to find only fragments of the pelvic girdle; moreover the fin rays are hardly ever found.



Text-figure 86.
Crushed fragments of an Arthrodire (not a *Dinichthys*), showing trace of pectoral fin (?).
fr, fin rays; *x*, pectoral fin (?); L, left and *R*, right plates of armor.

If all the above mentioned circumstances make the presence of pectoral fins in the Arthrodira presumable, there are some others making it problematical. For in some Arthrodires, as for instance *Acanthaspida* from Spitsbergen (Heintz 1929.1, .2) and *Coccosteus angustus* (Bryant 1929) from the Portage shale, N. Y., the body carapace extends very far downward and no cleft between the dorsal and ventral armor is developed. If, in these forms we place the pectoral fins behind the body carapace, they will be too far back and too close to the pelvic fins. The newly found *Acanthaspida* from Germany (Broili 1929–1930) shows an unusually perfect preservation; nearly the whole shell-covered body can be perfectly seen. Also the dorsal fin (or spine) is well preserved. But no traces of pectoral fins can be established. Moreover the pelvic fins are also absent.

Thus, nothing positive can be said about either the presence or absence of pectoral fins in the Arthrodira. We must wait for new and better preserved material to solve this question.

Finally, however, a few words may be said about the pectoral spines of *Dinichthys* described by Newberry (1889, p. 144, Pl. V). These remarkable long bones, usually found together with *Dinichthys* remains, belong, without doubt, to this fish. Newberry thought that they corresponded to the long spine-like "Ruderorgan" described by von Koenen (1883–1895) in *Coccosteus* from Germany. We now know that von Koenen's "Ruderorgan" is the spinal, which is well developed in *Dinichthys*, as in all other Arthrodirans.

Thus the pectoral spine can not be homologous with the "Ruderorgan." What this remarkable structure is, and where it was attached to the carapace, only new finds can show us.

It is interesting to point out that according to my discoveries the spinal in *Dinichthys* has entirely lost its character as a spine and has become a bone connecting the dorsal and ventral armor. There can be no question of its being homologous with the pectoral fins of other fishes.

THE GILL APPARATUS

Definite traces of the gill arches have never been found in theArthrodira. We may therefore suppose, that the gill arches in these fishes were not ossified. The question of the Arthrodiran gills is therefore a very disputable point. Miller, Pander, Traquair and Woodward (in "Catalogue") have said nothing about gill structures in the Arthrodira. But in calling our *PSO* plate in *Coccosteus* a "probable operculum" Woodward (1898) indirectly implied that he thought the gill openings were placed in the cleft between the head and body.

In a description of *Coccosteus* published in 1902, Jaekel spoke of the side plates of the body carapace (*ADL*, *PDL*, *AL* and *PL*) as "Elementen des Opercul-Apparates" and we are led to assume that he believed the gill openings were placed behind the body carapace. But in 1907 he changed his mind and wrote "Dass die Kiemen unterhalb der Platten der Wangenregion untergebracht waren, habe ich durch . . . die Auffindung der Kiemenbogen bei einem Wildungen Verwandten der Coccosteiden bestätigen können. Als äussere Kiemenspalte fungierte also der Schlitz zwischen der Wangenregion des Schädels und dem Vorderrand des Halspanzers." The "Verwandte der Coccosteiden" with "Kiemenbogen" mentioned in this paper was never described or figured in later papers by Jaekel. Therefore, we believe that he probably changed his opinion again.

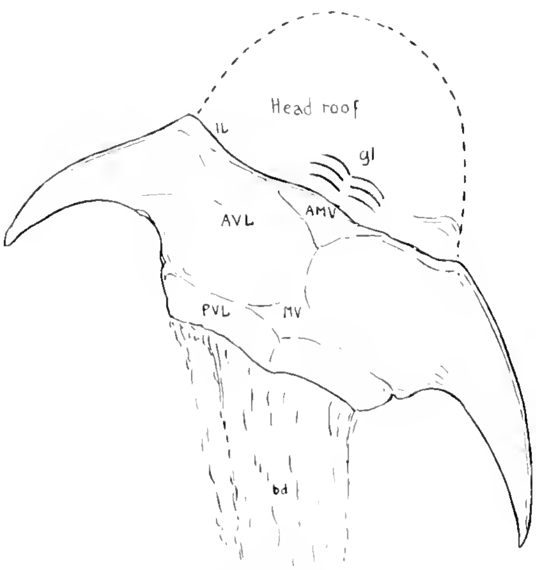
Kemna (1904) also thought that the gills were placed on the posterior part of the head and that the lower opening between the head and body carapace served as a gill opening. On the contrary, in Patten's opinion (1912), the whole body carapace of the Arthrodire, corresponding to that of *Bothriolepis*, must be regarded as a "branchial shield" which "served solely for the protection of the gills and heart." The openings for the "peribranchial chamber" were behind the body carapace.

But certainly most extraordinary is the opinion Jaekel expressed in his last papers (1925, 1926, 1927). In correlation with his theory about the descent of fishes from land-living animals, Jaekel tried to demonstrate that the oldest known fishes had no gills at all. He writes (1927, p. 284) that: "Auch bei *Coccosteus* und ihren Verwandten ist nichts von Kiemenspalten oder Oeffnungen bekannt. . . . Wir werden also auch hier mit der Möglichkeit rechnen, dass diese Fische . . . ohne äussere Oeffnungen atmeten."

Lastly, we may mention that Woodward (1922) and Stetson (1930) supposed the deep paired impressions (Text-figure 13, *PL*) on the hind part of the head of *Dinichthys* to be the "branchial chambers."

The only remains of a gill apparatus on record were described by Broili (1929) in a German Acanthaspid (*Lunaspis*). These are three small paired arch impressions placed very near the median line, immediately in front of the ventral shield (Text-figure 87). As Broili pointed out, very probably these arches are a part of the visceral skeleton.

Together with the majority of scientists, the present writer is of the opinion that the gill apparatus in the Arthrodira was placed under the head shield and that the split between *PSO* and *AL* is the gill opening. It is hardly possible that the body carapace served as a protector for the branchial region (corresponding to the opercular region in other fishes). In forms like *Acanthaspida* from Spitsbergen (Heintz 1929.1, .2) the body carapace is very long, making it unlikely that the gill openings would have been placed behind the body carapace, since they would have been pushed unnaturally far backward. The same would occur in *Coccosteus angustus*, described by Bryant (1929). On the contrary, in forms like *Heterostius* the whole body carapace is shortened and thickened, and there is no room for gills behind it (Heintz 1930.2).



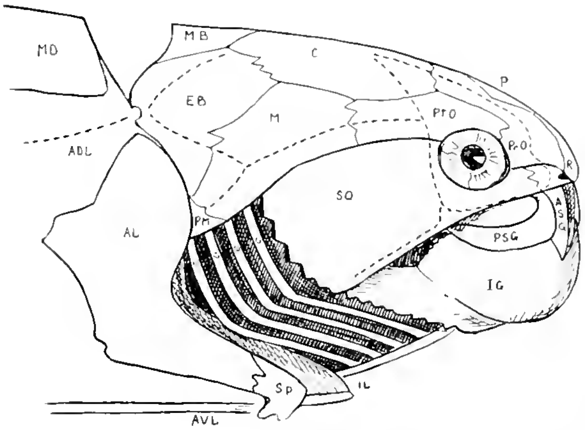
Text-figure 87.
Fragments of the head roof, the ventral shield and part of the body of *Lunaspis heroldi*.
Drawn to show *bd*, *body*; *gl*, gill arches (?),
(After Broili, 1929).

It has been remarked that there is too little room for the gill apparatus underneath the head shield. If we compare the heads of the Arthrodira with the heads of other fossil and recent fishes, it is easily seen that in the majority of forms the place for the branchial apparatus is not larger than that in the Arthrodira. In fact, behind the posterior part of *SO* and *PSO* and the front part of *AL* and *IL*, there is sufficient room to place an effective branchial apparatus.

Another circumstance makes the location of the gills in this region very probable. The surface of *IL*, as mentioned before, is the only place in the whole of *Dinichthys*, showing a distinctly superficial ornamentation. This ornamentation has been previously described (See Plate VIII, figure 22). We must suppose that it is a preserved skin part which covered this part of the bone. If we remember that in many other Arthrodires (Traquair 1890.4, Jaekel 1902, Heintz 1929.1, .2) this part of *IL* is sculptured like all other carapace plates—that is, it must be placed superficially—this supposition becomes a certainty. In that case there must have been an opening along *IL*, otherwise we could not find skin developed here. This opening can only be considered as a branchial opening. The remains of the visceral skeleton found by Broili are also placed in the same region. All these circumstances make it still more probable that the branchial apparatus in the Arthrodira was placed in the hind lower corner of the head.

The other question is: How was this apparatus formed? We have no remains to help us in solving this problem. We only know that the branchial apparatus was relatively strongly compacted. It consisted of cartilage. No real movable bony operculum was developed. The respiratory movements either functioned with the help of a special inner musculature or in combination with the lifting and dropping of the head in opening the mouth.

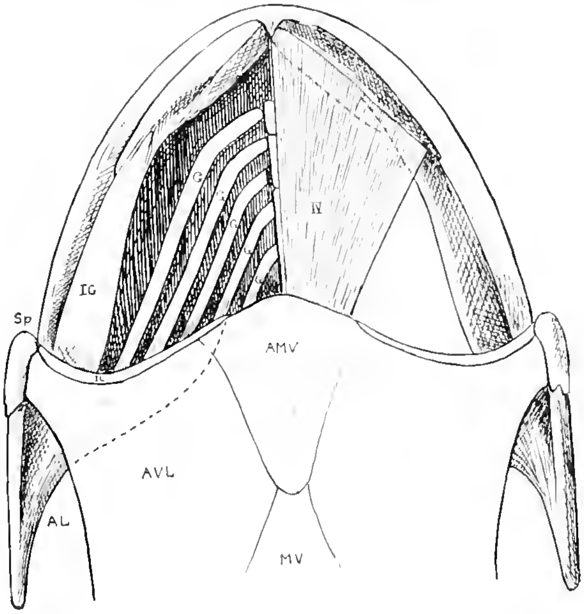
If the gill arches in the Arthrodira existed conformably with those in the fishes, they must have been placed like the arrangement in Teleostomous fishes, but not as in Elasmobranchs. This assertion becomes clearer if we look at the relative arrangement of the infero-gnathals (*IG*) and the front part of the ventral shield in the Arthrodira, and compare them with the corresponding parts in present-day fishes.



Text-figure 88.

The author's reconstruction of the possible arrangement of the gill arches in *Dinichthys*, in lateral view.

To show the gill arches (*G*), *PSO*, hind part of *SO*, *PIG*, and hind part of *IG* have been left off.



Text-figure 89.

A reconstruction of the possible arrangement of the gill arches in *Dinichthys* seen from below.

To show the gill arches (*G*), the musculus depressor gnathalis (*IV*) on the left side has been omitted.

This arrangement reminds us very much of that in the higher fishes. The intero-lateral, together with parts of the antero-lateral, corresponds with the clavicle; the infero-gnathal with the mandibular arches. The system of five or more gill arches can be placed between the infero-gnathal and the intero-lateral in accordance with the arrangement in the higher Teleostomi. The inner wings of *AL* and *IL* form the hind wall of the gill chambers. Along the median line, from *AMV* to the symphysis of the infero-gnathal, the basi-hyal elements may be placed. We know nothing about the presence or absence of hyoid arches. Their reconstruction as given by Jaekel (1919 1925) is very problematic. If the inferno-gnathal is only a superficial bone, not corresponding to the lower jaw in other vertebrates, we can not expect the Arthrodira to have developed hyoid arches.

To reconstruct the gill apparatus in *Dinichthys* in accordance with that of the Elasmobranchs is still more difficult. In all these forms the gill arches are placed behind and in immediate prolongation of the mandibular and hyoid arches. In the Arthrodira we cannot find the necessary room for the branchial apparatus behind the joint between the infero-gnathal and the post-sub-orbital. Another very probable possibility is that the Arthrodira had the branchial apparatus built after a principle unknown in recent fishes. Such extraordinarily constructed animals with such an unusual mouth mechanism may also have had their respiratory organs constructed on some equally remarkable plan.

The drawings given in Text-figures 88 and 89 of the arrangement of gill arches in *Dinichthys* must not be regarded as a reconstruction. They are only an attempt to show how the gill arches might have been placed in an Arthrodire. We have no direct facts in any way supporting this proposition.

THE BIOLOGY OF *DINICHTHYS*

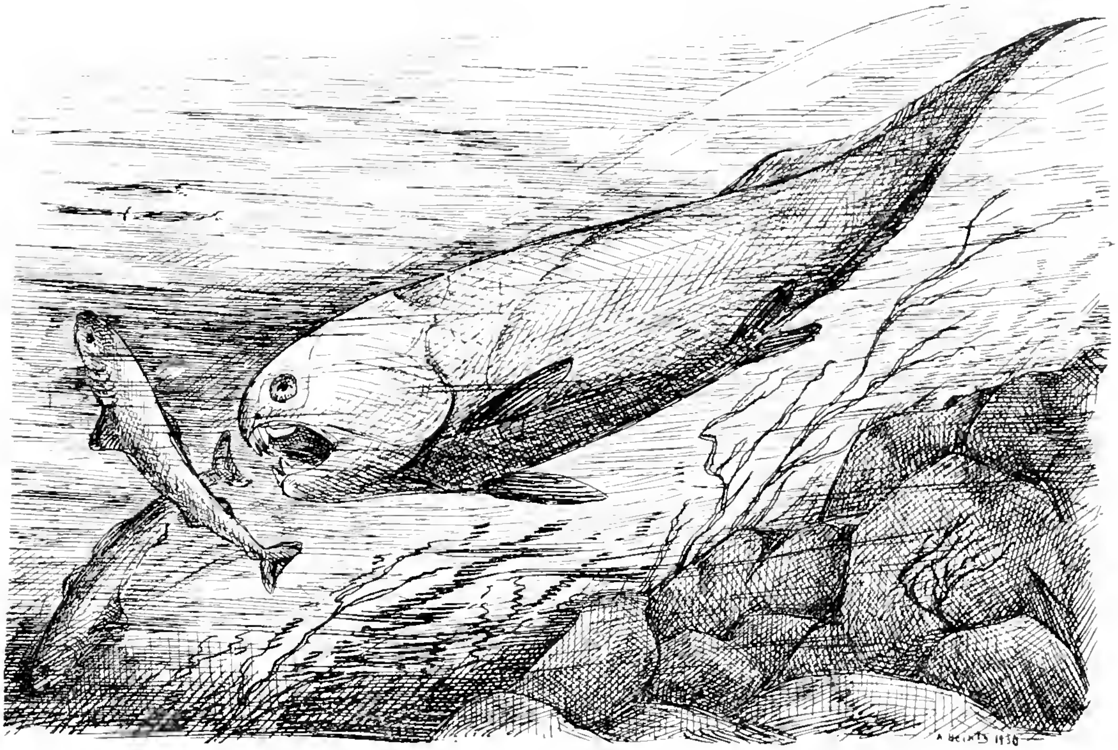
The complete body form of *Dinichthys* is unknown. But, with the help of *Coccosteus*, which in its structure was very like *Dinichthys*, we can make a relatively good picture of the animal. Very likely, *Dinichthys* had a macruriform body, that is, the highest and broadest part of the body was immediately behind the head. The posterior part behind the body carapace became narrower and narrower, finally culminating in a pointed tail. One dorsal fin and the paired pelvic fins were present. It is not excluded that also the paired pectoral fins were developed. But only the tail served as locomotor organ.

Dinichthys must certainly be regarded as a carnivorous animal. Only a look, for instance, at Text-figure 81, must convince us that such a perfectly armed mouth belonged to a carnivore. And, being a relatively good swimmer, it could actively pursue its prey. Text-figure 90 shows a tentative total reconstruction of *Dinichthys*.

THE RELATIONSHIPS AND SYSTEMATIC POSITION OF THE ARTHRODIRA

It is doubtful whether any other group has been assigned relationships to such a number of other animal groups as has been the case with the Arthrodira. At first determined as water beetles (reference in Agassiz, 1844, p. xxx), they were later described as fragments of reptiles (Kutorga 1835, 1837). Assmuss (1840) was the first who positively determined them as belonging to the fishes. After his time the Arthrodira were moved from one group of fishes to another. They were placed among the Ganoidei (Agassiz, 1833; Eichwald, 1860; Zittel, 1887): together with the Antiarcha were made an independent family of fishes, the Placodermata (M'Coy, 1848.3; Pander, 1857; Huxley, 1861; Traquair, 1888; Regan, 1904): were thought to be related to the Chondrostei (Baer, 1840; Jaekel, 1906–1929); to the Dipnoi (Newberry, 1875; Woodward, 1891.1; Dean, 1895; Eastman, 1900–1917); to the Holocephali (Jaekel, 1902); to the Elasmobranchii (Woodward, 1924; Stensiö, 1925); and to the Actinopterygii (Traquair, 1900.1; Bridge, 1904). Dean (1900–1901) and Hussakof (1905–1907) placed them as an independent class, the Arthrognathi, equivalent to the class Pisces. Finally, Jaekel (1906.1) wrote that: "Gerade die Organisation der Placodermen spricht deutlich für eine Abstammung der Fische von älteren, uns noch unbekannten, vierfüssigen Landwirbeltieren."

This compendium alone shows that the question of the relationship of the Arthrodires is a difficult one. The facts we know are so few that the subjective opinions of the investigators play too great a part in their conclusions. In the following sections I shall try to analyze all the different relationships of the Arthrodira.



Text-figure 90.
A total reconstruction of *Dinichthys* showing the fish in action.

THE RELATIONS BETWEEN THE ARTHRODIRA AND OTHER FISH GROUPS

When we know that the Arthrodira had no Dipnoi-like teeth, that the mechanism of their jaws was unusual and that they were not autostylic, their relation to the Dipnoi, based chiefly on these characters, must be regarded as improbable. Furthermore, they have so little in common with the Holocephali that it is difficult to find any relationship there.

The opinion of Jaekel that the Arthrodira are closely related to the Chondrostei, is based on the great likeness of the shoulder girdle of Rhynchodonts from Wildungen to that of the Acipenseridae, and to the body carapace of the Arthrodira. The likeness between *Rhynchodontus* and *Acipenser* is indeed quite great. Apart from the analogies in shoulder girdle structure as discussed by Jaekel, they also show close relationships in the structures of the neurocranium, head roof, gills and fins. On the other hand, it is much more difficult to find contact between these forms and the Arthrodira. The dentition of *Rhynchodontus* is quite different from that of the Arthrodira, reminding one much more of that of the Holocephali. Their jaw mechanism was certainly not Arthrodiran-like. The condyle on the plate corresponding with *ADL* is only developed as a spine. The shoulder girdle is far different from all plates usual in the Arthrodira. The plates corresponding with *PDL*, *PL*, *PVL*, *MV* and *IL* are absent. The Acipenser-like (Jaekel) head roof could not be Arthrodire-like.

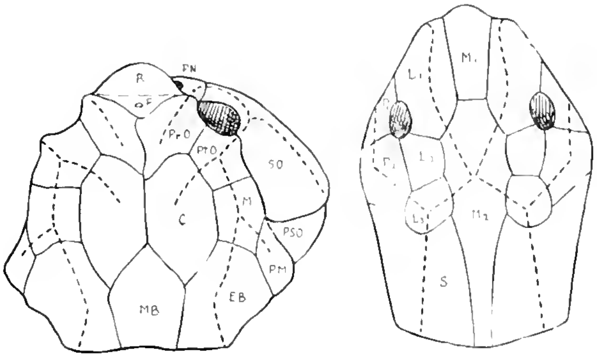
The difference between the Chondrostei and the Arthrodira is in reality very obvious. It is impossible to homologize the structure of their head roofs. The course of the sensory canals is also unlike. The position and mechanism of the jaws are of absolutely different characters. All these facts make any close relationship between the Arthrodira and the Chondrostei improbable.

It only remains to dispute the relationship between the Arthrodires and the Elasmobranchs. This was sharply advocated by Stensiö in his brilliant paper on the head of *Macropetalichthys*. According to his classical investigation, it is certain that *Macropetalichthys* was related to the Elasmobranchs. Regarding *Macropetalichthys* as closely related to the Arthrodira, Stensiö then draws the conclusion that the Arthrodires also were related to the Elasmobranchs. The present writer, however, cannot accept the opinion that *Macropetalichthys* was closely related to the Arthrodira. In fact, if we examine the structure of *Macropetalichthys*, it is hard to find much in common with the Arthrodira.

Beginning with the arrangement of the bony plates in the head roof of *Macropetalichthys*, we notice that all the attempts made by various authors (Eastman, Dean, Jaekel, Stensiö) to find an exact homology between these and the head roof plates of the Arthrodira, must be regarded as unsatisfactory. Arthrodirans, as we know, show an unusually constant plan in the arrangement of the head roof. From the oldest known *Acanthaspida* to the most recent *Dinichthys* we always find the same plates in the same relative position. The arrangement in *Macropetalichthys* is of an absolutely different type. To establish a homology between these two groups, Stensiö must assume that one plate in *Macropetalichthys* corresponds to a part of, or to many plates in the Arthrodira. For instance, M_2 in *Macropetalichthys*, would correspond to $\mathrm{L}+\frac{1}{2}$ of *B* and $\frac{1}{2}$ of *A* in the Arthrodira. Text-figure 91 is a schematic drawing, showing the homology proposed by Stensiö. In my opinion, this homology is not satisfactory and can in no way clearly establish the relationship between these two groups. The homology Dean proposed, wherein the head of *Macropetalichthys* corresponded with the fused head and body armor in the Arthrodira gives a better result. But Stensiö's investigation has made this theory absolutely impossible. As we know, the primordial neurocranium in *Macropetalichthys* goes to the hind part of the head. If the head of *Macropetalichthys* corresponds with the head and body carapace of the Arthrodira, we must expect to find that in them the neurocranium continues under *MD*. Surely nobody can accept this arrangement.

If we turn to the sensory canals, we find that they are also differently developed in the two groups. The homology proposed by Stensiö is only uncertainly probable, especially when we notice that his "pre-opercular canal" has only been found in a very badly preserved specimen of *Macropetalichthys*. The absolutely constant arrangement of the canals in the Arthrodira is not like that in *Macropetalichthys* (Text-figure 91).

No traces of the body carapace have ever been found in *Macropetalichthys*. We must suppose that it was not developed. If developed at all, it was certainly not movably connected with the head roof since no traces of joint sockets on the occiput are known. Thus, *Macropetalichthys* had no neck joint,—a trait most characteristic for the Arthrodira. This excludes also the possibility that the Macropetalichthyids had the same jaw mechanism as the Arthrodirans. Furthermore, the whole complicated visceral skeleton of an Arthrodiran (with its 14 plates) is unknown in *Macropetalichthys*.



Text-figure 91.
The head roofs of an Arthrodire (left) and of *Macropetalichthys* (right), to show the homologies between the single plates according to Stensiö. The positions of the sensory canals are shown by dotted lines.

$P_1 = PtO$, $P_2 = M$. $S = EB$, $L_1 = \frac{1}{2}\ PrO$. $M_2 = MB + \frac{1}{3}$ right $C + \frac{1}{3}$ left $C + \frac{1}{2}$ right $PrO + \frac{1}{2}$ left PrO, $L_2 = \frac{1}{3}\ C$; $L_3 = \frac{1}{3} C$.

R, *P*, *PM*, *SO*, *PSO*, and *PN* in an Arthrodire are without homologies in *Macropetalichthys*.

M_1 in *Macropethalichthys* has no corresponding plate in an Arthrodire.

I might remark here that in *Synosteus*, one of the Wildungen Arthrodira briefly described by Jaekel (1906.2), the head is secondarily fused with the body carapace. Therefore the head could not be moved in relation to the body, and the whole jaw mechanism must have been different. We may note here that in the first place this form is so incompletely figured and described that it is difficult to draw any conclusions. And in the second place, the whole arrangement of the plates, as far as it is possible to see it from Jaekel's drawing, is precisely Arthrodiran-like. This form, must have represented one of the most highly developed types of the Arthrodira, which, overspecialized, lost the most characteristic feature of the whole class. Nevertheless, it can be an Arthrodire, just as, for instance, the Struthioideae, though wingless, are still birds.

In Stensiö's opinion, *Phlyctaenaspis* and *Homostius* "seem to be most nearly related to *Macropetalichthys*." Both these forms are typical Arthrodires, and, in my opinion, are no more closely related to *Macropetalichthys* than are any other Arthrodira. The mere fact that the eye openings in *Homostius* are moved nearer to the median line and surrounded by *PrO*, *PtO* and *C*, instead of by *PrO*, *PtO* and *SO* as in other Arthrodires, does not make it any more like *Macropetalichthys*.

We can say nothing about the likeness or unlikeness between the structure of the primordial neurocranium in *Macropetalichthys* and the Arthrodira, so long as it is absolutely unknown in the latter forms. We can only point out in regard to the sensory organs, that the majority of the Arthrodira have the sclerotic rings, which are absent in *Macropetalichthys;* that the opening for the ductus endolymphaticus is known in *Epipetalichthys* but has never been observed in any Arthrodiran; and that an opening (or a deep impression) in the dermal bone for the pineal organ is always found in the Arthrodira, but never in *Macropetalichthys.*

If we recapitulate all the previously mentioned facts we find that *Macropetalichthys* had: (1) the dermal plates on the head placed differently from the Arthrodira; (2) had a different course for the sensory canals; (3) had no body carapace; (4) no joint articulation between head and body; (5) had an un-Arthrodiran-like arrangement of the jaws; (6) had developed no plates corresponding to the side plates of the Arthrodire head; (7) possessed no sclerotic rings; (8) had no opening for the pineal organ in the dermal bone; (9) but in some forms had openings for the ductus endolymphaticus, unknown in the Arthrodira. We also find that no intermediate forms between these two groups are known.

The resemblance between *Macropetalichthys* and the Arthrodira is thus based on mere facts that they are all fish-like vertebrates with the head covered by dermal bones, and that all lived during the Devonian Era. These facts, however, are not sufficient to prove them closely related forms.

As known, Stensiö thought also that the Ptycodontids (Rhyncodonts) and Jagorinids were nearly related to the Arthrodira. I have already pointed out that the relation between Rhynchodonts and Arthrodires is of a very doubtful character. As to *Jagorina* —a form from the Devonian of Wildungen, without dermal head roof or side plates on the head, whose body carapace according to Jaekel resembled that of the Chondrostei, and which had numerous small, independent Selachian-like teeth— it is even more difficult than in *Macropetalichthys* to find any resemblance to the Arthrodira.

My opinion is that the Arthrodira are not related to any of the above mentioned forms, and that therefore the conclusions drawn in studying these forms cannot be transferred to the Arthrodires.

If we now analyse the facts given by Stensiö (1925, p. 187) to show the relation between the Arthrodira and the Elasmobranchs, we shall see that but few hold good. The points based on the likeness between the structure of the neurocranium and of the brain are of no value for the Arthrodira, as the brain and neurocranium of these forms are too badly known. The blood vessels mentioned are also unknown in the Arthrodires. The position of the palato-quadrate can not serve as a proof, as the Arthrodira had no palato-quadrate at all. The dentition of Elasmobranchs and Arthrodires is as unlike as possible; the Arthrodires had no real teeth, hence enamel and dentine are unknown in their composition.[13] Their teeth-like tubercles on the jaws are made of real bone.

There are then left only two points; the position and relation of the olfactory capsule and the course and development of the sensory canal system. As to the first, according

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[13] Stensiö is of another opinion.

to Stetson's investigations, the nasal capsule in Arthrodires is like that in Elasmobranchs. Concerning the second point, we can only say that the course of the sensory canal system in the Arthrodira can not be compared in detail with that of the Elasmobranchs. In my opinion, if we recall the fundamental differences between Arthrodires and Elasmobranchs, obvious in their whole structures, these two points are not of any great significance.

THE ARTHRODIRA AS AN INDEPENDENT CLASS

The problem is—Are the Arthrodira agnathous or gnathostome forms? In other words, are their "lower jaws" homologous or only analogous to the lower jaws of other vertebrates? Let it be stated at once, that the proven facts give no absolutely certain answer to this question.

As known, it was Dean and Hussakof who especially defended the opinion that the Arthrodira are representative of an independent class, called Arthrognathi, whose jaws are only dermal plates, not modified gill arches as in all other fishes. In favor of this opinion the following facts can be mentioned:

1. The macroscopical and microscopical structure of the gnathal elements and of the dermal plates in *Dinichthys* are absolutely identical.

2. *Dinichthys lincolni* Cl. has on *ASG* very distinct tuberculations which are characteristic only of dermal bones.

3. In correspondence with all other dermal plates, on the gnathal elements there are never found traces of any kind of enamel or dentine. The "teeth" of Arthrodira, as also the cutting edges, are formed of true bone.

4. No traces of Meckel's cartilage have ever been found in the Arthrodira.

5. If one can speak of homology between the infero-gnathal and the dental or splenial, then without doubt the post-sub-orbital can not be regarded as homologous with the palato-quadrate or quadrate in other fishes. It is a typical dermal bone with definitely developed sculpture.

6. The whole jaw mechanism of the Arthrodira is constructed without the least resemblance to that of any other animal.

7. The symphysial connection of the infero-gnathal is also of an unusual type.

8. No traces of ossified hyoid arches or gill arches are known. In the majority of other fishes with such strongly ossified jaw elements, the other components of the visceral skeleton are also more or less ossified. This circumstance is still more remarkable if we remember that the gill arches in the Arthrodira (if present at all) represent a relatively highly developed type.

9. The relative position of the dermal cranial bones is difficult to homologize with the arrangement of cranial bones in other fishes.

All these arguments are of great importance and make Dean's theory quite probable. But there are other and contradictory facts which may be stated as follows:

1. In reality, the infero-gnathal was placed comparatively deep under the skin. Especially its hind corner stuck deep underneath the dermal plates (*SO* and *PSO*).

2. As seen, quite likely the post-infero-gnathal in many forms was cartilaginous. Possibly even in *Dinichthys* it was only superficially ossified. *PIG* may thus not have been a dermal bone, and we must suppose the same about *IG*, as *PIG* was placed on the outside of the latter.
3. In *Acanthaspida*, one of the oldest known Arthrodires, the jaw elements have never been found. Also in a previously mentioned specimen from Germany (Text-figure 87) showing a perfect preservation, no traces of them are seen. This indicates that the jaws of these oldest forms were perhaps made of cartilage.
4. The head shield of the Arthrodira is naturally divided into two parts; the head roof, and the side plates of the head. This division reminds us much of that in other fishes, where we find corresponding parts in the neurocranium and the visceral skeleton. These elements are perhaps homologous.
5. The sensory canal system of the Arthrodira is not so unlike that of other fishes. The homology is not clear, but still acceptable.

These are the facts we know. They are not of an indisputable nature, and the question about the relationship of the Arthrodira will in the end be settled by the personal judgment of the investigator. For myself, I hold to the opinion that the more completely the Arthrodira have been studied, the more striking appears their dissimilarity to all other types of fishes. Many characters show such fundamental differences that it is nearly impossible to correlate the Arthrodires with other fishes. In all cases, our knowledge of today yields no facts in proof of a sure relationship between them and other known groups of animals.

THE RELATION OF THE ARTHRODIRA TO THE ANTIARCHA (ASTEROLEPIDA)

The older investigators (Agassiz, Miller, Pander, Huxley, Eichwald, Zittel) have always placed the Arthrodira in close relation to the Antiarcha. But Newberry, who thought he could show a relation between the Arthrodira and the Dipnoi, detached the two groups mentioned above and placed them far from each other in the system. However as early as the beginning of this century many authors pointed out the great likeness between these groups and suggested their possible relationship (Jaekel, Dean, Hussakof, Patten, and more recently Stensiö and Stetson).

As a matter of fact, if the structure of the head and body armor in Arthrodira and Antiarcha can not be homologized in detail they show, nevertheless, similarities in their larger structural characters. These may be noted as follows:

1. They have both the head and forepart of the body covered by armor.
2. This armor is divided into head and body portions.
3. The head and the body armor are movably connected with the help of a double neck joint, a character unknown in other animals.
4. The armor is built of more or less isolated bony plates which are connected by squamosal sutures.
5. The eyes are protected by sclerotic rings.

6. The body armor of the oldest known Arthrodira greatly resembles that of the Antiarcha.
7. The armor plates and jaws are built only of true bone. Real teeth are unknown.
8. The gnathal elements in both groups seem not to be homologous with the jaw elements of other animals.

All these points permit us to accept a relationship between the Arthrodira and the Antiarcha. However, we must remember that it is not a very close relationship and that these two groups can not be regarded as forms derived from each other.

THE SYSTEMATIC POSITION AND DIVISIONS OF THE ARTHRODIRA

We have now seen that the Arthrodira can hardly be connected with any known fish group. Further, their structure shows so many exceptional characters that in my opinion we have not enough facts to consider them as belonging to the true fishes at all. Therefore, with Dean and with Hussakof, I propose to establish an independent class of animals which shall rank with Cyclostomes and Pisces. This class may be divided into sub-classes—Antiarcha and Arthrodira. In my opinion it is more natural to retain the old name Placodermata proposed for the same two groups by M'Coy (1848), than to adopt the new name Arthrognathi used by Dean (1900). I give the following definitions of this class and its sub-classes.

Class PLACODERMATA

Water-living, fish-like animals, with armored head and forepart of the body. The head armor is movably connected to the body armor by means of a double neck joint. The armor is composed of more or less separate bony plates, usually sculptured on the surface. The sensory canals, in the form of deep grooves on the surface of the plates, are always present. The eyes are protected by sclerotic rings. The opening (or deep impression) for the pineal organ and that for a double nasal opening are well developed. The gnathal elements are not homologous with the jaw elements of other vertebrates. No real teeth are developed. The hinder part of the body is naked or covered with scales. The dorsal fin is always present. The neurocranium, and other parts of the inner skeleton are never ossified.

The Placodermata are found only in strata of the Devonian Era.

Sub-class ANTIARCHA

The condyle of the neck joint is on the head; the fossa condyli on the body. The head is relatively small. The eyes are placed close together near the median line; the pineal organ is between them; the double nasal opening is in front. The gnathal elements are represented by two pairs of separate bones. The body armor is relatively long and narrow. In all forms it is made up of the same number of plates, arranged after the same plan. Two long, jointed appendages are movably connected to the anterior plate of the ventral carapace by means of a remarkable joint. No traces of paired fins are present.

The Antiarcha are found only in Middle and Upper Devonian.

SUB-CLASS ARTHRODIRA

The condyle of the neck joint is on the body; the fossa condyli on the head. The single plates and sensory canals are arranged on the same plan in all forms. The eyes are on the side, the pineal opening on the top, and the nostrils in front of the relatively large head. The gnathal elements are represented by three pairs of plates. In opening the mouth, the whole head moved upward and the movement of the lower jaw was relatively small. The jaws are armed with tooth-like tubercles, cutting edges or crushing plates. The gill arches are in the hinder lower corner of the head; the gill openings between the head and body carapace.

The Arthrodira range from Lower to Upper Devonian.

The division of the Arthrodira into smaller groups is a difficult problem, as the members of the whole sub-class are very similar and a great many of the forms are very imperfectly known. The proposed divisions must therefore be regarded as only provisional. The first order, without doubt, must comprise these forms, already known from the lower Devonian (Spitsbergen), which show many primitive characters. The definition is:

ORDER ACANTHASPIDA

Arthrodira with a relatively small head and long, narrow body carapace. The gnathal elements are unknown. The distance between the joints is short; the fissure between the head and body armor small. The process on *MD* is weak. The contact line between the dorsal and ventral carapace is long. The spinal is long and strong. No traces of paired fins are known. The body in some forms is covered with small scales.

The definitions of the various families and the genera in this order can be found in Broili (1929–1930) and Heintz (1929.1, .2). It must be noted that the names proposed by Heintz for the families, I. Monaspidae, II. Mediaspidae, and III. Polyaspidae, must be changed respectively to I. Jaekelaspidae, II. Phlyctaenaspidae, and III. Acanthaspidae— as corresponding better with the international nomenclature regulations.

The next equivalent group is:

ORDER COCCOSTEIDA

Arthrodira with the head and body carapace of nearly the same size. The gnathal elements are armed with tooth-like tubercles and cutting edges. The distance between the neck joints is large, as is also the fissure between the head and body. The keel on *MD* is strongly developed. The spinal is more or less reduced. The contact line between the dorsal and ventral carapace is short. The spinal column shows well calcified neural and haemal arches. The supports of the dorsal fins are also calcified. Calcified pelvic girdle and pelvic fins are present. The existence of pectoral fins is uncertain.

This order can be divided into families and genera as follows:

1. Family Coccosteidae with two genera: *Coccosteus* and *Dinichthys*.
2. Family Solenosteidae with genera: *Solenosteus*, *Stenognathus*, *Machaerognathus*, *Copanognathus*, and others.

3. Possibly many of the Wildungen Arthrodira can also be placed in this order, making a number of new families.

The classification of the other Arthrodira cannot be satisfactorily accomplished at the present; they are too incompletely known. We may merely indicate some groups.

Mylostoma and *Dinomylostoma*, together with the allied forms, should certainly compose a separate order, Mylostomida.

Titanichthys must be accorded the same treatment.

Homostius and *Heterostius*, which, according to the present writer's latest investigations, are some of the most highly specialized Arthrodires known, should very probably be considered as representatives of two independent orders.

Coming back to the first family of the order Coccosteida, we may give the following definition:

Family COCCOSTEIDAE

Arthrodira with armor composed of relatively thick, solid plates. The eyes were small, the sclerotic rings are broad. The sub-orbital is large, the post-sub-orbital small. The gnathal elements are relatively short, broad and thick. The side plates of the head are well separated from the head roof.

Genus COCCOSTEUS Ag.

Relatively small forms, with tuberculate armor plates. The infero-gnathal is without the large front tooth, but with well developed symphysial teeth. Median-dorsal with a medium sized keel, long, running into a point. On its surface, impressions of the sensory canals. Two sensory canals on the antero-dorso-lateral and on the antero-ventro-lateral. The spinal in the form of a small spine-like process.

Genus DINICHTHYS Nwb.

Relatively large forms, with almost non-tuberculate armor plates. The infero-gnathal with a well developed front tooth. The symphysial teeth if developed, small. Median-dorsal with large and massive keel, short and roundish. No sensory canals on *MD* and *AVL*. A single canal on *ADL*. The spinal is in the form of a small curved plate.

As seen from the following table, there have been described in all, 27 different species of *Dinichthys*. Among them only a few are really well known. The majority have as a type specimen a fragment of jaws or of the armor plates. To make a satisfactory definition of all these forms, a revision of all the old material and descriptions would be necessary. This would require a long and careful study, which is not the object of this paper.

THE TWENTY-SEVEN DIFFERENT SPECIES OF *DINICHTHYS*

	NAME	DETERMINED BY	YEAR	DETERMINED AS	REDETERMINED AS	REDETERMINED AS SYNONYM OF	BY	YEAR
1.	*Dinichthys herzeri*	Newberry	1868					
2.	*Dinichthys terrelli*	Newberry	1874					
	(*Dinichthys minor*)	Newberry	1878	*Dinichthys minor*	*Brachygnathus minor*		Hussakof	1909
3.	*Dinichthys eifeliensis*	Kayser	1880					
4.	*Dinichthys ringebergi*	Ringeberg	1884	*Dinichthys minor*	*Dinichthys ringebergi*		Newberry	1884
5.	*Dinichthys newberry*	Clarke J. M.	1885					
	(*Dinichthys gouldi*)	Newberry	1885	*Dinichthys gouldi*	*Stenognathus gouldi*		Hussakof	1908
	(*Dinichthys corrugatus*)	Newberry	1885	*Dinichthys corrugatus*	*Stenognathus gouldi*		Hussakof	1908
6.	*Dinichthys tuberculatus*	Newberry	1888			*Dinichthys pustulosus*		
7.	*Dinichthys curtus*	Newberry	1888					
8.	*Dinichthys intermedius*	Newberry	1889					
9.	*Dinichthys praecursor*	Newberry	1889			*Dinichthys tuberculatus*	Eastman	1897
10.	*Dinichthys pustulosus*	Newberry	1892			*Dinichthys tuberculatus*		
11.	*Dinichthys clarki*	Claypole	1892	*Gorgonichthys clarki*	*Dinichthys clarki*		Eastman	1900
12.	*Dinichthys lincolni*	Claypole	1893					
	(*Dinichthys gracilis*)	Claypole	1893	*Dinicthys gracilis*	*Stenognathus gouldi*		Hussakof	1911
13.	*Dinichthys canadensis*	Claypole	1893					
14.	*Dinichthys holmodeus*	Claypole	1893	*Coccosteus holmodeus*	*Dinichthys holmodeus*		Eastman	1900
15.	*Dinichthys prentis-clarki*	Claypole	1896					
16.	*Dinichthys trautscholdi*	Trautschold	1880	*Coccosteus megalopteryx*	*Dinichthys trautscholdi*		Eastman	1897
17.	*Dinichthys livonicus*	Pander	1857	*Coccosteus* aus Livland	*Dinichthys livonicus*		Eastman	1897
	(*Dinichthys kepleri*)	Claypole	1897			*Dinichthys herzeri*	Eastman	1900
18.	*Dinichthys pustulosus*	Eastman	1897					
19.	*Dinichthys bohemicus*	Barrand	1872	*Asterolepis bohemicus*	*Dinichthys bohemicus*		Eastman	1897
20.	*Dinichthys pelmensis*	Eastman	1897					
21.	*Dinichthys bulla*	Jaekel	1906	*Pachosteus bulla*	*Dinichthus bulla*		Eastman	1917
	(*Dinichthys dolichocephalus*)	Eastman	1907	*Dinichthys dolichocephalus*	*Stenognathus dolichocephalus*		Hussakof & Bryant	1918
22.	*Dinichthys subgracilis*	Branson	1911					
23.	*Dinichthys rowleyi*	Branson	1914					
24.	*Dinichthys missouriensis*	Branson	1914					
25.	*Dinichthys magnificus*	Hussakof & Bryant	1918					
26.	*Dinichthys tenuideus*	Hussakof & Bryant	1918					
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PLATE I

THE STRUCTURE OF *DINICHTHYS*

PLATE I

OUTSIDE VIEW OF THE HEAD ROOF OF *DINICHTHYS INTERMEDIUS* Nwb.

Figure 1

American Museum of Natural History, Specimen No. 32.

Compare with Text figure 12.

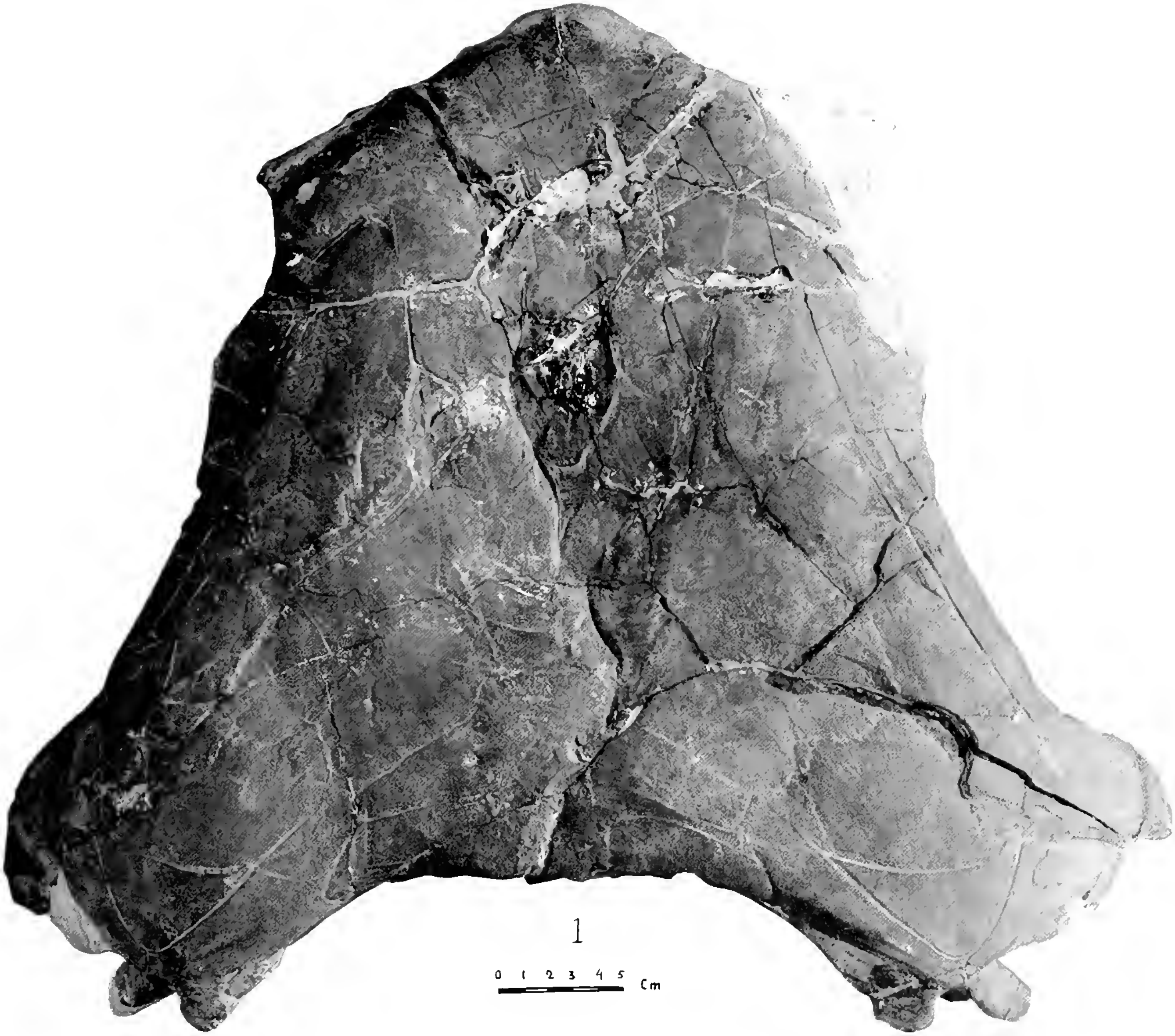

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PLATE II

THE STRUCTURE OF *DINICHTHYS*

PLATE II

INSIDE VIEW OF THE HEAD ROOF OF *DINICHTHYS INTERMEDIUS* Nwb.

Figure 2

American Museum of Natural History, No. 32.

Compare with Text figure 13.

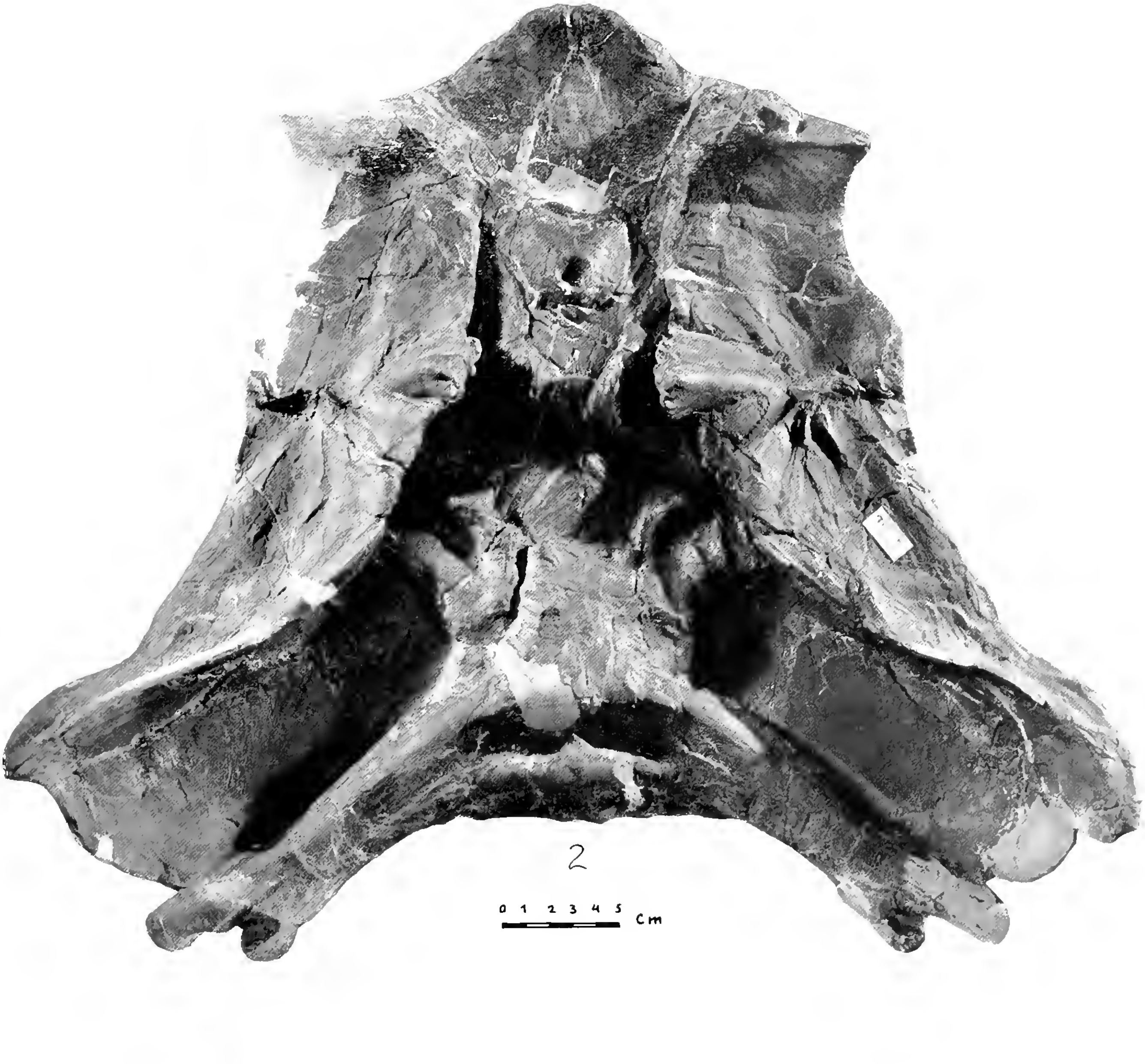

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PLATE III

THE STRUCTURE OF *DINICHTHYS*

PLATE III

THE STRUCTURE OF VARIOUS PARTS OF THE HEAD ROOF

Fig. 3 Plaster cast of the post-nasal plate of *Dinichthys* (?) *intermedius* Nwb. seen from the outside.

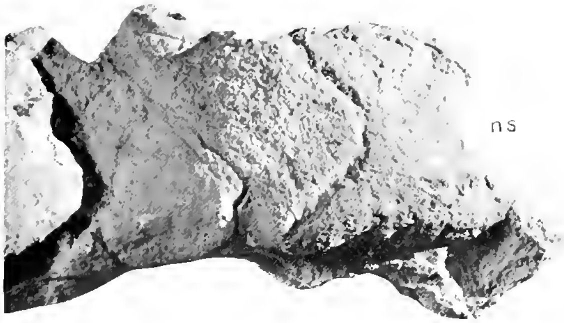
Fig. 4. The same viewed from the inside.
SO, top of sub-orbital, *ns*, nasal impression.

Fig. 5. Inside view of nearly complete sclerotic ring of *Dinichthys* sp.
American Museum of Natural History, No. 5071G.

Fig. 6. Outside view of the post-nasal plate of *Dinichthys terrelli* Nwb.
ns, nostril impression, *pto*, process touching post-orbital plate.
American Museum of Natural History, No. 3562.

Fig. 7. Left hind corner of the head roof of *Dinichthys* sp.
M, marginal plate; *PM*, post-marginal plate; *EB*, corner of externo-basal plate.

All figures in natural size.



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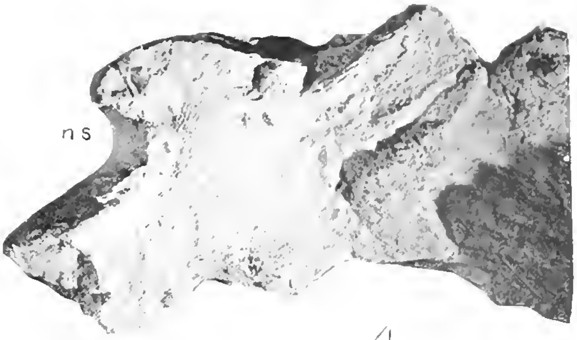

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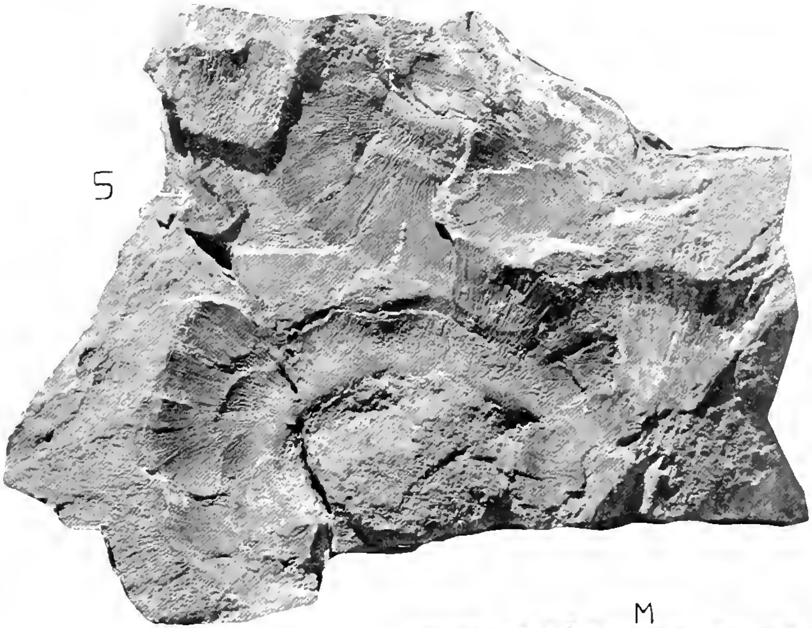

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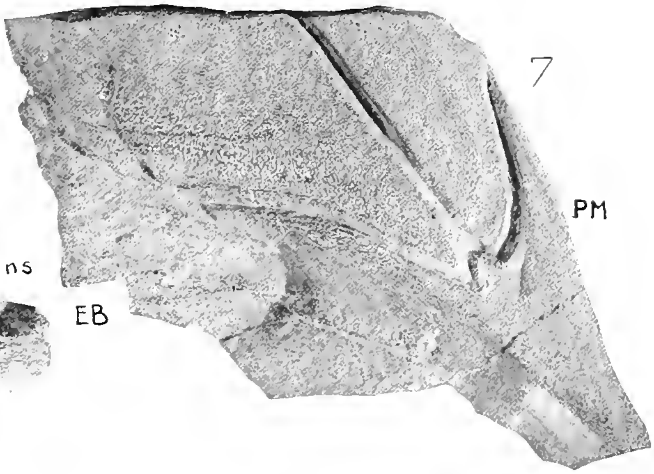


PLATE IV

THE STRUCTURE OF *DINICHTHYS*

PLATE IV

THE POST-SUB-ORBITAL PLATE OF *DINICHTHYS TERRELLI* Newb.

Fig. 8. A photographic view of the inside of this plate.

Fig. 9. A photographic view of the outside of the same plate.

Compare with Text-figure 26.

Both figures in natural size.

8

9

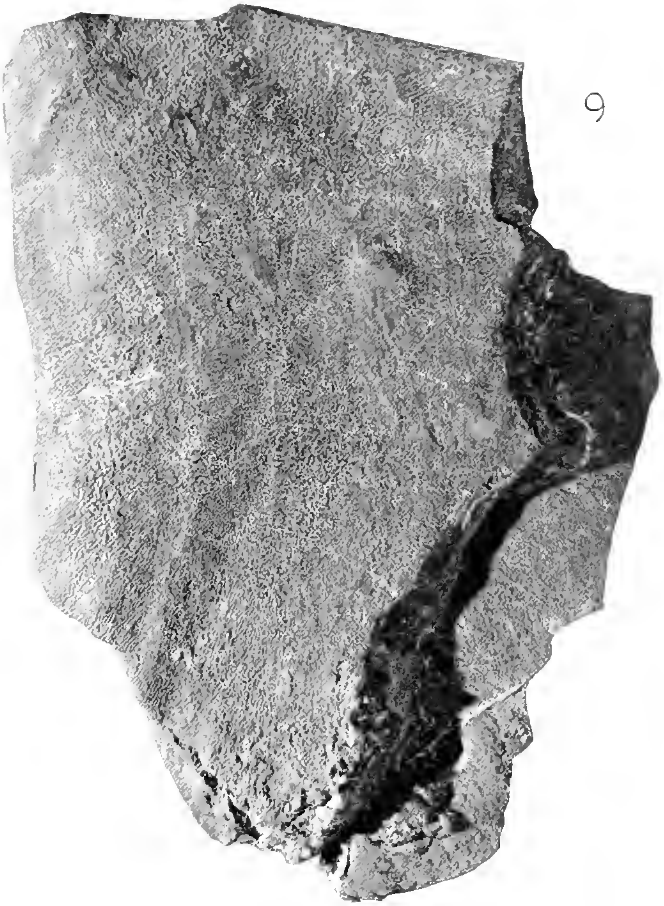


PLATE V

THE STRUCTURE OF *DINICHTHYS*

PLATE V

PHOTOMICROGRAPHS OF SECTIONS OF THE GNATHAL ELEMENTS

Fig. 10. A section of the postero-supra-gnathal plate.

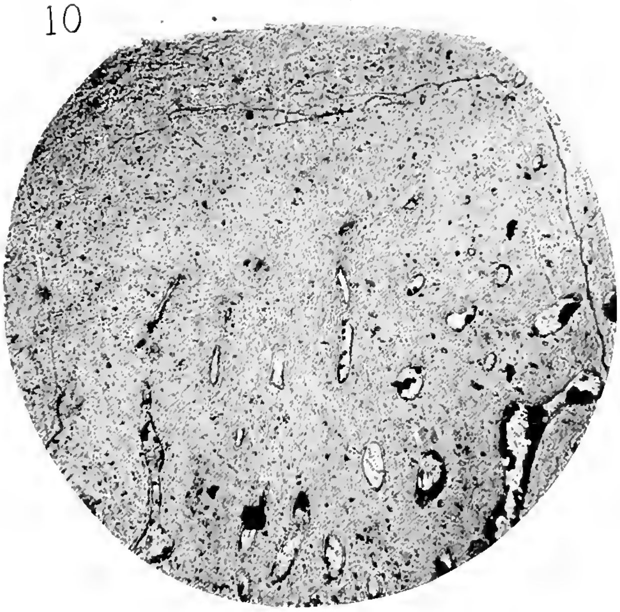
Fig. 11. A section of the same plate under higher magnification. The nearly straight line along the top represents the cutting edge.

Fig. 12. A section through the "pick" of the infero-gnathal plate.

Fig. 13. A more highly magnified section from the same plate.

Figures 1 and 3, ×32; 2 and 4, ×110.

10



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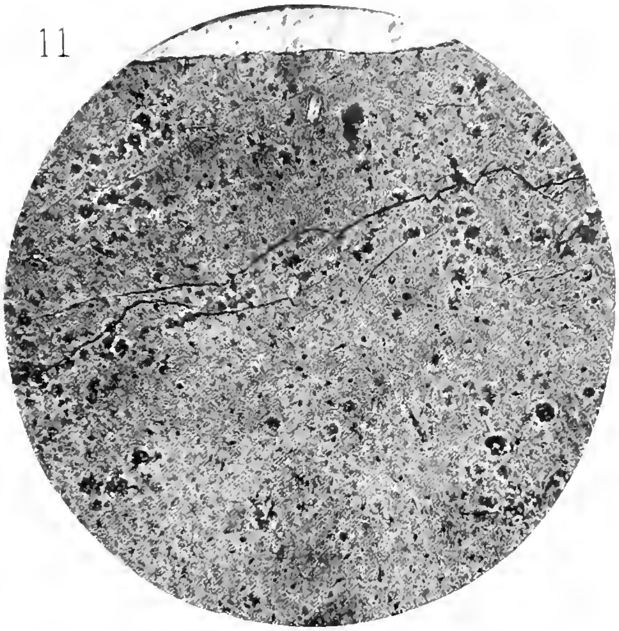

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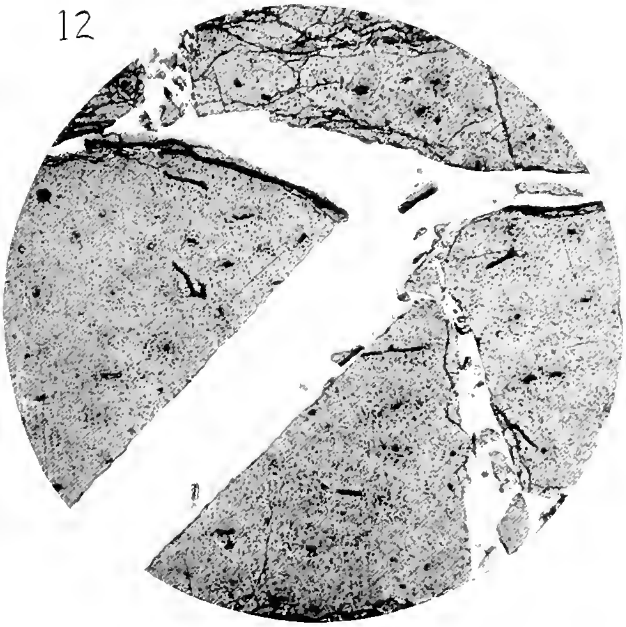

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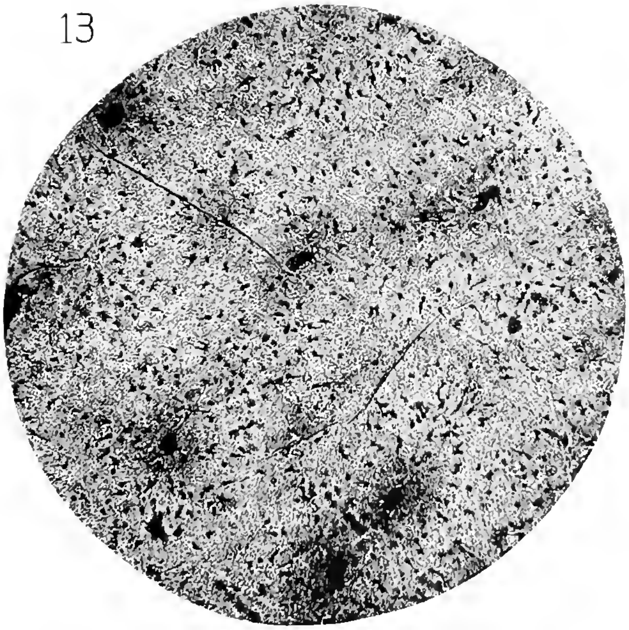


PLATE VI

THE STRUCTURE OF *DINICHTHYS*

PLATE VI

PHOTOMICROGRAPHS OF SECTIONS OF GNATHAL AND CARAPACE PLATES

Fig. 14. A section through the "pick" of the antero-supra-gnathal plate.

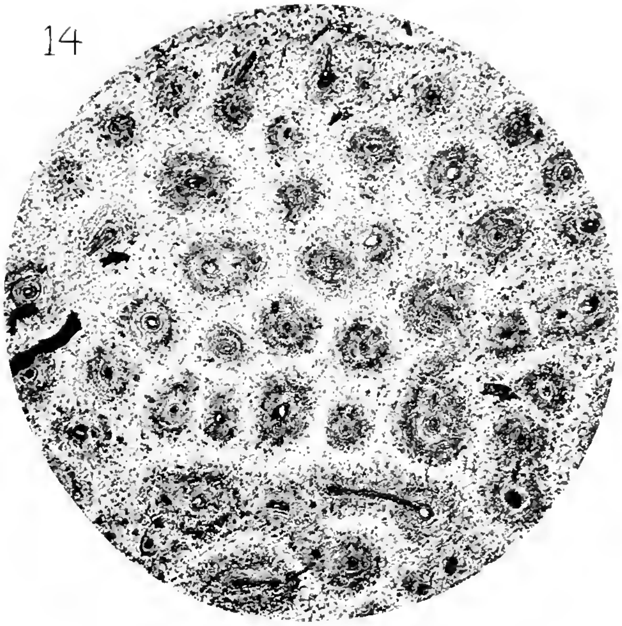
Fig. 15. A more highly magnified section of the same plate.

Fig. 16. A section through the middle part of the intero lateral plate.

Fig. 17. A section of the same plate under higher magnification.

Figures 1 and 3, × 32; Figures 2 and 4, × 110.

14



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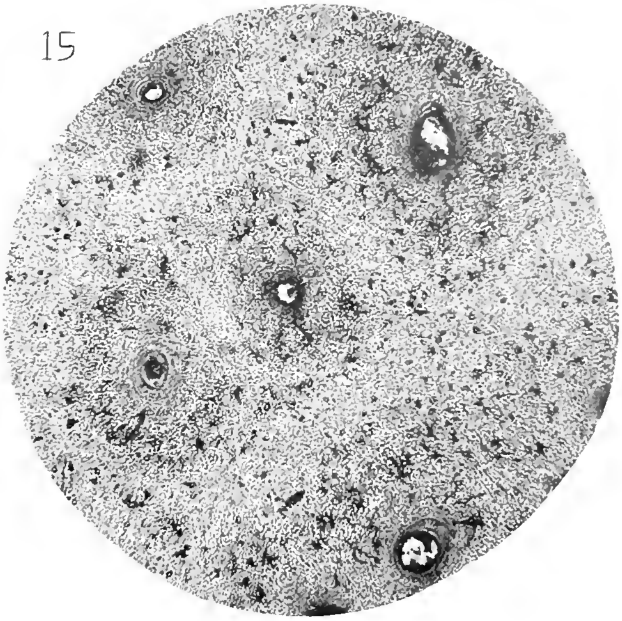

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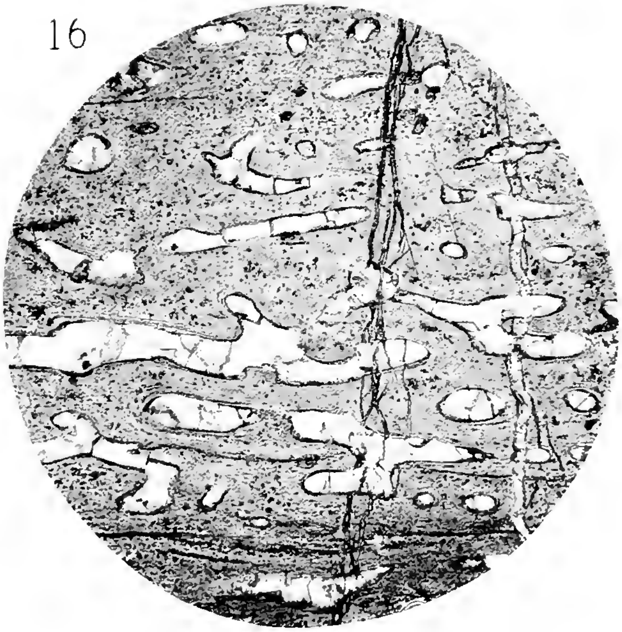

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PLATE VII

THE STRUCTURE OF *DINICHTHYS*

PLATE VII

THE INFERO-GNATHAL AND THE POSTERO-INFERO-GNATHAL PLATES OF *DINICHTHYS INTERMEDIUS* Nwb.

From a specimen in the American Museum of Natural History.

Fig. 18. The left plate from the outside.
Fig. 19. The right plate from the inside.

Compare with Text figures 30 and 31.

18

19

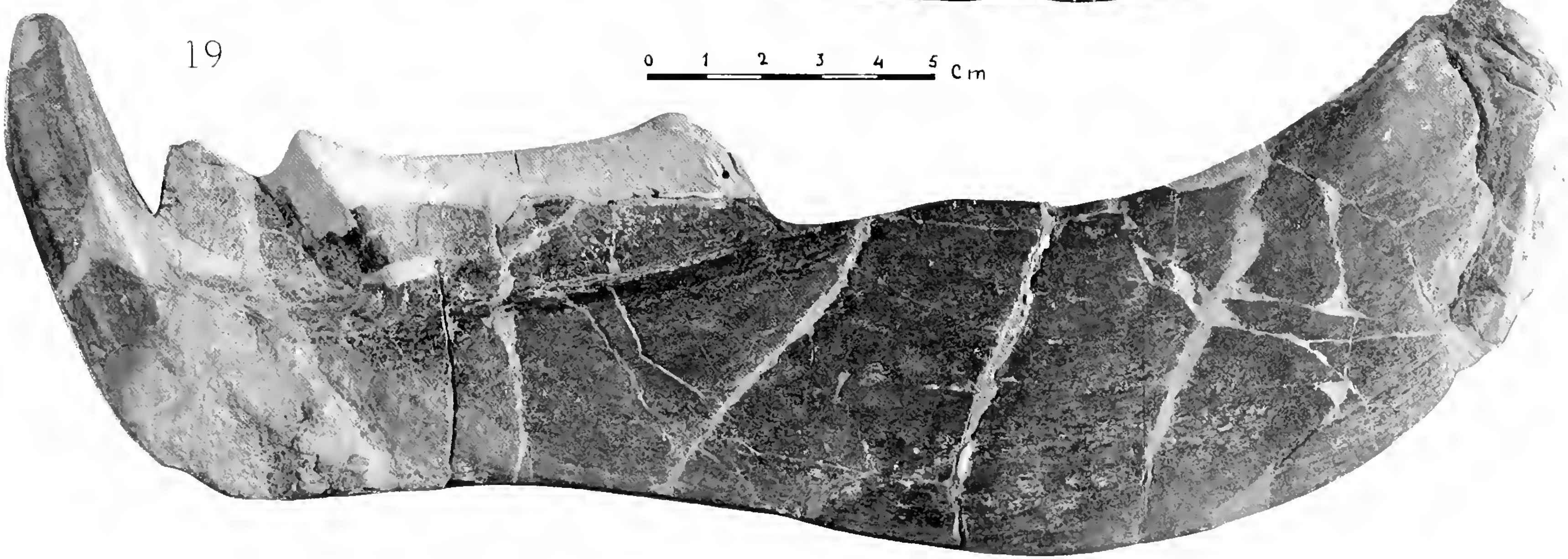


PLATE VIII

THE STRUCTURE OF *DINICHTHYS*

PLATE VIII

THE INTERO-LATERAL PLATES OF *DINICHTHYS CURTUS* Nwb.

American Museum of Natural History, No. 7895.

Fig. 20. This intero-lateral plate seen from the outside.

Fig. 21. The same from the inside.

Compare with Text-figure 81.

THE INTERO-LATERAL PLATE OF *DINICHTHYS TERRELLI* Nwb.

From a specimen in the American Museum of Natural History.

Fig. 22. A part of the outside of this plate showing the superficial sculpture.

Figures 1 and 2, natural size; figure 3, ×3.

20

21

22

PLATE IX

THE STRUCTURE OF *DINICHTHYS*

PLATE IX

THE STRUCTURE OF THE SPINAL PLATES

Fig. 23. External aspect of the left plate of *Dinichthys intermedius* Nwb.

Fig. 24. The right plate seen from the outside.

Fig. 25. The left plate from the inside.

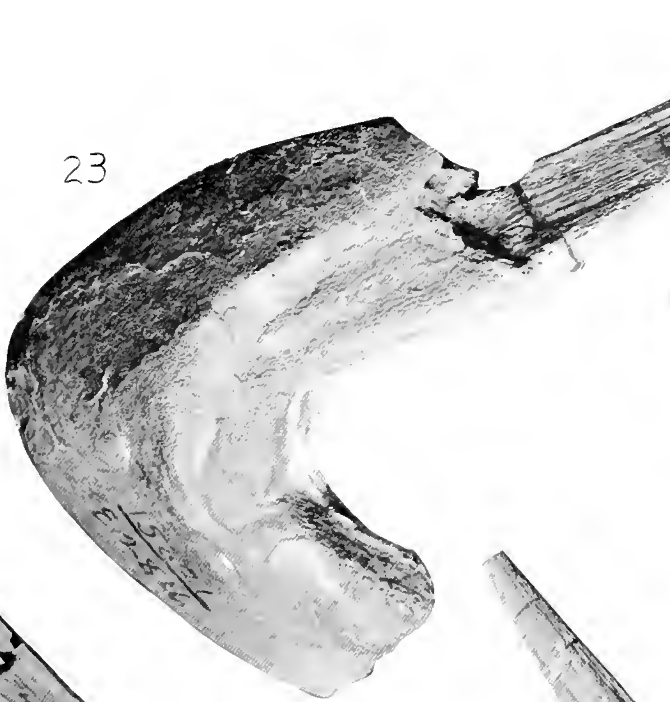
Buffalo Museum, No. 15261 E2816.

Fig. 26. Outside view of the right plate of *Dinichthys curtus* Nwb.

American Museum of Natural History, No. 8795.

All figures natural size.

23



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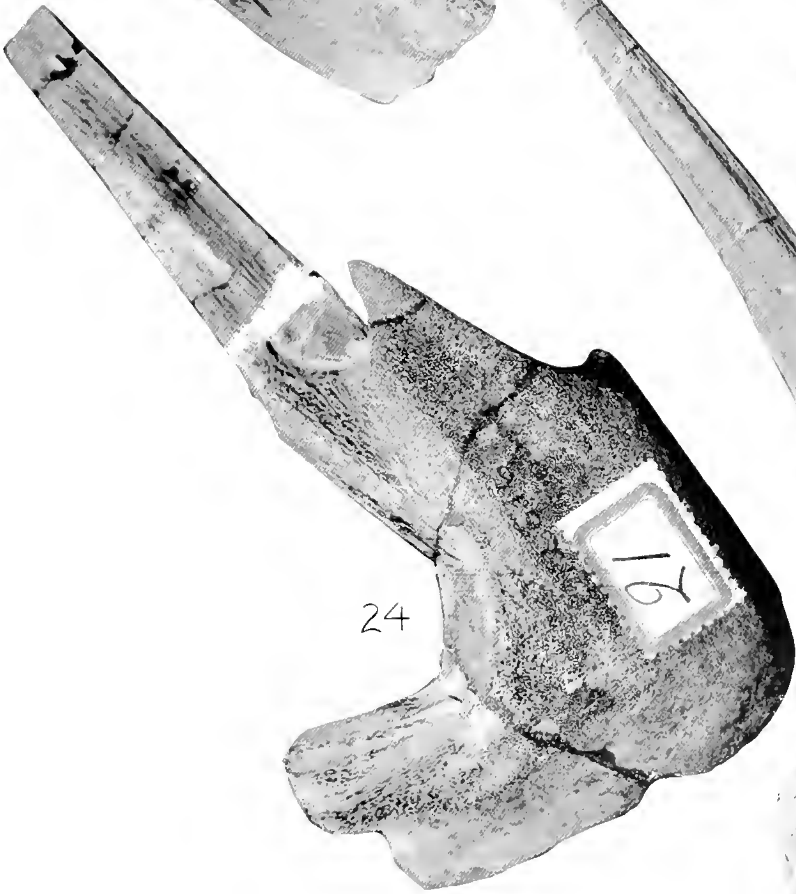

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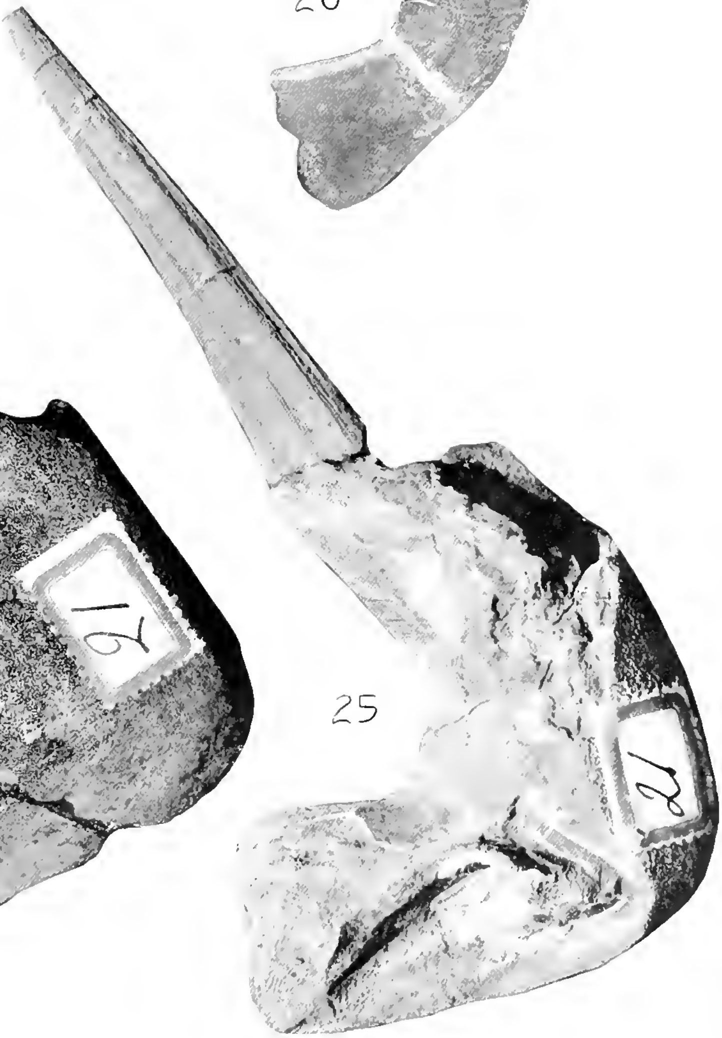

THE

BASHFORD DEAN MEMORIAL VOLUME

ARCHAIC FISHES

Edited By
EUGENE WILLIS GUDGER

ARTICLE V

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NEW YORK

PUBLISHED BY ORDER OF THE TRUSTEES

Issued November 23, 1933

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CHLAMYDOSELACHUS ANGUINEUS

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INTRODUCTION

Considering the primitive position of *Chlamydoselachus* among vertebrates and the widespread interest aroused by the first published description, it is surprising that no comprehensive account of the natural history of this shark has been published in all the years since Samuel Garman (1884.1 and 1885.2) first figured and described it.

Because the fish has been rarely taken outside of Japanese waters, and then only in scattered localities, there have been few opportunities other than in Japan for any study of its natural history. Unfortunately no Japanese ichthyologist has yet undertaken this task. Had Dr. Bashford Dean lived, he would presumably have prefaced his contribution to the embryology of *Chlamydoselachus* with such an introduction, using mainly the data obtained at first hand during his sojourns in Japan in 1900–1901 and again in 1905—data recorded only sparingly in his notebooks but held doubtless in his capacious memory. The writing of such a natural history would have been a task for which he was peculiarly fitted because of his wide experience as collector and student of primitive fishes. But unfortunately the only article Doctor Dean found time to publish on *Chlamydoselachus* was the abstract of a preliminary report (1903) read before the American Society of Zoologists. As it is, the known facts about *Chlamydoselachus* are widely scattered through the literature from 1881 to 1931.

Preliminary to our study of the external development of this fish, based on Doctor Dean's drawings, we have thought it well to bring together in orderly form this widely scattered knowledge of *Chlamydoselachus* as a background and foundation for our projected work. We have tried from our studies of the literature to synthesize the natural history of *Chlamydoselachus*—the fish and its life in nature. As the reader will see, the data have been continually checked against Doctor Dean's notes and against all of our available material. This material consists of three adults and six large embryos in the collections of the American Museum, and in addition a finely preserved adult head, kindly loaned by Prof. J. H. McGregor, from the zoological cabinet of Columbia University. All these specimens were brought by Doctor Dean from Japan or sent from Misaki to him. These specimens have been of the greatest service to us, for while we have checked each published description and statement against every other one, in every possible case the fishes themselves have been the ultimate source of our information.

DISCOVERY OF *CHLAMYDOSELACHUS ANGUINEUS*

It has long been erroneously held that the late Samuel Garman was the first scientific man to see and describe (1884.1) the "Japanese frilled shark." However, in going through the literature, we have found that L. Döderlein brought to Europe a large collection of Japanese fishes secured in the years 1879 to 1881. These were described by Steindachner and Döderlein,[1] but they nowhere mention a fish that can be identified with *Chlamydoselachus.* In the "Einleitung," Döderlein says the most important part of his collection was deposited "in der K. K. zoologischen Hofmuseums [Wien]."

At the end of the "Einleitung" there is a widely set-off paragraph signed by Steindachner, in which he says that he took over Döderlein's collection and the editorship of his manuscript. But there is still no trace of *Chlamydoselachus.* However, Röse (1895), in the introduction to his paper on the development of the teeth of *Chlamydoselachus*, says that Döderlein gave him (Röse) an embryo, which was taken from the body (*Leibe*) of one of two specimens obtained by Döderlein from Tokyo Bay in 1881. Röse says:

> Late in the year 1882, Döderlein described the two adult animals and entrusted the handwritten description to Hofrath Steindachner in Vienna, who was to look after its publication and who received along with many other rare fishes the two specimens of *Chlamydoselachus* from Professor Döderlein. Döderlein's description has not been published and since then [1882] nothing has been heard of the two *Chlamydoselachus* in Vienna.

From the above it is clear that the credit for the discovery of this fish belongs to Döderlein. He, and even more Steindachner, must have known that it was a great ichthyological rarity. Why one, or both, did not publish this description at once is an unsolved mystery. Our first thought was that the specimens might have been destroyed or lost, but we find that Collett (1897.1, p. 9), who has listed all the specimens of *Chlamydoselachus* in European museums, records these first of all as "Mus. Vienna, 2 specimens, Tokio, 1881." Collett does not say that this information came from Vienna (he states his authority for counts in other museums), and since he quotes Röse, it may be that he got the data from him. That these specimens are still in the Naturhistorisches Museum at Vienna, we are informed in a recent letter from Dr. Victor Pietschmann.

Since Döderlein's description was never published, the credit for first naming *Chlamydoselachus* and publishing a description of it must go to the late Samuel Garman, curator of fishes in the Museum of Comparative Zoology of Harvard College, who, in two articles published in 1884, first made this rare and extraordinary fish known to the scientific world. These descriptions were based on an adult female specimen, 1511 mm. (59.5 in.) long, "purchased by the Museum of Comparative Zoology from Professor H. A. Ward, who gives Japan as the locality." Garman published a figure of this strange fish, and, since this is the earliest known, it is reproduced herein as our Text-figure 1. As will be seen later, the tail of this fish is defective.

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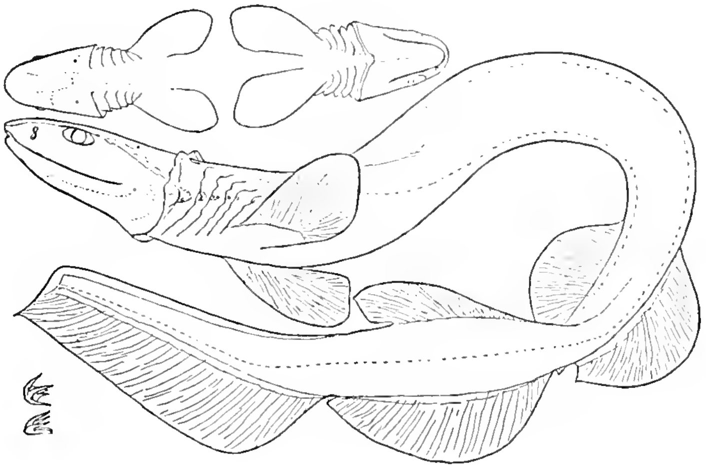
[1] Steindachner, Franz, und Döderlein, Ludwig. Beiträge zur Kenntniss der Fische Japans (I). *Denkschriften K. Akademie Wissenschaften Wien*, 1883, vol. 47, (Einleitung, pp. 211-217).

GEOGRAPHICAL DISTRIBUTION

In bringing together the scattered data setting forth the distribution of the rare shark, *Chlamydoselachus*, it seems best to present the records for each region in chronological order. These regions are few outside of Japan.

IN JAPANESE WATERS

As we have seen, Döderlein's two specimens came from Tokyo Bay in 1881, but Garman's fish (1884) is merely labelled "habitat, Japanese seas." For many years thereafter, these waters were the sole source of this rare and remarkable shark, and indeed to this day, so far as we have been able to ascertain, with one exception all the specimens upon which anatomical work has been done have come from Japan.



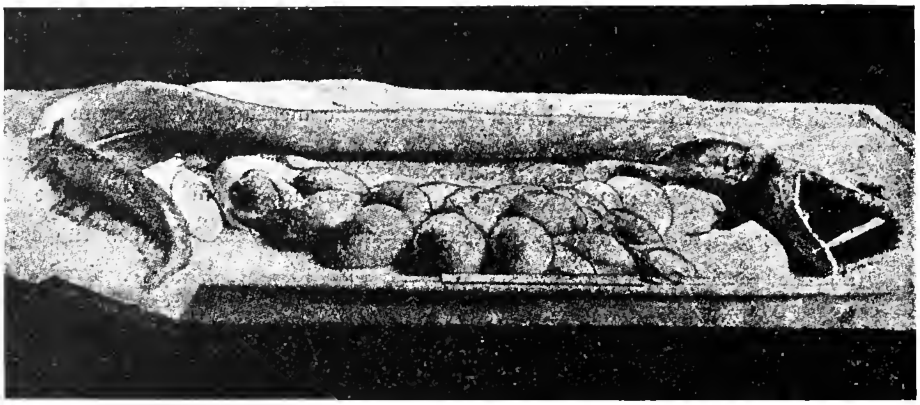
Text-figure 1
The first published figure of *Chlamydoselachus anguineus*. In this drawing, the head and tail are shown in lateral view, but the body is twisted in order to give a dorsal view of both pelvic fins and a latero-ventral view of both pectoral fins. The tail is abnormal. In separate drawings, the head is portrayed in both dorsal and ventral views. A tooth is shown in oblique front and lateral aspects. The size is that of the original figure.
After Garman, 1884.1, .2.

In this connection it may be well to state that, although the specimen described by Garman was an eviscerated female, he has given in the papers above mentioned and in later publications (all of which are listed in our bibliography) the most comprehensive account of the fundamental structures of the fish, and in our judgment a sounder discussion of its affinities than any writer who has followed him. These were based not only on the fish above mentioned but on a later specimen (a female 1345 mm., 53 in. long) brought to the Museum of Comparative Zoology from Japan in 1887 by a Japanese graduate student, Saitaro Goto. From this specimen, Garman corrected his error about the tail and confirmed certain unusual structures described from his first fish. Garman had two drawings made of his first specimen. His first (1884.1) was the outline reproduced as our Text-figure 1. His second (1885.1) was a more finished picture, as may be seen in our Figure 16, plate V. These two drawings are the first figures of *Chlamydoselachus* ever published.

The next capture of this shark was recorded by Günther in his report on the deep-sea fishes collected by the Challenger (1887). His three specimens were taken in deep water in Yeddo Bay off Tokyo. His splendid figure, probably the best today, is reproduced herein as Figure 1, plate I. This figure was drawn half-size from a fish measuring 1473 mm. (58 in.) long. This drawing shows a perfect tail ("measuring two feet"), whereas Garman's first specimen lacked the distal part of this organ.

Dean, in his "Fishes, Living and Fossil" (New York, 1895, page 87), reproduced (in a line drawing in reversed right and left) Günther's excellent figure. Of it Dean wrote with his usual discernment:

> *Chlamydoselache* [Günther's name] derives its great interest from its late discovery (1884, Garman), rareness, and Pleuracanthid type of teeth; but now that it has been taken in numbers—comparatively—in deep water [of Tokyo Bay], one is inclined to believe that many of its 'primitive' characters, like its eel-like shape, may partly be due to its environment: its resemblance, moreover, to the Pleuracanth has since been found to be of a superficial character.



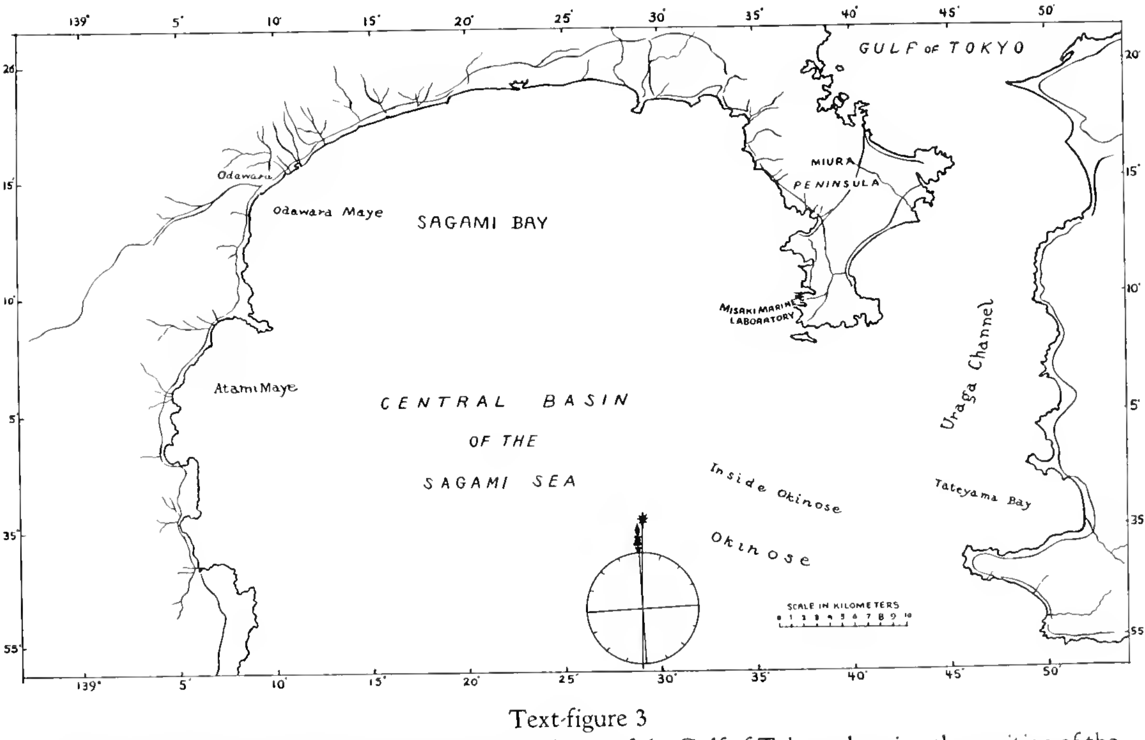
Text-figure 2
A female *Chlamydoselachus* with the eggs which have been cut out of her body.
This figure has been carefully retouched to make the outlines clearer.
After Nishikawa, 1898.

Passing by Röse (1895), whose 340-mm. embryo was taken from the body of one of Döderlein's fishes obtained at Tokyo in 1881, we come to Nishikawa (1898), who figured (Text-figure 2 herein) a female specimen of *Chlamydoselachus* with about twelve eggs taken from her body. He noted that this shark seemed to be confined to the Sea of Sagami, but specific localities were not designated save that it was occasionally brought to the Tokyo market from the east side of the Bay of Tokyo, and that it was sometimes (though rarely) taken by the fishermen of Misaki. He specifically stated that he had seven female fish with eggs and it would seem from the context that he had several other fish, either non-gravid females or males. Goto, who edited Nishikawa's article, spoke of "a specimen brought some time ago to my laboratory."

At this time Dean was in the full swing of his work on the morphology of the early fossil fishes, and on the embryology of the Cyclostomes and Ganoids, primitive vertebrates, for whose eggs and embryos he was searching far and wide. It seems to us probable that the publication of Nishikawa's paper on *Chlamydoselachus* turned Dean's attention to this primitive shark and led him to go to Japan to study the fish.

Dean's notes do not clearly indicate when all his specimens were taken, but fortunately Mrs. Dean was with him in Japan, and she tells us that they were at Misaki (on the peninsula between Sagami and Tokyo Bays) from July to October 1900, and from March to July 1901. They were not there all the time; some months they were in residence continuously, some months intermittently. In 1905, they were again at Misaki, from June to October, not steadily, but for the most part as on the first trip. Furthermore, fishing for *Chlamydoselachus* was carried on for Dean during his absences; thus in 1902, 1903, 1905 and 1906, as we ascertain from his notes.

Two articles by Dean, describing his first visit to Japan, cast light upon his methods of obtaining this rare material. In the second (1904), he speaks thus: "Happily, too, the collector of the station [Misaki], Kuma Aoki, is an ex-fisherman, for, knowing the townspeople, he serves as a diplomat, suggesting regions which should be fished, and often accompanying the expeditions." Further on he speaks of Kuma's remarkable knowledge of the fishing grounds. In the earlier article (1901), he speaks of Misaki as an excellent fishing ground for *Chlamydoselachus*, and then he concludes: "Professor Mitsukuri



Text-figure 3

A map of the Sagami Sea, the Miura Peninsula, and part of the Gulf of Tokyo, showing the position of the Misaki Laboratory in which Doctor Dean worked, and the waters from which his specimens of *Chlamydoselachus* were obtained.

From an old chart compiled by Prof. I. Ijama.

arranged that should by any chance specimens escape me at Misaki, they should be captured for me a little later in the fish market in Tokyo. In this way I finally secured a number of the much prized embryos."

That the reader may get a clear idea of the location of the Misaki Biological Station, where Dean resided while studying *Chlamydoselachus*, and of the waters from which his specimens were obtained, we give here in mere outline as Text-figure 3 a reproduction of a map drawn by Prof. I. Ijama and found among Dean's materials.

We cannot state exactly how many specimens Dean obtained while in Japan, nor how many were taken for him during his absences. However, in his notes we find an undated table listing twenty-one adult specimens of both sexes. Another list (written, we believe, by the Japanese collector) records ten fish, of which some were taken in 1902, some in April 1903, and others in February and April 1905—all while Dean was in America. Elsewhere, Dean lists three specimens taken in 1905—apparently not the same as the above. Among these notes is a letter from S. Fujita recording the capture in 1906 of a large female with five embryos, and speaking of the sending of embryonic material to Dean in America.

Scattered throughout Dean's notebook are various dated notes recording the capture of specimens with embryos or their purchase in the market at Tokyo. Thus, in his handwriting, we find this interesting record: "1905, Kuma fished for about 5 weeks in the best ground off Odawara [on the west side of Sagami Bay]—special tackle—squid bait,—depth from 300–600 fathoms. Took 3 fish,—several *Heptanchus*." The internal evidence indicates that these three fish are undoubtedly the three specimens of *Chlamydoselachus* listed in the notebook and dated 1905, with the notation "Odawara."

We find this man Kuma named in Dean's notes in several places. Knowing Dean's habits when in the pursuit of rare embryological material, we conclude that Kuma was in Dean's employ. Thus in another place we find this note: "Kuma, 300–400 fathoms: average 350 *hiro*[2] [1650 feet]—up to 500 [2500 feet]. 18 days fishing, two *Rabuka* [native name for *Chlamydoselachus*], Odawara, to Oct. 1, 1905."

Thus we cannot be sure how many specimens were obtained by Dean, but eliminating what we believe to be entries referring to the same fish, we find pretty definite proof that he obtained 39 specimens of both sexes. Some of these entries may possibly be duplicates. On the other hand, from Fujita's letter it is plain that other unlisted specimens were taken, their eggs and embryos cut out and sent to Dean. It is of course unfortunate that we do not have more complete records of Dean's specimens; but we believe that the list of 39 is at least not an exaggeration. He himself (1904, p. 204) says of Misaki: "In the course of a year the neighborhood yields about a dozen specimens of the frilled shark, *Chlamydoselachus*." It should be recorded that one of Dean's fish, a female, measured 1960 mm. (77.1 in., 6 ft. 5.1 in.) "over all." This is the largest *Chlamydoselachus* of which there is any record.

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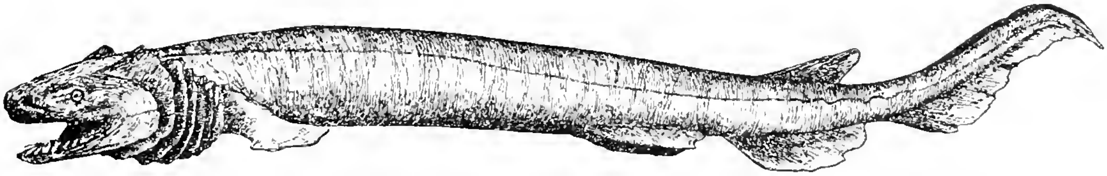
[2] A *hiro*, the Japanese fathom, is five feet, the fisherman's measure of depth taken on a fishing line held in the hands stretched out horizontally.

Our next reference to the taking of *Chlamydoselachus* in Japanese waters is from Doflein's book of travels in the Orient (1906). He stated that "On the Odawara ground, the rare *Chlamydoselache anguinea* is caught in winter, that shark with the three-pointed teeth whose nearest kin are known to be of the Cretaceous period." This matter-of-fact statement would indicate that, thanks to Dean's employment of Kuma and other fishermen, the fish was becoming well known. Doflein's excellent figure is reproduced herein as Figure 2, plate I.

There is before us a price list of 895 different species of Japanese fishes, issued by Alan Owston of Yokohama in 1905. In this he quoted "*Chlamydoselachus anguineus*, 100-200 shillings" ($25–$50). From this, one may judge of the relative facility with which this rare fish could be procured 28 years ago. In fact it would seem that Owston and Japanese dealers carried on a regular business in handling specimens of *Chlamydoselachus*, for in every article but one quoted herein, dealing with the internal structure of this shark or with its embryos, if any statement is made as to the source of the material, Japan is always named.



Text-figure 4

A drawing of the mounted "Krausenhai" in the Senckenberg Museum, Frankfurt am Main.

After Mertens, 1921.

Furthermore, Japan has been the source of the greatest number of museum specimens, mounted or unmounted, as will be shown in tables later. Of the former, the only one figured, so far as we know, is in the Senckenberg Museum at Frankfurt am Main. This has been described by Mertens (1921). That it may be compared with the other figures, his drawing is reproduced herein as Text-figure 4. This specimen is a female and measures about 1585 mm. (62.4 in.).

Since the above was written, the American Museum has received from the Japanese Fisheries Society volume I of an elaborate work, "Illustrations of Japanese Aquatic Plants and Animals" by Kumatarô Ito, published in 1931. On Pl. IV, fig. 3, of this volume, *Chlamydoselachus* is represented in color. This illustration is reproduced herein (from a photograph) as our Text-figure 5. Our discussion and criticism of this figure will be found later in this article in sections dealing with the various structures. The short descriptive text gives no new data whatever, and we are not able to state whether this figure was made from a fresh or from a preserved specimen; possibly it was copied from some other drawing.

Since this article went to press, Dr. E. Grace White, of Wilson College, Chambersburg, Pennsylvania, has returned from the Misaki station, bringing to the Museum an adult specimen of *Chlamydoselachus* captured by Kuma. This, like our specimens, is a female. Its total length is about 1398 mm. (55 in.). It came to our attention too late to receive more than incidental mention in various sections in this paper.

As already stated, Japan has been in the past and is today the chief, and indeed the only dependable, source of supply of the frilled shark; nevertheless, as we shall now relate, this shark has been taken from waters other than Japanese.

Text-figure 5
The Japanese frilled shark, *Chlamydoselachus anguineus*.
From a drawing in color by Ito, 1931.

AT FUNCHAL, MADEIRA

The first capture outside of Japanese waters was recorded by Collett (1890). This specimen, an eviscerated young female 610 mm. (24 in.) in total length, was found in a small collection of fishes obtained (mainly by purchase from the fishermen) at Funchal, Madeira, by the Prince of Monaco, in March, 1889. Unfortunately there is no record of the depth from which this *Chlamydoselachus* was taken. It is notable as being the smallest specimen ever captured.

Collett stated that its length (610 mm., 24 in.) is approximate, and that it is preserved in the collections of the Prince of Monaco. In Roule's paper (1912) on the sharks preserved in the Musée Océanographique (at Monaco), two specimens of *Chlamydoselachus* are listed. The source of one of these will be satisfactorily traced later, but of the other Roule said "A female, length, 570 mm., source unknown." Despite the difference (40 mm., 1.5 in.) in length, we consider this to be the Madeiran specimen. This disparity in length may be explained by shrinkage due to long immersion (22 years) in alcohol and by inaccurate measurement. However, the matter of greatest interest in connection with this specimen is that its capture at Funchal demonstrated that *Chlamydoselachus* is not confined to Japanese waters.

ON THE ARCTIC COAST OF NORWAY

In 1897 Collett again had an opportunity to describe a *Chlamydoselachus* from waters other than those of Japan. This magnificent specimen, a female, was taken at a depth of 100–150 fathoms in the Varanger Fjord, on the Arctic coast of Norway, in August, 1896. It was 1910 mm. (75.4 in., 6 ft. 3.4 in.) long over all; and it is second in size only to Dean's largest fish (1960 mm.) also a female. Collett's photograph of his fish is excellent and gives such a natural representation that we have reproduced it here as Figure 3 of plate I. As our bibliography shows, Collett has referred to this capture and has described this fish in various publications (1897.1. 1897.2, 1905). This same specimen has been described also by Grieg in a popular paper published in 1897. His figure, however, is a poor reproduction of Günther's (1887) drawing (see our Figure 1, plate I). A year later (1898) Palmen published what is practically a review of Collett's account. The fish, partly dissected, is preserved in the zoological museum of Christiania (Oslo) University.

IN THE BAY OF BISCAY

In 1914 Pellegrin and Loppé made known the capture in the Gulf of Gascony near Rochelle of a large specimen 1490 mm. (58.75 in.) long over all. This fish (sex not noted) was brought in fresh to the Muséum Fleuriau at Rochelle, and a mount was made of it. The depth at which it was taken was not ascertained, but the authors infer that it must have been not more than 200 meters since the fishing there is not done below that depth. This is the only known capture of this archaic shark in French waters.

OFF THE IBERIAN PENINSULA

There are now to be noted four captures of *Chlamydoselachus* in waters adjacent to Spain and Portugal. This is interesting because nowhere else, outside of Japanese waters, do we find so many captures recorded within waters of equal extent. The first of these was put on record by Carlos de Bragança, King of Portugal, in 1904. This specimen was a male, 920 mm. (36.25 in.) long, taken off Cezimbra, Portugal. It was caught by the fishermen on a hook and line at a depth of about 580 meters (1790 ft.) in July, 1900. According to Pellegrin and Loppé (1914), this specimen was presented by the king to the Muséum d'Histoire Naturelle in Paris, where it now is. Unfortunately no figure of it was made. It is one of the smallest specimens ever taken.

Three years later, Bolivar put on record (1907.1, .2) the capture of a frilled shark off Corunna, Spain, in the summer of 1906. The sex of this specimen is not noted in the text, but Bolivar's photograph (our Figure 4, plate I) shows that it is a male. Its length was 1140 mm., or 45 inches. No statement is made as to the depth at which it was taken, but it was captured by Sr. Estaban Bertrand some distance from land and evidently in fairly deep water. This fish was presented by Sr. Bertrand to the Prince of Monaco, in whose museum it is preserved. It is the first specimen listed by Roule (1912), who gives its length as 1240 mm. instead of 1140, the source as Corunna, and notes it as a gift but does not state the giver's name.

Last of all for Spanish waters, Luis Bertrand (1926) recorded two new specimens. Referring to the 1140-mm. male specimen listed from Corunna in 1906 by Bolivar, he stated that a female 1121 mm. (44.1 in.) long "was captured two months later at exactly the same place" by Sr. E. Bertrand. The second *Chlamydoselachus* was taken off San Sebastian on Dec. 15, 1925. This specimen was a female, 1860 mm. (73.25 in.) long. It is, then, so far as available records go, the third largest specimen ever taken. Bertrand did not give the sex, but his figure (our Figure 5, plate II, herein) made from a photograph shows it to have been a female as were the two other large fish already noted. This 1860-mm. fish is preserved in the oceanographic museum of Donostia (the Basque name for San Sebastian).

Finally, we are indebted to the splendid volume of Lozano Rey (1928) for an excellent résumé of the data on the occurrence of *Chlamydoselachus* in Iberian and surrounding waters, and also for a number of references to the literature cited in this subsection. But for his book these references would have remained unknown to us. We are also in his debt for the figure of *Chlamydoselachus* reproduced herein as Text-figure 6. Whether this is an original drawing of a Spanish fish, or whether it is a reproduction of Günther's drawing, we cannot say.

Text-figure 6
A lateral view of *Chlamydoselachus anguineus*. This is possibly drawn from Günther's lithographed figure (our Figure 1, plate I).
After Lozano Rey, 1928.

IN MOROCCAN WATERS

From the coasts of Morocco, two specimens of *Chlamydoselachus* are on record. Osorio (1909, p. 48) first made known the capture of a specimen 1600 mm. (63 in.) long. We have been unable to locate in any American library Osorio's article, the reference to which we quote from Lozano Rey (1928, p. 300). Since the title says "deep-sea fishes taken near to the Portuguese coast," we infer that the fish must have been captured in the Moroccan waters nearest to Portugal, i.e., in the Atlantic.

In 1913, Seabra recorded a 1300-mm. (51.2-in.) specimen of *Chlamydoselachus* taken by a commercial fishing boat on the coast of Morocco. Unfortunately neither the sex of the fish, the depth at which it was taken, nor the particular locality is indicated. However, since his title reads "Fishes from the Coasts of Morocco and Portugal," it is probable that this specimen also came from some point on the Atlantic coast of Morocco near to Portugal. Lozano Rey specifically says that both fish came from the coasts of Morocco.

SUMMARY OF GEOGRAPHICAL DISTRIBUTION

Up to the present, *Chlamydoselachus* has been taken in but two general regions—in Japanese waters, and in those around western Europe. The smaller number of captures, 9 in all, is from the latter region: from Norway, one specimen; from the Bay of Biscay, one; around the Iberian peninsula, four; in Moroccan waters, two; at Madeira, one. From Japan has come an apparent total of 77 specimens as recorded in our Tables I and II and listed in Doctor Dean's notebooks, plus the specimen recently brought back by Doctor

White. There is some slight uncertainty as to whether four of these sharks came from Japan, though the evidence favors this source. Of the 39 fish recorded in Doctor Dean's notebooks, 4 adults and 6 embryos are also listed in Table II. Therefore, this reduces the total number of recorded specimens from 86 to 76. Nishikawa and Goto dissected numbers of the fish, while Owston and other dealers for years supplied specimens—some of which undoubtedly are among the fish listed in Tables I and II.

In conclusion it may be said that so far as our investigations go (and we have searched the literature minutely) there are no captures on record for regions other than those listed above, and no captures in extra-Japanese waters other than those given. However, it may be noted that David G. Stead gave an oral report before the Linnaean Society of New South Wales in 1907 on the remains (a skull and about 150 vertebrae) of a ten-foot shark, which had come ashore at Port Jackson, Sydney Harbor, and which he believed to have been *Chlamydoselachus*. But the latest and fullest check-list of Australian fishes (1929) has no reference to this fish, so the identification may be considered erroneous.

As stated above, with a single exception (Collett's Norwegian specimen), all the known *Chlamydoselachus* material dissected for anatomical study has come from Japan. As will be shown later, all museum specimens, with the exception of the eastern Atlantic examples listed in European museums, have come from Japan. The eastern coast of Japan—especially Tokyo and Sagami Bays—is still the only dependable source of supply of this archaic fish.

DEPTHS AT WHICH *CHLAMYDOSELACHUS* HAS BEEN TAKEN.

Intimately connected with the matter of geographical distribution is that of the vertical distribution—the depths at which *Chlamydoselachus* has been taken. Some of these depths have been incidentally noted. In this section we have brought together all the available data.

It is well known that sharks are mainly littoral forms or surface-dwelling (pelagic) fishes out at sea. However, some sharks are deep-water forms and among these *Chlamydoselachus* undoubtedly belongs. From the structure of his specimen (especially from the small size of the spiracle), Garman, for whose fish no depths could be noted, conjectured that it was probably descended from a bottom-dwelling form. Günther noted that his specimens were taken in "deep water" in Tokyo Bay, but apparently did not have records of even approximate depths. Nishikawa (1898), who ought to have given the depths, which he probably knew, merely said "brought up from the deep." Doctor Dean's notes, made in Misaki, give us more definite information. He referred to examples from 200 fathoms and to Kuma's fishing off Odawara at "depths from 300–600 fathoms" (1800 to 3600 ft.). Elsewhere he listed specimens taken at depths of from 80 to 500 *hiro*. As explained elsewhere, a *hiro* is the Japanese measure of a fishing line held between the outstretched hands, and since the Japanese are men of rather small stature this is about five feet—their fathom. Hence these depths varied from 400 to 2500 feet.

Further, Dean in his first account of Misaki (1901) made the following interesting statement: "In this favorable neighborhood there are several scores of fishermen who are in the habit of supplying the Tokyo market from the deeper waters (300 to 700 fathoms), and there was thus a daily chance for a collector to obtain rare and interesting forms." He stated elsewhere that these men fished with trawl lines which were miles long and carried thousands of hooks.

For some of the eastern Atlantic specimens we have definite records. No depth was given for the Madeiran fish (Collett, 1890), but for that from the Varanger Fjord, Norway, Collett (1897.1) gave the depth as "some 150 fathoms." Pellegrin and Loppé (1914) had a fish which was taken in an arm of the Gulf of Gascony at a depth not below 200 meters—that being the limit for trawlers there. For the waters around the Spanish peninsula there are several records. Thus the specimen of Carlos de Bragança came from a depth of 580 meters off Cezimbra, Portugal. Bertrand (1926) gave no depth for his specimen taken near San Sebastian, and Lozano Rey made no statement other than that *Chlamydoselachus* is adapted to deep zones and hence ought to be widespread.

Along this line of thought, Collett (1897.1, p. 8), in discussing the specimen caught off Madeira, had noted that *Chlamydoselachus* was thus proved to frequent the waters of almost similar latitudes in the two hemispheres of the globe. Referring to the capture of a specimen in that part of the Arctic Ocean which washes the northern Norwegian coast (74° N. Lat.), he stated that this proves the truth of "the remarkable phenomenon which has often been previously observed and mentioned, that, unaffected by latitude or parts of the Earth, there exist forms of animal life which appear unchanged at great depths in all waters where like temperatures exist, whether under the Equator or up under the Poles."

Subsequent captures of *Chlamydoselachus* in the Gulf of Gascony and in the waters surrounding the Iberian peninsula (the deepest from 580 meters) amply justify Collett's generalizations.

SPECIMENS IN MUSEUMS AND THEIR SOURCES

For the sake of any readers of this article who may be interested in examining the fish, we list the museums and universities which have or have had specimens, and give the localities whence these were obtained. For European museums (Table I) we have used Collett's list (1897.1) of eleven museums and fifteen specimens without feeling obliged to ascertain if those specimens are still in existence or if others have since been added to these collections. To this list we have added about an equal number of European institutions and specimens. Table II for American institutions is, however, brought up to date.

TABLE I

SPECIMENS OF *CHLAMYDOSELACHUS* IN EUROPEAN MUSEUMS

No.	In the Collections of	Number	Source	Date	Authority
1	Zool. Mus., Vienna	2 adults	Tokyo	1881	Collett
2	British Museum (Nat. Hist.)	3 adults	Tokyo	1887	Collett
3	Musée Océanographique, Monaco	1 young	Madeira	1889	Roule
		1 adult	Corunna	1906	Roule
4	Anat. Instit., Moscow	2 specimens	Japan?		Collett
5	Mus. Zool., Liége	1 adult	Japan		Collett
6	Mus. Hist. Nat., Bruxelles	1 adult	Japan		Collett
7	Böhm. Mus., Prague	1 adult	Japan		Collett
8	Mus. Fritsch, Prague	1 adult	Japan		Collett
9	Mus. Acad. Imp., St. Petersburg	1 adult	Japan		Collett
10	Mus. Zool., Christiania	1 adult	Norway	1896	Collett
11	Mus. Hist. Nat., Paris	1 adult	Portugal	1900	Pellegrin
12	Mus. Fleuriau, Rochelle	1 adult	Near Rochelle	1914	Loppé
13	Comm. Cent. Pêches Marit., Lisbon	2 adults	Morocco	1913	Seabra
14	Oceanog. Mus., San Sebastian	1 adult	Spain	1925	L. Bertrand
15	Mus. Oceanog., Corunna	1 adult	Spain	1906	Bolivar
16	Senckenberg. Mus., Frankfurt	1 adult	Japan		Mertens
17	Zool. Mus., Univ. Jena	2 adults	Japan?		Maurer
18	Zool. Stattsammlung, München	1 adult	Japan		Luther
19	Liverpool Univ.	1 adult	Japan		Hawkes
20	Birmingham Univ.	3 adults	Japan		Hawkes
	Total	29	16 (+4?) Japan		

The history of the specimens collected by Döderlein at Tokyo in 1881 and deposited in the Naturhistorisches Museum at Vienna has been referred to earlier in this article. No further study of them seems to have been made, but in a recent letter from Dr. Victor Pietschmann we learn that they are still there.

TABLE II

SPECIMENS OF *CHLAMYDOSELACHUS* IN AMERICAN MUSEUMS

No.	In the Collections of	Number	Source	Date	Authority
1	Mus. Comp. Zool., Cambridge	1 adult	Japan	1884	Garman
		1 adult	Japan	1887	Garman
2	Mus. Comp. Zool., Cambridge	1 embryo	Japan	1905	T. Barbour
		1 embryo	Japan	1907	T. Barbour
3	Mus. Zool., Stanford Univ.	2 adults	Japan	1900?	A. W. Herre
4	U. S. Nat. Mus., Washington	1 adult	Japan		B. A. Bean
5	Amer. Mus. Nat. Hist., New York	3 adults	Japan		Gudger
6	Amer. Mus. Nat. Hist., New York	6 embryos	Japan		and
7	Zool. Mus., Columbia Univ.	1 adult head	Japan		Smith
	Total	17	Japan		

DISTINCTIVE MORPHOLOGICAL CHARACTERS

In this section we endeavor to synthesize the scattered observations of many writers on the morphology of *Chlamydoselachus*, in order that students may be able to get a clear idea of the general form and make-up of this little-known selachian. The statements of every author have been checked against our three adult female specimens, and for head parts also against the well-preserved specimen from Columbia University. On many points, notably on teeth and caudal fin, because of our abundant material, we have the good fortune to record more extensive data than any preceding students. This part of our article will then form a very definite basis for the future study of the anatomy of the adult and for an exposition of the main features of the outer development of the embryos.

THE ANIMAL AS A WHOLE

In studying the natural history of *Chlamydoselachus*, we must first consider the animal as it would appear to the eye of an observer on first beholding the fish.

GENERAL FORM AND APPEARANCE

"Is it a sea serpent?" was the question asked by many who saw Garman's specimen (1884.1) for the first time (Text-figure 1; Figure 16, plate V). The elongate, slender, eel-like body, the flattened sub-triangular head, the sinister eye, the anterior mouth (almost terminal in position), the enormous gape, and the jaws beset with slender hooked teeth, do give *Chlamydoselachus* a certain superficial resemblance to the pythons among snakes. But fins and gill-openings at once proclaim that the creature is a fish. Then the shagreen that covers the body and lines the mouth, the multiple gill-straps, and the fundamental internal structures conclusively show it to be a shark. Yet *Chlamydoselachus anguineus* ("the snake-like frilled shark") is the most slender and eel-like selachian known to science. Even in our specimens that have been in formalin and alcohol for about thirty years, the body is fairly flexible.

This extremely slender form may be clearly demonstrated by bringing together the few records of ratios based on length and diameter. Thus Günther's largest male specimen (1473 mm. long) was in length about 16.4 times the depth of the body (see Plate I, figure 1); Collett's female fish was 1910 mm. over all and 165 mm. in depth, giving a ratio of 11.5 to 1. Carlos de Bragança's specimen, a male 920 mm. long, was "about" 75 mm. in depth, a ratio of 12.3 to 1, which strikes a fair average between the other two ratios.

However, there are now to be considered two fish whose dimensions give ratios which depart widely from the above. L. Bertrand's very full-bodied female measured 1860 mm. in length and 240 in greatest depth, giving a ratio of 7.7 to 1. This exceptional ratio is to be explained on the ground that the fish is a female and is presumably gravid. We base this conclusion on the full-bellied appearance of the fish as seen in Bertrand's illustration (made from a photograph reproduced as our Figure 5, plate II). For the Japanese fish shown in our Text-figure 5, the proportion of length to depth based on the measurements given is 12.7, but our measurements of the illustration give the figures 267 mm. in length and 40 mm. depth—a ratio of 6.67 to 1. This fish is also a female and judging from the full abdomen it is gravid.

Such slenderness of body as is exemplified in three of these specimens is found in no other species of shark. While in size this animal does not measure up to the popular conception of a "sea serpent," still the size of the adult specimens referred to is considerable. For further data see Tables III–VI. It will be noted that in some extreme cases the fish reaches a length of more than six feet.

LENGTH OF *CHLAMYDOSELACHUS*

In Tables III, IV, and V we have brought together all data available to us pertaining to the length of *Chlamydoselachus*. From the length, the size may be roughly inferred by consulting the illustrations, or the ratios of length to depth already given. The specimens are tabulated by sexes and by lengths in ascending order. We note also the country of origin, the authority on whose word the fish is listed, and the institution in which it is or was preserved. These tables will also give some idea of the number of specimens that have come into the hands of scientists. For other lists showing the locations of museums containing specimens, and the number therein, see Tables I and II.

TABLE III

LENGTHS OF *CHLAMYDOSELACHUS*, SEX UNKNOWN

No.	—Length—		Source	Authority	In collections of
	Millims	Inches			
1	950	37 4	Japan	Collett	Bohm. Mus., Prague
2	1300	51 2	Morocco	Seabra	
3	1330	52 4	Japan?	Maurer	Zool. Mus., Univ. Jena
4	1350	53 1	Japan	Collett	Mus. Nat. Hist., Brussels
5	1490	58.75	Bay of Biscay	Pellegrin & Loppé	Mus. Fleuriau, Rochelle
6	1500	59	Japan	Collett	Mus. Fritsch, Prague
7	1600	63.	Japan	Collett	Mus. Zool., Liége
8	1600	63	Morocco	Osorio	
Av.	1390	54.7			

It is to be regretted that the authors cited as authorities for the length, source, and present locations of the specimens listed in Table III did not give the sex of each fish, so that it might be placed in either Table IV or Table V.

Since Tables III, IV, and V were formulated, averages made, and the data incorporated in various sections of this article, we have learned from Dr. Victor Pietschmann that the Vienna Museum contains a male 1241 mm. long and a female of 964 mm. These are the specimens obtained by Döderlein and listed by Collett.

We have also made a cursory examination of the female specimen brought recently from Japan by Doctor White (see page 253). This measures 1398 mm. (55 in.) in total length. Since the specimen has been coiled up in a container and is rather stiff through preservation in alcohol, this measurement is approximate only. It may be noted that this fish is only slightly below the average in length.

With a few scattering exceptions, we have been able to ascertain the lengths of the fish studied by the scientific men listed in our bibliography, also the lengths of those fish found in a large number of the museums of Europe and the United States. In our tables only 8 specimens have to be listed under "sex unknown," while definite data are given for 15 males and 35 females. Little need be said of the first class. Their sizes run from 950 to 1600 mm. (two specimens) or from 37.4 to 63 inches. Barring No. 1, which is only 950 mm. long, these fishes are of fair size (1300 to 1600 mm.). Five are from Japan, two from Morocco, and one from the Bay of Biscay.

TABLE IV

LENGTHS OF MALE SPECIMENS OF *CHLAMYDOSELACHUS*

No.	—Length—		Source	Authority	In collections of
	Millims	Inches			
1	920	36.25	Portugal	Bragança	Mus. Hist. Nat., Paris
2	1050	45.25	Japan?	Braus	Zool. Mus., Univ. Jena
3	1140	44.9	Spain	Bolivar	Mus. Océanogr., Monaco
4	1168	46.0	Japan	B. A. Bean	U. S. Nat. Mus., Washington
5	1240	48.8	"	B. Dean	
6	1250	49.25	"	Collett	Brit. Mus. (Nat. Hist.)
7	1300	51.2	"	B. Dean	
8	1320	52.0	"	Goodey	Univ. Birmingham
9	1330	52.4	"	B. Dean	
10	1335	52.6	"	" "	
11	1380	54.3	"	" "	
12	1400	55.1	"	" "	
13	1450	57.2	"	" "	
14	1474	58.0	"	Günther	Brit. Mus. (Nat. Hist.)
15	1650	65.0	"	B. Dean	
Av.	1293	50.9			

The 15 males run from 920 to 1650 mm., 36.25 to 65 inches. The average is 1293 mm. or 50.9 inches. Omitting No. 1, the smallest fish, the average becomes 1320 mm. or 52 inches. Of the 15 fish listed, 12 are definitely from Japan, and 8 of these were taken for Dean and their measurements are listed in his notes. These measurements were presumably made from freshly caught fish, and are probably accurate; some if not all of them were certainly made by Dean himself.

For female fish we present the surprising number of 35 measurements. Of these fish 32 are from Japan and 21 measurements are from Dean's specimens. These latter measurements were all made from newly caught fish and are certainly accurate.[3] Here again the table begins with (in this case two) specimens far below the usual size, and the

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[3] What has become of all this valuable material is unknown. Dean undoubtedly brought a number of these fish back to America with him, or had later catches sent. This is the probable source of our three adult specimens and of the head at Columbia. Dean was for many years the source for *Chlamydoselachus* material in America and Europe. Thus Allis (1893, p. 123) says he obtained "several heads" from Dean for his work. This in part will account for the disappearance of some of these specimens. But one should remember that Dean was primarily interested in obtaining embryos. Perhaps some male specimens were ignored, and some female specimens discarded after they had been examined for embryos.

range is from 610 and 845 mm. (24 and 33.25 in.) to 1960 mm. (77.2 in.). The average length of these 35 fish is 1532 mm. (60.3 in.). Leaving out the two unusually small ones, whose combined lengths do not equal the average, the average for 33 adults is 1579 mm. (62.25 in.)—a length practically equal to that of No. 24 of the table.

TABLE V

LENGTHS OF FEMALE SPECIMENS OF *CHLAMYDOSELACHUS*

No.	Millims —Length—	Inches	Source	Authority	In collections of
1	610	24.	Madeira	Collett	Mus. Océanog., Monaco
2	845	33.25	Japan	A. W. Herre	Mus. Zool., Stanford Univ., Calif.
3	1220	48.0	"	Garman	Mus. Comp. Zool., Cambridge
4	1350	53.1	"	Gudger & Smith	Amer. Mus. Nat. Hist., N. Y.
5	1380	54.3	"	B. Dean	
6	1390	54.75	"	Collett	Brit. Mus. (Nat. Hist.)
7	1396	55.0	"	B. Dean	
8	1420	55.9	"	" "	
9	1460	57.5	"	" "	
10	1485	58.4	"	Gudger & Smith	Amer. Mus. Nat. Hist., N. Y.
11	1500	59.0	"	A. W. Herre	Mus. Zool. Stanford Univ., Calif.
12	1500	59.0	"	B. Dean	
13	1510	59.5	"	" "	
14	1510	59.5	"	Garman	Mus. Comp. Zool., Cambridge
15	1520	59.8	"	B. Dean	
16	1520	59.8	"	Collett	Mus. Acad. Imp., St. Petersburg
17	1550	61.0	"	B. Dean	
18	1550	61.0	"	Gudger & Smith	Amer. Mus. Nat. Hist., N. Y.
19	1565	61.6	"	B. Dean	
20	1565	61.6	"	" "	
21	1565	61.6	"	" "	
22	1574	62.0	"	Mertens	Senckenberg. Mus., Frankfurt
23	1575	62.0	"	B. Dean	
24	1580	62.25	"	" "	
25	1620	63.8	"	" "	
26	1670	65.8	"	" "	
27	1670	65.8	"	" "	
28	1700	67.0	"	Nishikawa	
29	1740	68.5	"	B. Dean	
30	1770	69.7	"	" "	
31	1770	69.7	"	" "	
32	1770	69.7	"	" "	
33	1860	73.25	Spain	Bertrand	Mus. Oceanog., San Sebastian
34	1910	75.4	Norway	Collett	Zool. Mus., Univ. Oslo
35	1960	77.2	Japan	B. Dean	
Av.	1532	60.3			

Taking the tables as they stand, it is evident that the females average larger than the males (35 females average 1532 mm.; 15 males, 1293 mm.). If now, omitting the unusually small and presumably immature fish of both sexes, we compare the average for the 33 remaining adult females (1579 mm. or 62.25 in.) with the average for the 14 remaining adult males (1320 mm. or 52 in.) we see that the females still average larger than the males, and that the difference is greater than in the preceding case. The average female is 259 mm. or 10.25 in. longer than the average male, based on the measurements of the 14 males and 33 females in our tables. The average female is 1.2 times longer than the average male.

That the female of this fish should be larger than the male is in keeping with the general rule in fishes. However, in *Chlamydoselachus* there seems to be a particular reason found in its method of reproduction (viviparity); for the female has to build up the enormous eggs and then accommodate and incubate them within her slender body during the many months before the young are born. For an idea of the capacity required for this see Text-figures 2 and 5 and Figure 5, plate II, showing dissected and unopened females respectively.

TABLE VI

DETAILED COMPARATIVE MEASUREMENTS OF *CHLAMYDOSELACHUS ANGUINEUS**

Describer	Gudger & Smith			Goodey	Collett	Bragança	Bertrand
Sex	Fem. I	Fem. II	Fem. III	Male	Female	Male	Female
Total length	1350	1485	1550	1320	1910	920	1860
From tip of snout to upper edge first gill-slit	140	140	150	—	195	122	—
From tip of snout to hind edge last gill-slit	240	240	240	195	260	150	210
From tip of snout to front edge dorsal fin	955	1060	975	826	1260	590	1210
From tip of snout to front edge pelvic fins	640	770	750	648	990	440	—
From tip of snout to front edge anal fin	810	950	940	808	—	565	1200
From tip of snout to front edge anus	750	860	855	686	—	515	1100
Mouth (length?)	—	—	—	—	132	80	135
Height of body	—	—	—	—	165	75*ca*	240
Base of dorsal fin (length?)	—	—	—	—	172*ca*	70	—
Greatest height of dorsal fin	—	—	—	—	45	—	—
Length of pectoral	105	114	150	—	165	73	—
Length of base of anal	145	155	160	—	245	108	—
Distance anal fin to tip of tail	537	540	670	—	470	—	—
Distance hind edge of anus to tip of tail	535	558	632	—	—	405	—
Length of caudal fin	327	345	370	—	—	265	—
Maximum depth of caudal	120	115	122	93	135	80	—
Eye orbit, longitudinal	20	23	17	—	28	—	—
" " vertical	17	14	14	—	15	—	15
Interorbital space	80	80	80	—	90	—	90

The smallest fish are two females of 610 and 845 mm. (24 and 33.25 in.). The smallest male is 920 mm. (36.25 in.) long. The only other unusually short specimen is one of unknown sex measuring 950 mm. (37.4 in.). All other fish listed are above 1000 mm. in length. The largest of the "unknown" class measures 1600 mm. (63 in.). The largest male is 1650 mm. (65 in.). However, there are 10 females larger than this fish. Of the three largest females, one (Spain) is 1860 mm. (73.25 in.) long, another (Norway) is 1910

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*Measurements in millimeters.

mm. (75.4 in.), and the largest (Japan) is 1960 mm. (77.2 in.). The average length of the 58 (8+15+35) specimens of *Chlamydoselachus* for which we have definite measurements is 1450 mm. (57 in.). In view of all these facts and figures, one must conclude that Doflein (1906) was remarkably close to the truth when he said underneath his figure of a male fish (Figure 2, plate I) "Natürliche Länge *ca* 1½ m. [1500 mm., 59 in.]."

In addition to the tables of lengths only, we have compiled our Table VI showing the comparative measurements (in millimeters) of different regions and organs in four specimens from authors, plus the like measurements in our three specimens—fish which have been long in preservative.

It must be distinctly understood that the measurements of our three specimens are approximate only. These specimens have for at least 25 years been coiled up in barrels of alcohol. To straighten them out and get even approximate measurements is a matter of no small difficulty; to get absolutely accurate ones is an impossibility. After making due allowance for errors of measurement, there are individual variations which must be recognized. The depth of body of our three specimens cannot be measured because they have been eviscerated, but it is apparent that No. II has proportionately a more slender body than the others.

COLOR OF THE FRILLED SHARK

Unfortunately no one has definitely described the color of a newly caught *Chlamydoselachus*, but for preserved fish there is great uniformity of report. Perhaps it will be best for us to let the describers speak for themselves—taking Japanese specimens first. Thus Garman (1884.2, 1913) says "Uniform brown, darker at the edges of the fins." Günther (1887) unfortunately makes no reference to the coloration. Nishikawa (1898), who figures a freshly caught female (our Text-figure 2), makes no statement, nor do we find any in Dean's fragmentary notes. Jordan and Fowler (1903, p. 597) say of their small specimen (996 mm. or 39.1 in.)—"Color in spirits uniform brown." Mertens (1921) speaks in one place of the color of his specimen as "dark" and in another as "a beautiful uniform purplish-black (Purpurschwarz)." This statement is however an isolated one. Finally, the colored figure in the Japanese work referred to (Ito, 1931) shows, and the descriptive text states, "color uniformly dark-brown, darker at thin margins of fins," while the under parts are almost white.

The color of eastern Atlantic specimens agrees with that of Japanese fish. Collett unfortunately makes no reference to the color of his preserved specimens from Madeira (1890) and Norway (1897.1). Pellegrin and Loppé (1914) give no color for their fish, though Loppé saw it while it was fresh. For specimens from Iberian waters we have more definite data. Bolivar (1907) says of the first fish taken at Corunna, Spain, that "The head, the back, the fins and tail are of a dull brown color, while the underneath parts are much lighter." As we understand it, this applies to the preserved fish. Bertrand (1926) makes a curious statement about the color of his specimen which he apparently saw while it was fresh or at any rate shortly after it had been captured. He writes: "La linea lateral, muy marcada, es de color pardo oscuro, algo mas claro por debajo." This we translate thus: "The strongly marked lateral line is of a dark-brown color, but it is lighter below." The lateral line *is* strongly marked as may be seen in our Figure 5, plate II, a reproduction of his figure made from a photograph by the well-known ichthyologist, Gandolfi-Hornyold. But what we believe Bertrand means is that 'The body is of a dark-brown color *above* the strongly marked lateral line, but is lighter in color below.' Speaking generally for Spanish and Portuguese specimens, Lozano Rey (1928) says "The general color is a uniform brown, darker on the edges of the fins, and somewhat lighter on the ventral surface of the body."

As our Table VI shows, there are in the American Museum three adult specimens, presumably brought or procured from Japan by Dean prior to 1906. These, after at least twenty-five and probably thirty years in alcohol and formalin, are somewhat diverse in coloration. The largest fish (1550 mm.), which has been in a copper tank, has teeth and skin colored green from impregnation with copper salts. Above the lateral line its color is dark-brown tinged with green, below this a greenish brown-gray. The two other fish have been stored in wooden barrels and hence lack the greenish tinge. The second (1485 mm. long), in a poor state of preservation, is everywhere a dark muddy-brown, darker (approaching black) below. Our smallest fish (1350 mm. over all) is in a better state of preservation. It is dark-brown on the dorsum, lighter coppery-brown or tan below the lateral line, and darker again on the belly.

The head from Columbia University, which has been beautifully preserved in formalin, is a light coppery-brown approaching tan. Still lighter brown or tan over the body are our six embryos after twenty-five or thirty years of preservation. Their fins are darker and therein they agree with the fin-coloration of our adults.

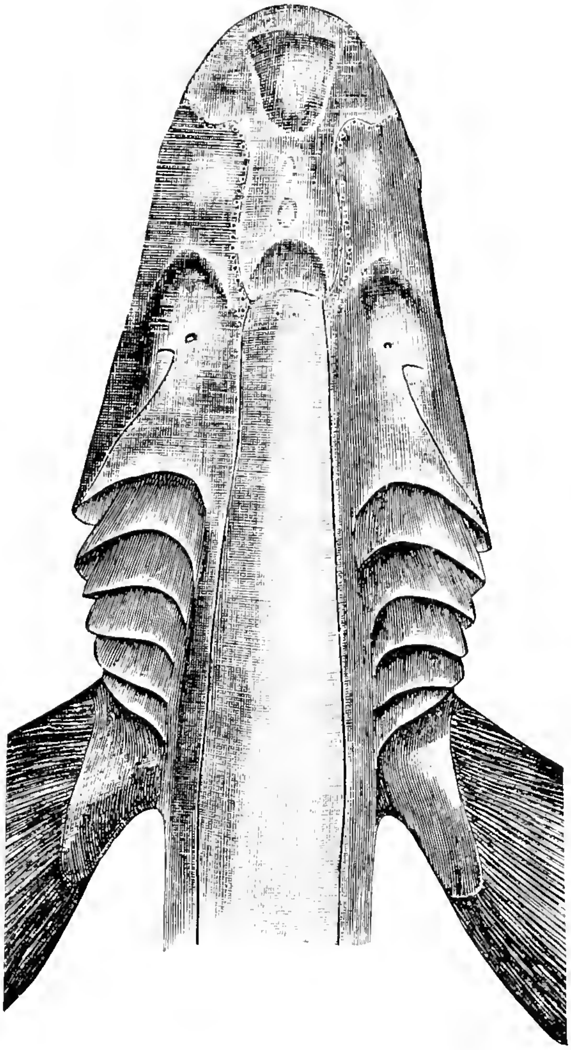
THE HEAD OF *CHLAMYDOSELACHUS*

The head of the Japanese frilled shark, in keeping with the unusual form of the body, differs in many respects from that of any other shark known to us.

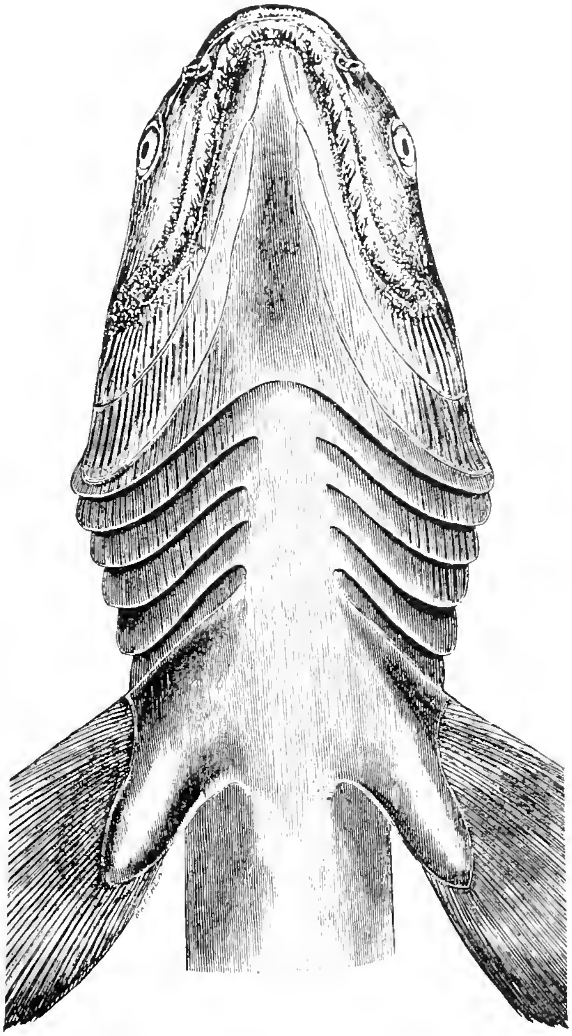
GENERAL FORM

In our large embryos the head is rather blunt, but in our three full-grown adults it is somewhat pointed and is remarkably flat on top and wide behind. Indeed it is flatter and wider than in any other shark known to us. In both young and old it is widest behind in the region of the first gill-opening, as shown in the small figures reproduced from Garman in our Text-figure 1. A better showing of the dorsal aspect of the head is found in our Text-figures 7 from Garman (1885.2), and 21 from Allis (1923).

From these, and from the figures of the whole shark previously given, it can be seen that Garman has grounds for saying of the head of *Chlamydoselachus* that it "has a look about it that reminds one of some of the venomous snakes." This, it may be noted, has been remarked by every visitor who has seen our specimens. It is particularly true when the mouth is wide open, for then the teeth stand out and the hinder part of the head spreads widely.



Text-figure 7
Dorsal view of the head of *Chlamydoselachus*. Note the position of the spiracles, the form and number of the gill-slits, the position of the lateral line and of the pectoral fins.
After Garman, 1885.2.



Text-figure 8
The head of *Chlamydoselachus* as seen from below. Note the long narrow lower jaw, the position of the nostrils and of the eyes, and the long gill-covers—the first being "free from the isthmus."
After Garman, 1885.2.

MOUTH AND JAWS

The mouth is nearly terminal in position in the flat sub-triangular head. This is in marked contrast with its position in most other sharks, where the mouth is ventral and set so far back that it leaves an overhanging snout. The lower jaw is loosely articulated, both at its apex and also proximally where it is attached to the head. This may be seen in every lateral view of the shark, particularly in Günther's drawing (Figure 1, plate I). It is especially well portrayed in Collett's lateral view of the head (Figure 6, plate II), and also in Allis's representation (Figure 7, plate II). The angle of the lower jaw literally reaches back behind the skull into the region of the gill-arches. As may be seen in Text-figure 8 from Garman, the lower jaw is, for a shark, remarkably long, narrow and pointed. Furthermore it is rather frail as one may see in Collett's figure (Figure 6, plate II). One could by hand easily break the lower jaw of one of our preserved specimens.

In marked contrast with the form of the mouth of *Chlamydoselachus* as seen in all other figures reproduced in this article, and as observed in all our specimens, is that shown in Ito's drawing (1931) reproduced herein as Text-figure 5. The figure calls for no comment, save that we are unable to offer any explanation for it.

The peculiar structure of the jaws has been admirably characterized by Goodey (1910, p. 550) as follows:

> Perhaps the most important point in regard to the specialization of the skull of *Chlamydoselachus* is to be seen in the extreme length and mobility of the jaws. These are exceptionally long, extending from the anterior, almost terminal mouth to a point well behind the posterior limit of the cranium. This extension is remarkable; in fact, one quarter of the total length of the jaws is found in this region, and it is this feature, connected with the exceptional length of the hyomandibular, which gives the jaws their great mobility. Indeed, their disposition relative to the cranium is quite different from that found in any other Selachian whose skull I have been able to examine or to see a figure of. It resembles nothing among the Vertebrates so much, perhaps, as the general disposition of the jaws in certain of the Ophidia.

In this connection it will be of interest to set forth the measurements of the mouths (Table VII) of our three fish and those of the head from Columbia University. It should first be stated that in our fish the jaws have been hardened shut, and although we have forced them open the measurements are undoubtedly smaller than they would have been in live or in freshly caught fish. On the other hand the mouth of the head from Columbia, preserved open, is probably more widely distended than is natural.

TABLE VII

MEASUREMENTS OF THE MOUTH OF *CHLAMYDOSELACHUS ANGUINEUS*

Mouth of	Front to Back	Side to Side	Length of Fish
American Museum Specimen I	93 mm. 3.6 in.	80 mm. 3.1 in.	1350 mm. 53.1 in.
" " " II	100 " 3.9 "	80 " 3.1 "	1485 " 58.4 "
" " " III	105 " 4.1 "	95 " 3.7 "	1550 " 61.0 "
Columbia University Specimen	70 " 2.7 "	90 " 3.5 "	

Both upper and lower jaws possess rudimentary lip-like structures. Concerning these Allis (1919, p. 146) says:

> In *Chlamydoselachus* the lips are much thicker at the angle of the gape of the mouth than in their anterior portions, the angle of the gape thus being a relatively long line. The inner end of this line forms the functional angle of the gape when the mouth is widely opened, and the outer end of the line the functional angle when the mouth is closed and from this outer angle the outer edge of each lip converges toward the inner edge until the lips attain their

> normal thickness. This is readily seen in the accompanying figures [Allis, 1919, Pl. I, figs. 1 and 2] . . . and it is there also seen that what is actually a portion of the external surface of the head when the mouth is widely opened, becomes enclosed between the lips when the mouth is closed.

Allis (1919) speaks of "primary" and "secondary" lips in *Chlamydoselachus*, but his description is too involved for consideration here. The reader is referred to his text (1919, pp. 146–147) for his exact wording. However, if the reader will consult our Figure 7, plate II, a reproduction of Allis's drawing of the head in lateral view, and will contrast this with Allis's view of the wide-open mouth (our Figure 9, plate III), he will see these rudimentary lips represented. In both figures the wrinkles at the angles of the mouth are well shown, as are the dense patches of shagreen around the angle. All these structures we find in our adult specimens.

The peculiar organization of mouth and jaws above described gives *Chlamydoselachus* a gape which is enormous for such a remarkably slender-bodied shark. Looking at this fish head-on, one sees practically nothing but the wide-open mouth looking like the entrance to a tunnel. For this, see Garman's figure (our Figure 8, plate III) and Allis's head-on figure (our Figure 9, plate III). Even more striking than either of these is our Figure 10, plate III, made from a photograph of the open mouth of the head from Columbia University, in which the distention is greater than in either of the other figures.

In both Garman's and Allis's figures, the shape of the mouth is about normal, judging by the shapes which the mouths of our three specimens take when distended. The mouth of the Columbia specimen has been much enlarged laterally. Later, these figures will be referred to for other points.

BREATHING VALVE

We have found in the mouths of our preserved specimens of *Chlamydoselachus* a structure which, at first, we thought had escaped the notice of all previous investigators. There is in the mouth at the apex of the upper jaw, in all five of the fish we have examined, a thin crescentic fold or shelf which we interpret as a breathing-valve. This fold extends to the third and fourth rows of teeth on either side, and projects posteriorly into the front upper part of the mouth. There is quite a recess or pocket between it and the front part of the roof of the mouth, which extends forward in our specimens dorsal to the jaw-cartilages and between them and the skin. The shelf or breathing-valve is of course very much contracted in our specimens, which have been thirty years in alcohol. But it may be plainly seen in Figures 11 and 12, plate IV, made from photographs of our specimens. In Figure 11 the valve is seen to be posteriorly angled like the head of a broad arrow,[4] while in Figure 12 it is more rounded. Both, however, are quite evident. The similar structure in our third specimen, and that in the Columbia head, are shown in Figures 11 to 15, plates IV and V. Similar folds of tissue are found in the mouths of many bony fishes—especially those which breathe with the mouth partly open.

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[4] Doctor White's specimen possesses a similarly angled breathing-valve. (See Figure 14, plate IV).

In all five of our preserved specimens, the tongue (Figures 8 and 9, plate III) does not in any case reach far enough forward to come into apposition with this valve-like structure. But in all of these specimens, on each side between the tongue and the lower jaw, there is a prominent loose fold of tissue which during expiration might come into contact with the crescentic fold, and thus enable the shark to breathe with its mouth partly open. Somewhat similar structures are known to occur in skates and rays. Also, Gudger has found in various teleostean fishes at Tortugas, Florida, similar dorsal breathing-valves and similar loose folds of skin alongside the tongue. He has verified the function of these structures in living fishes. We infer therefore that the structures we have just described in *Chlamydoselachus* function exactly like the similar structures present in living fishes.

At the time the above was written, we believed that we had discovered a structure hitherto unnoticed in *Chlamydoselachus*. However, our study of an article by Allis (1914), based in part on *Chlamydoselachus* material supplied by Dean, showed that we had been partially anticipated. In his specimens Allis found across the front part of the roof of the mouth what he describes (p. 354) as

> a nearly horizontal shelf across the anterior portion of the large and deep subethmoidal depression on the ventral surface of the neurocranium. This subethmoidal depression is shown in both Garman's and Goodey's figures, but is not there as pronounced as I find it in all of the several specimens that I have examined.

Continuing he says:

> The mucous membrane of the mouth cavity lines the walls of the subethmoidal depression and is reflected, first posteriorly and then anteriorly, to clothe first the dorsal and then the ventral surface of the horizontal palatine shelf, a mucous fold with a supporting core of cartilage thus being formed, dorsal to which there is a large and deep suprapalatine recess in the roof of the mouth cavity. When the mouth is opened and shut some slight movement must necessarily be given to this mucous fold, and the overlying recess must be correspondingly enlarged or diminished in capacity.

In the closely related form, *Heptanchus*, Allis found "a large pocket . . . in the roof of the mouth cavity. . . [which] extends but little if at all dorso-anterior to the dorso-posterior edge of the palatine process." Returning to *Chlamydoselachus*, he states:

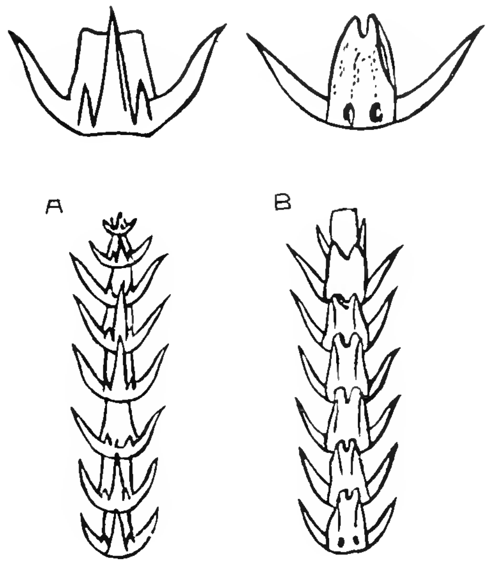
> The palatine process of *Chlamydoselachus* does not definitely articulate with the lateral edge of the solum nasi, simply resting against its ventral surface in certain positions of the upper jaw, and probably sliding slightly upon it in a latero-mesial direction. If this sliding contact were to become a definite articulation, such as is to be found in teleosts and bony ganoids, it is evident that that part of the palatine process that lay mesial to the line of contact would be a hindrance to the free articular movements of the parts concerned, and that it would accordingly tend to become detached or resorbed; and if resorbed it would evidently leave a fold in the mucous lining of the mouth cavity that would strikingly resemble the maxillary breathing valve of many teleosts.

Then Allis goes on to say definitely that he believes this structure in *Chlamydoselachus* to be the homologue of the maxillary breathing-valve found in teleosts. We have found his line of reasoning rather difficult to follow and have thought it best to quote him quite fully. He gives no figures of this breathing-valve.

Our conception of the action of this breathing-valve is as follows: when the creature is resting quietly on the bottom, with the mouth slightly open, the breathing-valve doubtless helps to prevent the regurgitation of water during the process of expulsion of the water through the wide-open gill-slits.

TEETH OF *CHLAMYDOSELACHUS*

The fang-like teeth are arranged in rows extending obliquely from front to back across each jaw, as may be seen in Figures 8, 9, and 10, plate III; also in Figures 11—14, plate IV; and lastly in Figure 15, plate V. A single row of teeth, about 1.8 times the natural size, is portrayed in both dorsal and ventral aspects in Text-figure 9. These are enlargements of the teeth found in Günther's drawing (Figure 1, plate I). They have been retouched by our artist to make them sharp and clear-cut. The single teeth have been enlarged about 3.4 times.

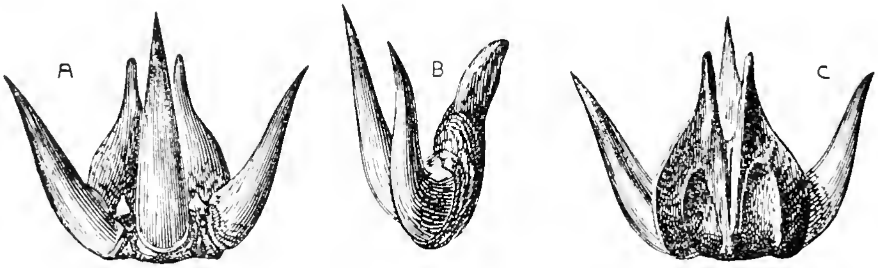


Text-figure 9
The teeth of *Chlamydoselachus* in rows: A, from above and in front; B, from below. Note how the base of each tooth is anchored underneath the base of the tooth behind it, to resist a pull tending to tear it out. The single teeth are × about 3.4, the tooth rows × about 1.8.
After Günther, 1887.

The rows are separated by toothless spaces, which are in width about equal to the width of the adjacent rows of teeth. Posteriorly the spaces become narrower, and at about the seventh or eighth row of teeth, the toothless spaces become very much reduced and the rows of teeth are so closely set that it is difficult to distinguish the rows. The teeth in these posterior rows are very small and are rudimentary in structure. In the symphysis of the lower jaw there is a median row of teeth. At the point of each jaw the outermost teeth of each row are bent so far out beyond the margin of the jaw that they are on the exterior when the mouth is closed. This is particularly true of the lower jaw. For all these points see Plate III, figures 8, 9 and 10.

In their form the teeth are unlike those found in any other existing shark. Each tooth has three slender, curved, inwardly directed cusps or denticles set on a broad base (Text-figure 10) which projects behind and interlocks with the base of the tooth posterior to it, so that it cannot ordinarily be overturned by an outward pull. There are a central and two lateral cusps of approximately the same size, and between the central and each lateral cusp is a rudimentary cusp or denticle. For these details of the structure of the teeth of *Chlamydoselachus* see our Text-figure 10 where a tooth is drawn in dorsal, lateral and ventral aspects; and our Figure 15, plate V, in which the teeth are by photography enlarged to about 13 mm., i.e., about three times natural size.

As will be seen in our table No. VIII, different authors have given different counts of the rows of teeth in the jaws of their specimens. Mertens (1921), who is not included in the table, gave 16 rows only for each jaw, upper and lower, of his fish. This is manifestly an error, due apparently to his failure to count the rows in the corners of the mouth, where the teeth grade into shagreen. Garman (1884.1) counted 28 rows above and 27 below, but later (1885.1) corrected this to 26 and 25 respectively. From our illustrations showing mouth and teeth (Plate III, figures 9 and 10), it is understandable why there is an odd number of rows below, due to the median row at the symphysis of the lower jaw.



Text-figure 10
An individual tooth of *Chlamydoselachus* × 6: A, upper front view; B, lateral view; C, ventral view.
After Garman, 1885.2.

The figures also make it clear that toward the angle of the jaw the teeth become smaller, the arrangement in rows more obscure, until finally it is only with great difficulty that one can distinguish the rows and differentiate the teeth. We have found this true in trying to count the rows of teeth in the jaws of our specimens, and only after days of work did we succeed in developing a technique that enabled us to produce counts which, when checked, gave the same numbers time after time for the same specimen.

TABLE VIII

NUMBER OF ROWS OF TEETH IN JAWS OF VARIOUS SPECIMENS OF *CHLAMYDOSELACHUS*

No.	Specimen	Sex	Source	Upper Jaw	Lower Jaw	Teeth in each Row
1	Garman, 1884	Female	Japan	13-0-13—26	12-1-12—25	6
2	Günther, 1887	Male	"	12(13)-0-12(13)—24	12(13)-1-12(13)—25	6 and 5
3	Collett, 1897	Female	Norway	11-0-12—23	10-1-10—21	variable
4	Jordan & Fowler, 1903	——	Japan	13-0-13—26	11-1-11—23	not more than 6
5	Hawkes, 1907	——	Japan	13-0-13—26	13-0-13—26	" " " 6
6	Bertrand, 1926	Female	Spain	—23	—23	
7	Lozano Rey, 1929	——	Iberia	13-0-13—26	12-1-12—25	
8	Amer. Mus. I	Female	Japan	13-0-13—26	13-1-13—27	variable
9	Amer. Mus. II	Female	"	11-0-8—19	12-1-11—24	"
10	Amer. Mus. III	Female	"	13-0-12—25	12-1-13—26	"
11	Columbia Univ.	——	"	13-2-13—28	11-1-12—24	"

Study of Table VIII reveals the fact that there is considerable variation in the number of rows of teeth. For the largest fish but one ever taken (a female, 1910 mm. long), Collett has the lowest count, 11–0–12 above, and 10–1–10 below. The latter is the lowest count for either jaw in any fish. The largest count (13–1–13—27 above) is found on our specimen No. I, a female only 1350 mm. long, or 100 mm. shorter than the average of 58 measured fish. Jordan and Fowler's count (1903) is normal for the upper jaw, but rather scant for the lower, being next lowest in rank to that for Collett's specimen but agreeing in total count with Bertrand.

The varying counts in the table, and particularly certain abnormalities shown only partly therein, call for statement and discussion. Garman's first and erroneous count has already been referred to. His figures in our table are those of his final and more accurate count. He found one more row of teeth on each side on the upper than on the lower jaw, but found one central row below and none above. Günther had difficulty in getting the exact count at the angle of the jaws. Collett's figures are consistent, but he added in a footnote that "In the present specimen the second side row of the left lower jaw is abnormal, being double (with two closely adjoining rows, all the teeth in them being somewhat smaller than normal teeth)." In this connection it is a matter of regret that Collett's fine figure of the head and jaws in lateral view (our Figure 6, plate II) was not made of the left side instead of the right.

Mrs. Hawkes (1907) found the teeth in all her specimens (two in the Liverpool University, and three in the British Museum) bilaterally symmetrical with no median row in the lower jaw, but she added (presumably referring to the lower jaw) that "In every specimen examined, however, there was a torsion of the left front row of teeth toward the right side; and in one case this resulted in a median row of teeth as described by Garman, but the total number of rows of teeth was still 52." Bertrand and Lozano found no such abnormalities in their specimens, and their counts call for no comments.

There are left our specimens, three adult fish listed elsewhere in our table of sizes, and the head of a fourth adult kindly loaned from the zoological museum of Columbia University. Our counts of the teeth in these vary so greatly among themselves and in comparison with the specimens already considered, and the Columbia specimen has such a marked abnormality, that it is necessary to go into details.

Like other investigators, we have had much trouble in making counts, especially in our specimens I, II, and III, in which the jaws had hardened in a closed position. By distending each mouth as widely as possible, by focussing a light on the angle of the jaws and by using a magnifying glass, and above all by much practice, we have finally obtained counts which are found to be correct by repeated checkings. To count the very small teeth in the crowded rows at the angle of the jaw, one must get in position to look down the length of the row; failure to do this is probably one explanation for the divergent counts recorded in Table VIII.

In our first fish (a female, 1350 mm. long) there are 13 rows of teeth on each half-jaw, upper and lower, plus a central row at the symphysis of the lower jaw, which gives

27 rows below. In the angles of the jaws, on both lower right and left and in the upper left, we find the last row of teeth imperfectly developed. On the left side above and below, the last row has only the central cusps developed, while in the right lower side the last row has the central and outer cusps only. In fish No. II (a 1485-mm. female) we found 11 and 8 rows on the sides of the upper jaw, and beyond the last row rudimentary structures which our best efforts were unable to differentiate as either teeth or shagreen denticles. The lower jaw has only 12 rows on the right and 11 on the left, with a central row of teeth at the symphysis. Our fish No. III (1550 mm.) shows nothing unusual save a reversal of the count—the right side having 13 rows above and 12 below, the left 12 above and 13 below. There is also in the center of the lower jaw the usual single row of teeth.

The Columbia University specimen (a head only) has a remarkable abnormality, the exact counterpart of which has not been found in any other fish. The lower jaw has 11 rows on the right, and 12 on the left, with the usual median row. The upper jaw has 13 on each side plus 2 rows of small teeth almost in the center of the symphysis. This double row, as may be seen in Plate III, figure 10, is slightly displaced toward the right—the distance between the right-hand teeth of the right-hand central row and their neighbors being 5 mm., while on the left the distance is 8 mm. The teeth of the double row are very small, measuring (height or length of central cusp) 2.25 mm. in each row, whereas the perfect central cusps of the neighboring normal teeth measure 4.5 mm. in length. These teeth are shown enlarged about two times in Figure 13, plate IV. From this one may judge that an extra tooth *anlage*, which might have produced a single central row of normal-sized teeth, has produced an abnormal double row of teeth, each tooth half the normal size. Furthermore this double row of small teeth corresponds plainly to the abnormality described by Collett, though the double row of teeth referred to by him constitutes the second side-row of the left lower jaw, while ours is found at the center of the upper jaw. He unfortunately gives neither figure nor measurements, merely saying "somewhat smaller than normal teeth."

In Doctor White's specimen, elsewhere referred to, we find an abnormality much like that just described. In the upper jaw of this female 1398-mm. specimen, about half way from the exact center of the symphysis to the first right lateral row of normal teeth, there is a single row of teeth half the normal size for this jaw—i.e., the central cusps are 2 mm. long instead of 4. There are 6 teeth in this pygmy row and 5–6 in the rows of normal teeth—some rows have the outer tooth broken off. It would seem that the cause of this abnormality is very similar to that which produced the teratological tooth-rows just described. It is interesting to note that these variations in both fish are found in the same position, i.e., to the right of the center of the upper jaw. In Doctor White's specimen (Figure 14, plate IV), the abnormal tooth *anlage*, which in the other fish produced two rows of half-sized teeth, equivalent to a full-sized single row, has here brought forth a single row of half-sized teeth. The other row has been suppressed.

In one of our (American Museum) specimens, another interesting abnormality is found. As may be seen in Figure 15, plate V, there is, just anterior to the hinder edge of the breathing-valve, a transverse row of minute denticles across the hinder base of the symphysis. These are in pairs, but at the right of the line three are found which look like a tri-cusped tooth. Between the second and third rows of teeth in this right upper jaw, far back toward the "gum" behind the teeth is what appears to be a very small three-cusped tooth. All these spinose structures we interpret as imperfectly developed teeth. A row of four single-cusped teeth, very similar to those shown in Figure 15, plate V, is found in the upper jaw of Doctor White's specimen immediately anterior to the V-shaped breathing-valve. All this is excellent evidence supporting the commonly accepted belief that the teeth of a shark are strongly metamorphosed dermal denticles.

In this connection we have carefully examined the six embryos in our possession (ranging in length from 190 mm. to 374 mm.). These all have tooth-pads through which the teeth have not yet broken, but not one of them has such a pad in the middle of the upper jaw. Each one does have such a central pad at the point of the lower jaw—however, in one fish only this pad is slightly twisted to the left. So slight is this that the twisting is possibly due to displacement while the specimen was being hardened in formalin.

In our four adult specimens and in the head from Columbia University, we find the ventral surface of the breathing-valve covered with shagreen as may be seen in Figure 13, plate IV, and in Figure 15, plate V. Moreover the folds of tissue which form the "gum" behind the teeth, and also the tongue and in general the lining of the mouth, are covered with shagreen in some cases closely simulating teeth.

Authors report varying numbers of teeth in the various rows. These enumerations are exceedingly difficult to make, but we have accurate counts for three sets of jaws in which we were able to distinguish the teeth in every row. For a fourth (our fish No. II), we were able to get the count in the lower jaw only, the last rows of both sides of the upper jaw having the small teeth and the adjoining tissues so torn and mangled (possibly when caught on a hook) that no accurate count could be made (only 95 teeth could be recognized). Our results are set in order in Table IX.

When one studies Table IX, where the rows are analyzed to show the number of teeth to a row, one must conclude that in the matter of the teeth, both in the number of rows and in the number of teeth in each row, *Chlamydoselachus* is in a plastic condition.

It is significant that, unlike what is found in almost all other sharks, practically all the visible brier-like teeth in every row in the mouth of *Chlamydoselachus* are functional at once, hence a large number are usable and are used. For this see all the figures of the open mouth. In our specimen No. I there are 140 teeth in the upper jaw and 134 in the lower, 133 on the right and 135 on the left plus 6 in the center; a total of 274 for the mouth. The table and its footnotes explain why complete figures cannot be given for fish No. II. In the jaws of No. III, there are 122 teeth in the upper jaw and 128 in the lower. These are also thus divided: 122 on the right side, 122 on the left, with 6 in the center; and the totals are 250 in each count—upper-lower and right-left. In the Columbia University specimen we find 144 teeth above and 118 below, total 262. These are divided as follows: 122 on the right, 122 on the left, plus 18 in the center—a total of 262.

TABLE IX

NUMBERS OF TEETH IN ROWS IN THE JAWS OF FOUR SPECIMENS OF *CHLAMYDOSELACHUS*

	Amer. Mus. No. I				Amer. Mus. No. II				Amer. Mus. No. III				Columbia Univ.			
No. of teeth	R. Upper	Center	L. Upper	Total	R. Upper	Center	L. Upper	Total	R. Upper	Center	L. Upper	Total	R. Upper	Center	L. Upper	Total
6	7 rows		7 rows	84	4 rows		3 rows	42	5 rows		3 rows	48	3 rows	2	3 rows	48
5	5 "		4 "	45	2 "		3 "	25	2 "		4 "	30	7 "		9 "	80
4	1 "		1 "	8	5 "		2 "	28	6 "		5 "	44	3 "		1 "	16
3			1 " *	3	***		***									
Total	13 "	0	13 "	140	(11)	0	(8)	95	13 "	0	12 "	122	13 "	2	13 "	144
	R. Lower		L. Lower		R. Lower		L. Lower		R. Lower		L. Lower		R. Lower		L. Lower	
6	3 rows	1	5 rows	54	5 rows	1	4 rows	60	4 rows	1	5 rows	60	4 rows	1	2 rows	42
5	5 "		5 "	50	2 "		2 "	20	4 "		4 "	40	5 "		3 "	40
4	4 "		2 "	24	2 "		3 "	20	2 "		2 "	16	2 "		7 "	36
3	1 " **		1 " *	6	3 "		2 "	15	2 "		2 "	12				
Total	13 "	1	13 "	134	12 "	1	11 "	115	12 "	1	13 "	128	11 "	1	12 "	118

*Central cusps only. **Central and outer cusps only. ***Tooth region mangled, no count possible.

Taking then our largest number of teeth, 274 for fish No. I, each tooth with its 3 cusps (in theory), we have a total for the mouth of 822 spine-like fangs—all functional at once. While this count does not equal Garman's estimate of 51 rows of teeth with 6 teeth in a row, or 306 teeth (918 cusps), it does present an impressive number of teeth and fangs. In fact it is (so far as we know) exceeded only by the much smaller but vastly more numerous comb-like teeth of the whale shark, *Rhineodon typus*, which in the jaws of a 40-ft. specimen may number 6000 to 7000; and possibly by those of *Cetorhinus maximus*, the basking shark.

The many small teeth of *Chlamydoselachus*, each with its three slender recurved cusps, evidently function (like the simpler but vastly more numerous and smaller teeth of *Rhineodon*) for retention only, in contrast with the chopping service rendered by the one or two rows of broad teeth of *Charcharodon* and *Galeocerdo*. In conclusion we note that the wide gape, the many hooked teeth, the large shagreen-lined mouth and gullet, all indicate that *Chlamydoselachus* may seize and swallow living prey of a diameter nearly equal to its own.

There are no differences correlated with sex either in the form of the teeth or in their number and arrangement in rows.

The function of these teeth being clear, the matter of the apposition of the teeth in the jaws must be noted. *A priori* it was thought that when the mouth is closed a row of teeth in one jaw would fit between two rows in the other. How this may be in the live fish we cannot say, but in our preserved specimens it is not so. It is true that these jaws are somewhat distorted in the hardening process, but in them the tooth rows tend to fit *against* each other.

EYES OF *CHLAMYDOSELACHUS*

The eyes are large and elongate, and are situated on the side of the head approximately over the space between the fifth and seventh rows of teeth. In Garman's figures (our Text-figure 1 and Figure 16, plate V), the eye is represented about midway between the tip of the snout and the angle of the mouth. This location is true of the eye in our three adult specimens and in the head from Columbia University. A number of the specimens of which figures are reproduced in our paper seem to have the eye in about this position. However, the eye is placed forward of the median point in Lozano Rey's drawing (Text-figure 6), and in those of Günther and Doflein (Figures 1 and 2 of plate I); also in that of Collett (Figure 6, plate II). Examination of our embryos shows that in them the eye is slightly behind the median point. In this particular matter, either the fish is subject to considerable variation or the artists have been inaccurate in their drawings.

The eye is elongate in all our adult specimens, but is round in our embryos. Nearly all the illustrations of the fish show it elongate. Notable however are the round eyes in Mertens' (1921) and Ito's (1931) figures (our Text-figures 4 and 5). These we believe to be incorrectly drawn. As may be seen in our Table VI, the aperture is greater in its horizontal than in its vertical diameter.

The eyes are placed so as to look laterally and somewhat dorsally. When the head is viewed from above they are nearly invisible. Set in oblong apertures, with overhanging brows, devoid of eyelids and even of the nictitating membrane found in many sharks, the eyes of *Chlamydoselachus* have a fierce, staring expression like that of some snakes (see Plate II, figure 6).

We have stated above that *Chlamydoselachus* lacks eyelids as do all sharks known to us. Garman does not in any way refer to eyelids, simply noting the absence of the nictitating membrane, the so-called "third eyelid." However, Mrs. Hawkes (1906, p. 966) says:

> There are both upper and lower eyelids, but no nictitating membrane. The infolding of the skin in both cases is sudden and distinct, that of the lower lid is remarkable for its depth, extending almost to the back of the eye. The infolded membrane both above and below the eye is deeply pigmented, the lower being also provided with fine scales. This pigmentation, which on the under side of the eye is as deep as that of the surface of the body, together with the presence of scales, indicates that the infolded portions become, at times (that is when the eye is protruded), a part of the superficial skin. Those portions of the inner surface of the eyelids which are never evaginated are quite smooth and of a light colour. The eye can easily be protruded, and when in this position does not look outwards but upwards, a position made possible by the large conjunctival fornix. It is known that *Chlamydoselachus* is a deep-sea fish, in which case an eye which could look upwards would be of the greatest advantage.

On this point Allis (1923, p. 150) states that: "This [subdermal] membrane [which bridges over the space between the antorbital and postorbital processes] and the overlying dermal tissues form, in *Chlamydoselachus*, the upper eyelid of the fish, and when the eyeball is rolled upwards its dorsal half, approximately, lies beneath this tissue, the ventral portion of the eyeball being exposed in the small external opening of the eye." No writers listed in our bibliography, other than Hawkes and Allis, refer to such an eyelid.

Here is what we find in our four adult heads. The external opening of the eye, corresponding roughly to the palpebral aperture in man, is oblong and its edges are sharp and distinct. In every case (in our preserved specimens) where the eye is rotated upward, the cornea in this position is almost completely hidden, and the greater part of the exposed portion of the sclera is covered with shagreen. Even in our preserved specimens, slight pressure from below with the finger is sufficient to rotate the eye completely upward, so that the cornea is entirely hidden. We infer that this fish, presumably a bottom-dweller, usually has its eyes turned somewhat upward. Evidently *Chlamydoselachus* does not close his eyes by means of lids, but by rotating the eyes upward until the cornea is hidden leaving the shagreen-covered sclera to afford protection to the eyeball. We find no structures in the eyes of *Chlamydoselachus* that seem able to function as lids. We agree with Allis (1923, p. 150) that there is probably little if any real protrusion of the eyeball due to change of its position.

NOSTRILS OF THE FRILLED SHARK

The nostrils, placed near the front of the snout, open on a surface that faces anteriorly, ventrally, and laterally, which is about the most favorable location imaginable for an organ whose function depends on a rapid intake and egress of water. Garman figures the nostrils (our Figure 8, plate III; and Figure 16, plate V) and describes them (1885.1, p. 2) as follows:

> Each nostril is vertically elongate, and so constructed that the upper half opens forward and the lower half backward. Internally the nasal chamber is not divided. During forward motion the water enters through the upper section of the nostril, passes downward behind the partition and out again through the lower section. Backward motion reverses the current. The partition divides the opening but not the chamber; it is formed by a sharp fold pushing backward from the middle of the front wall to meet a similar fold from the opposite side. In the Notidanidae the structure is similar. Commonly among Selachians the anterior fold takes the form of a flap partially covering the nostril.

These figures and this description fit our specimens fairly well. Our fish are too distorted by being coiled up in barrels and by the action of preservatives to permit good drawings of the nostrils to be made. We think these organs are admirably shown in Allis's drawing—Figure 9, plate III.

SPIRACLES OF *CHLAMYDOSELACHUS*

The spiracles, which are typical elasmobranch respiratory organs representing a modified anterior pair of gill-slits, are present though almost vestigial. Each spiracle lies near the top of the head at the middle of a line joining the upper surface of the eye with the medial dorsal edge of the first gill-fold.

Our largest fish has had the top of the head much bruised and cut, especially on the left side, where we can find no trace of the spiracle. On the right side we find an aperture, 2 mm. in diameter, which we believe to be the spiracle. In our second largest specimen (1485 mm.), the spiracles are about the same size as in the former. The head of our smallest fish (1350 mm.) shows the spiracles most clearly, although they are somewhat smaller. In the well-preserved head from Columbia University they are definite oval slits about 3 mm. in length. Through one of these we inserted a bristle which came out into the pharynx through a fairly large opening (large enough to admit the blunt end of a pencil) in series with the other branchial clefts and situated in front of the hyomandibular. In our 304-mm. embryo the spiracles are visible under a reading glass, but cannot be identified with the naked eye. Of these organs, Garman remarks (1884.2, p. 116) as follows: "The spiracles are so small as to be almost useless; but, being present, they point toward an ancestor, a bottom-feeder, in which they were more developed."

The position of the spiracle (according to our specimens) is correctly shown by Garman in our Text-figure 7, and by Allis in our Text-figure 21. But it is placed entirely too far back in Collett's plate (our Figure 6, plate II). Either there is great variation in the position of the spiracles, or the artist has taken great liberties with his subject.

GILL OPENINGS OF THE FRILLED SHARK

Although in most sharks five pairs of gill-openings are present, in *Chlamydoselachus* there are six. This at once places *Chlamydoselachus* in the same category with the other primitive selachians, *Hexanchus* (with six gill-openings) and *Heptanchus* or *Heptranchias* (with seven).

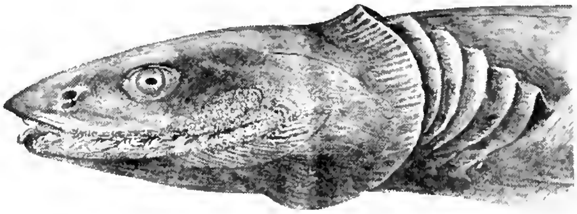
Each gill-opening is guarded by a thin caudally projecting fold or flap which doubtless serves as a valve in addition to providing protection for the delicate gill-filaments. The gill-openings are very large, so that when the great mouth is open for seizing prey, water entering it may readily pass out through the gill-apertures. The members of each series of gill-covers overlap like the shingles of a roof, and each is supported by a number of branchial rays (Figure 6, plate II). In embryonic forms, the gill-filaments project beyond the gill-covers, and even in adults the filaments tend to show beyond the free edges of the gill-flaps. This we have found in some very old and much faded photographs of adult specimens of *Chlamydoselachus* among Dean's materials. These we think he must have brought from Japan. Moreover, Allis (1923) shows the ends of the gill-filaments projecting from under the gill-flaps (Figure 7, plate II). This and the other heads on which Allis worked came either from Dean, or from Japan through Dean's kind services (Allis, 1925, p. 123). None of our adult specimens show extended gill-filaments, so it is evident that not all specimens have them. In this respect as in many others, *Chlamydoselachus* is decidedly variable.

The gill-covers constituting the first (the anterior or opercular) pair require special consideration. These begin a little further dorsally than the others (Text-figures 7 and 8; Figures 6 and 7, plate II; and Figure 16, plate V), and extend so far ventrally that they meet and are continuous across the median line, forming a frill or ruffle (Text-figure 8). In this respect the frilled shark differs from all others of its kind, for in no other selachian does the first pair of gill-folds extend so far ventrally as to meet and form a structure whose free edge is continuous across the isthmus. Thus in *Chlamydoselachus* alone among sharks, does the first or opercular pair of gill-folds foreshadow the condition found in many teleosts where "the gill-membranes are free from the isthmus." However, it may be noted that in the giant basking shark, *Cetorhinus maximus*, the gill-clefts arise high on the dorsum, as they do in *Chlamydoselachus*, and extend so far ventrally as almost to meet. Still Garman says even of the anterior pair in *Cetorhinus* that they are "narrowly separated on the back and on the throat." In *Chlamydoselachus* the gill-covers posterior to the first pair fail to meet ventrally, although their ends approach closer on this surface than on the dorsum—as may be seen in Text-figure 8.

We have noted that *Chlamydoselachus* has an extremely large mouth correlated with voluminous gill-openings. Similar structures are found in the basking shark, *Cetorhinus maximus*, which feeds on small pelagic organisms caught with its large mouth while it is swimming at or near the surface. The whale shark, *Rhineodon typus*, also is known to feed on such food, and it has a mouth which may correctly be characterized as cavernous; its gill-openings, too, are unusually large. But any inferences regarding the feeding habits of *Chlamydoselachus*, drawn from a comparison between its mouth and gills and those of *Cetorhinus* and *Rhineodon*, are likely to be misleading if we neglect to compare the teeth. For the two latter sharks have many thick-set minute teeth, while *Chlamydoselachus* has relatively few teeth, each with several (3—5) slender, recurved barb-like cusps or denticles, obviously adapted for holding rather large prey struggling to escape.

In *Chlamydoselachus* the peculiar structure of the gill-covers is so conspicuous as to form one of the most distinctive characters of the animal. The resemblance of the opercular fold to a short cloak or mantle suggested to Garman the generic name *Chlamydoselachus* of which the common name "cloaked shark" or "frilled shark" is a free translation. The dorsal portion of each gill-flap is thrown into a projecting fold which is particularly conspicuous in the first pair. Presumably this is to allow for a large expansion when the mouth is open and a large volume of water is passing through. These folds can be seen on all the figures of the fish in this paper. However, they are particularly well shown in Text-figures 7, 8, and 11; in Figures 6 and 7, plate II; and in Figure 16, plate V.

Correlated with these gill-flaps in the feeding-respiratory activities of the frilled shark is the curious crescentic maxillary fold, which as we have suggested (page 269) may function as a breathing-valve. When the mouth is partly closed on prey merely "nipped" by the outer front teeth, the breathing-valve perhaps helps to prevent the regurgitation of water during the process of expulsion of the water through the wide-open gill-slits.



Text-figure 11
A side view of the head of *Chlamydoselachus* to show the position and length of the lower jaw, the position of the nostril and of the eye, and the position and form of the gill-covers.
After Garman, 1885.2.

THE TRUNK OF *CHLAMYDOSELACHUS*

The trunk of *Chlamydoselachus*, or that part of the fish extending from the head to the end of the body-cavity, is in many ways different from that of other sharks. Its structures and their position and arrangement present a number of interesting variations and include at least one organ not previously noted in other fishes—the tropeic folds

GENERAL FORM

The absence of an anterior dorsal fin, together with the bunching of the single dorsal, the anal, and the pelvic fins behind the middle portion of the body as a whole and in close contiguity to the caudal fin, gives the fish a somewhat three-tailed appearance when viewed from the side, and leaves the body proper entirely unobstructed almost from head to vent. Garman (1885.1, p. 1) says of his 1511-mm. (59.5-inch) specimen (Text-figure 1) that for a distance of almost two feet the body was entirely unrelieved by fins. This is better shown in Garman's drawing reproduced as our Figure 16, plate V. In Collett's

(1897.1) 1910-mm. specimen (Figure 3, plate I), the body from last gill-slit to vent measures about 975 mm. (38.4 inches), as nearly as we can determine from his data. Carlos de Bragança's specimen (1904) was 920 mm. long (36.25 in.), and from the hinder edge of the pectorals to the front edge of the pelvics measured 265 mm. (10.4 in.). Lastly, Maurer's fish (1912) was 1330 mm. (32.4 in.) in length, of which 500 mm. (19.7 in.) was the distance from the shoulder-girdle to the anus.

The measurements of the unobstructed portion of the bodies of our three long-preserved specimens (from the hinder edge of the base of the pectoral to the front edge of the base of the pelvic) are: No. I (1350 mm. or 53.1 in. long over all), 381 mm. or 15 in.; No. II (1485 mm. or 58.4 in.) 483 mm. or 19 in.; No. III (1550 mm. or 61 in.) 483 mm. or 19 in. Note that while fish No. III is 65 mm. (2.5 in.) longer than No. II, the above measurements are the same. These measurements, though made on fish long in preservative and very much bent, are fairly accurate, and they clearly show that here as in other measurements and structures of this fish there are variations.

The body, from pectoral to pelvic fins, is everywhere about the same diameter. This may be noted in Garman's specimen (Text-figure 1), in Günther's and Collett's specimens (Figures 1 and 3, plate I), in Bolivar's reproduction of a photograph (Figure 4, plate I), in Mertens' drawing (Text-figure 4), and in Lozano Rey's fish (Text-figure 5). However, it is not true of Bertrand's full-bodied specimen (Figure 5, plate II) which is a female and probably gravid as was Nishikawa's fish (Text-figure 2). It is also not true of the Japanese fish figured by Ito (1930), which is a female, and which because of the very large abdomen we believe to have been gravid (Text-figure 6). We cannot give girth measurements for our three specimens because they have all been opened and partly eviscerated.

We have noted that the placement of the locomotor organs around and behind the cloacal aperture gives the body a somewhat three-tailed appearance when viewed from the side. This, taken in conjunction with the practically uniform diameter of the body proper, accentuates the elongate form. This appearance is helped also by the fact that there is little or no compression save in the region behind the cloaca. In general appearance, our shark is more eel-like than any other known to us.

In *Chlamydoselachus* the pointed sub-triangular snake-like head, the slender sinuous body devoid of an anterior dorsal fin and having about the same diameter throughout, the flexible make-up of the fins and their bunching far behind where the body is smaller, fit the fish for gliding eel-like in and out of crevices in rocks and wrecks. It is evident that it could worm its way out through the fairly large meshes of a beam or otter trawl, and this may in part account for the fact that so few have been taken in such trawls even in localities where the fish is known to live and where such fishing is carried on. Further, we conjecture that its motion in swimming must be sinuous and is probably rather slow.

We, like others before us, have pointed out certain superficial resemblances between *Chlamydoselachus* and an eel, but Dr. W. K. Gregory, in a personal communication to the writers, comments on this matter as follows:

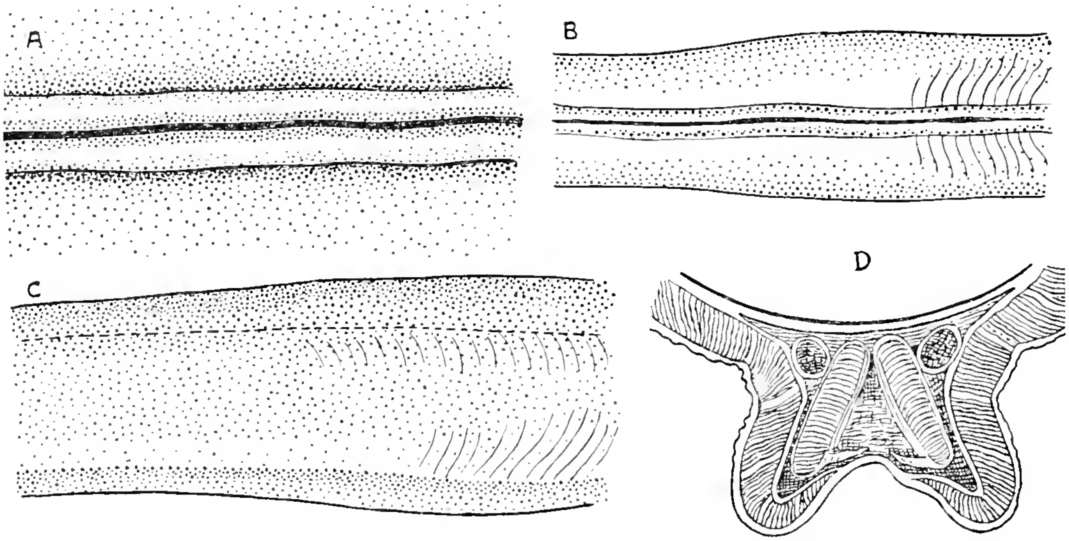
> *Chlamydoselachus* differs profoundly from all eels in the possession of large well developed flat pelvic fins, of stout shark-like pectoral fins and of a heterocercal tail utterly unlike the gephyrocercal tail of eels. The cross sections of its head and body differ widely from those of eels. Therefore I cannot believe that its motion is especially eel-like. Its vertebrae are utterly different from those of eels and therefore unfavorable to the extreme flexure of the body. The musculature of *Chlamydoselachus* is thoroughly shark-like and it seems to me that the eel-analogy has been greatly overdone in the literature and that it is simply an elongate shark in movements as in anatomy.

TROPEIC FOLDS

These curious structures, found in no other shark so far as we know, were first described by Garman (1884.1, p. 51) in his 1511-mm. female fish as follows: "Under the middle of the belly, the skin forms two closely approximated rolls or ridges separated by a groove, and inside of these the muscle is thicker than toward the flanks." Garman for the same fish (1885.2, p.3) again refers to the fact that "A prominent doubled or grooved keel along the median line of the belly adds considerably to its depth. Toward the pectoral arch and the pelvics the keel loses its prominence. It is largest near the middle of the total length, where it projects three-quarters of an inch, and the groove has a depth of one-third as much." Garman found these folds on his second (female) specimen (1887), but the only other investigators who have noted them are Collett (1897), who found them "very indistinct" in his (1910-mm). female specimen, the largest but one ever captured; and Braus (1898) who studied the innervation of the muscles of this region and concluded that the groove between the folds is formed by an infolding of the body-wall.

We have examined all our specimens for these folds and present the following findings. Our fish No. II (a female, 1485 mm. long) shows only a trace of the folds reaching from the middle point of the abdomen for about 125 mm. (5 in.) forward. This fish has been split down the center line of the belly, and we at first thought that this had obliterated the folds. But had this slit been made along the groove, the elevations would show on either flap. However, our fish No. I (1350 mm.), also a female, shows these folds well developed. They extend from about a line joining the posterior edges of the bases of the pectorals backward 340 mm. (13.3 in.) to a point about 25 mm. (1 in.) in front of the bases of the pelvics. This fish has been split open to the left of the folds and the right abdominal wall is very much crumpled, which may in part account for the shallowness of the anterior fourth of the groove; back of this, the groove is quite uniformly 4 mm. in depth except at the end where it shallows out. Finally, our largest fish (No. III, 1550 mm. long), also a female, has had the ventral wall split to the right of the tropeic folds. These extend from a line joining the middle parts of the pectorals backward 385 mm. (15.1 in.) to flatten out about 45 mm. (1.75 in.) in front of the bases of the pelvics. The groove varies from about 2 mm. to about 4 mm. in depth. It should be borne in mind that all our measurements are made on specimens badly shrunken by long immersion in preserving fluids and much crumpled by being curled up in containers.

All the above notes pertain to adult females—Garman's and Collett's specimens and our three. There are now to be considered our six embryos. Our two larger specimens, a male 374 mm. long and a female 320 mm. long, have long been in strong formalin. The keel in each is very marked, 3–4 mm. high, with only slight indications of a median groove on its outer surface. However, our four small embryos (males, 305 mm., 245 mm. and 210 mm. respectively, and a female only 190 mm. in total length) all have well-developed keels with equally well-developed grooves along the mid-line. In these embryos, especially in our two larger, these keels are so marked as to give the abdomen of each a very definite resemblance to the lower V-shaped hull of a racing yacht.



Text-figure 12
The tropeic folds of *Chlamydoselachus*: A, of an adult from below; B, of an embryo from below. In both, the central dark line is the bottom of the fold, the white lines mark the top of the fold, and the outer dark lines the outside bases of the fold. C is a lateral view of a part of the side of an embryo showing the lateral line, the myomeres, and the side of the fold. *D* is a section of the tropeic fold in an adult, copied from Garman, 1885.2.

To illustrate these structures we have had drawings made (Text-figure 12). The legends to these make unnecessary any further description. The structure of these unusual organs will be further described in an article on the anatomy of *Chlamydoselachus*.

As to the function of this curious structure, but two conjectures have been made. Garman (1885.2, p. 3) first described this from a fertile female and stated that "the prominence of the keel and its folds was looked upon as a possible sexual development, appearing when the young are carried." However, its marked appearance in our male embryos, plus the fact that such folds have never been found in any other shark even at breeding season, completely disprove this conjecture. Collett suggested that possibly the huge liver becomes enlarged at times and may then obliterate the ridges and groove—i.e., that they are a sort of "expansion-joint" structure. This does not appeal to us since no shark, much less this one, is known to have such periodic volumetric changes in the liver. On the whole it seems possible that the tropeic folds may have somewhat the same function as the keel of a ship.

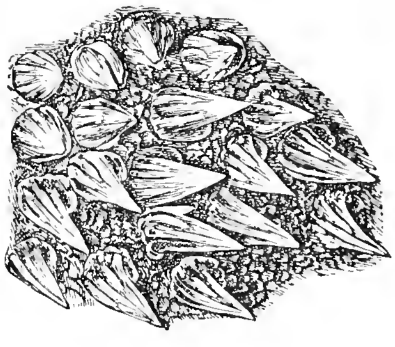
CLOACAL APERTURE AND ABDOMINAL PORES

The cloacal aperture is situated between the posteriorly placed pelvic fins, hence it is posterior to the center of the body as a whole. This aperture in the male fish is portrayed in Günther's drawing (our Figure 17, plate V) as an elliptical opening. In our embryos it consists of a longitudinal slit with somewhat turgid lips. The abdominal pores, a pair of canals leading from the abdominal cavity to the exterior, open on each side of the hinder part of the aperture, each at the summit of a small elevation. In our three adult females we find the abdominal pores in the same place as in our embryos. Each pore is protected on the side by the pelvic fin, and behind by a fold of integument extending from the base of the fins to the ventral surface of the body.

Garman's drawing (1885.2) of the abdominal pores in external view in a female is reproduced herein as Figure 18, plate V. Here, judging by our specimens, the pores are entirely too large. Furthermore, they are shown embedded in a common mass of tissue and in the hinder part of the cloacal aperture, whereas in our specimens they are always separate and situated on the lips of the cloacal aperture in front of its hinder edge. In another plate (his No. XII) Garman (1885.2) figures a dissection of the pelvic fins, cloaca, and abdominal pores of his first specimen. Here these pores are situated one on the hinder part of each side-wall of the cloacal opening.

In the matter of the position of the abdominal pores with reference to the cloacal aperture, we find considerable variation. The position of the pores on Garman's fish and on our three is, we believe, the normal one. Günther (1887), in his Fig. 1, pl. LXV, shows the pores as paired papillae placed behind the hinder rim of the cloacal aperture. A closely similar condition is found in Doctor White's specimen.

Still greater variations, amounting to undoubted abnormalities, are now to be reported. Günther, in one of his male fish from Yeddo Bay, found but one abdominal pore, that on the left side. Furthermore, it was outside of and behind the cloacal aperture. No statement was made as to his third specimen (a female). In our fish No. 1 there are two papillate structures on the side-walls of the cloacal opening just anterior to its hinder end. That on the right is plainly a normal abdominal pore, but no opening could be found in the left papilla. These structures may be made out clearly in our Figure 19, plate V. These openings, together with


Text-figure 13
The dermal denticles at the angle of the mouth (×5). Note the faint resemblance to the form of the teeth.
After Garman, 1885.2.

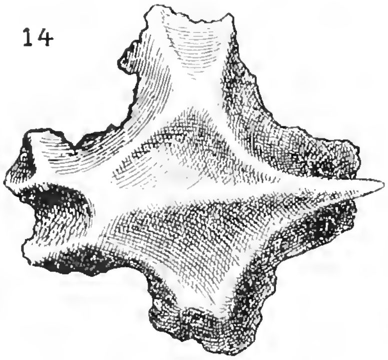
others in the cloacal region, will be further considered in the article on the anatomy of the frilled shark.

DERMAL DENTICLES

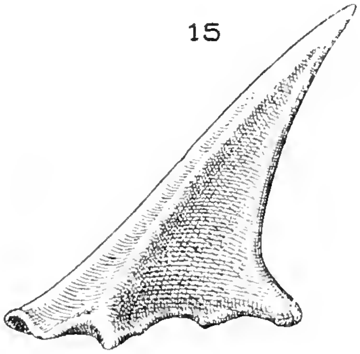
The placoid scales or dermal denticles cover the entire body, including the fins and that part of the sclera which is exposed when the eyes are turned upward; also they line the mouth, gullet, and branchial arches. In sharks generally, the skin with its close-set denticles comprises what is called shagreen. The dermal denticles of *Chlamydoselachus* have been studied by two investigators, Garman and Röse. The former (1885.7, pp. 6 and 7) says:

> Over the entire body the scales are small and irregular in size and shape. On the flank and belly they are polygonal plates, or depressed lumps . . . surmounted by one, two, or three sharp prominences, the median of which is stronger, in places becoming a keel. On the tail this keel is produced beyond the base as a spine. This spine is very sharp, has three longitudinal ridges, and is excavated slightly or flattened beneath. About the mouth and in particular around its angles the spines are larger, more conical, and more erect—more like teeth. [Garman's Pl. VI, fig. 12 reproduced as our Text-figure 13]. Each of a few of these scales has a small cusp near its base. In the mouth, just behind the last row of teeth, there are spines which are more slender, and which have broader bases. . . . From each side of the lateral line elongate scales with chisel-shaped or truncate ends reach out to meet similar ones from the other side, thus forming a cover or protection for the canal. [Garman's Pl. VI, fig. 10—our Text-figure 18.]

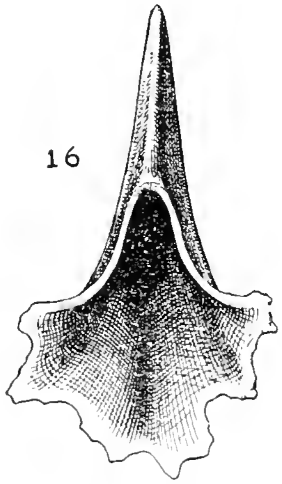
The scales have been studied by Röse (1895) in connection with his work on the teeth. These scales came from a 340-mm. (13.4-in.) embryo taken from the "uterus" of



Text-figure 14
Dorsal view of a placoid scale (×130) from the flank of a 340-mm. uterine embryo of *Chlamydoselachus*.
After Röse, 1895.

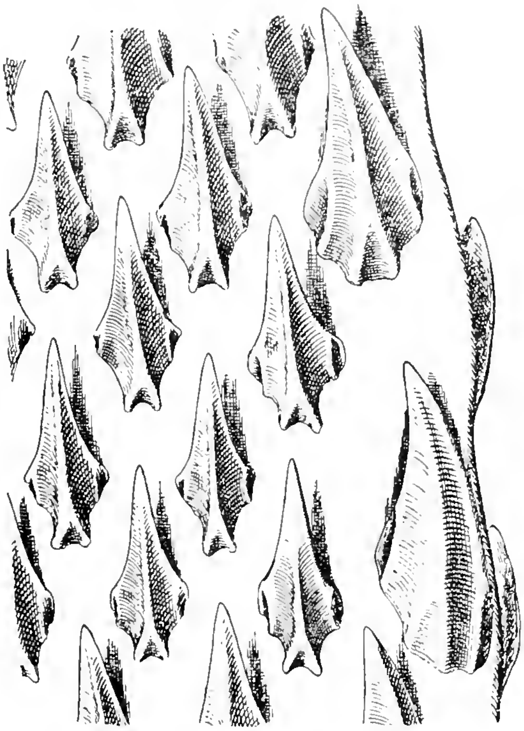


Text-figure 15
Lateral view of a dermal denticle (×130) from the tail region of a 340-mm. uterine embryo of *Chlamydoselachus*.
After Röse, 1895.



Text-figure 16
The scale seen in Text-figure 15 in the same enlargement but viewed from beneath.
After Röse, 1898.

one of Döderlein's specimens previously referred to. Röse's observations in general agree with Garman's, but his figures are drawn to larger scale and are much clearer. We reproduce here his figures 1, 2, 3, and 4 as our Text-figures 14, 15, 16, and 17 respectively. Text-figure 14 shows a placoid scale from the flank. This (viewed from above) shows the prominent spine and the ridges extending from the base to the apex of the spine. These ridges are four in number, three visible and one concealed by the spine itself. Text-figure 15 shows a dermal denticle taken from the side of the tail. In this, the ridge on the right of the figure is the ridge which is concealed when viewed from above as in Text-figure 14. In Text-figure 16, the scale from the caudal region is viewed from beneath and shows the pulp-cavity. Text-figure 17 shows some large dermal denticles from the region of the dorsal fin. Viewed from above in their natural position and orientation, they give an excellent idea of the appearance of the shagreen in a region where this is well developed.

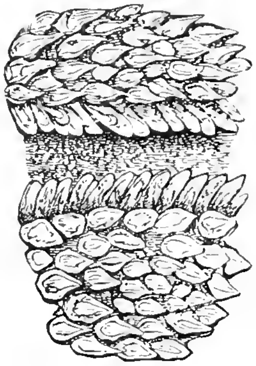

Text-figure 17
Dermal denticles (×30) from the dorsal fin of a 340-mm. uterine embryo of *Chlamydoselachus* shown in their natural arrangement.
After Röse, 1898.

Certain well-developed and highly specialized scales form the "armature" (as Garman designates it) found on the anterior edges of the dorsal fin and of the dorsal lobe of the caudal fin. These are portrayed by Garman (1885.2) in his Pl. VI, fig. 11—our Text-figure 23. For a discussion of these scales see our description of the caudal fin (page 294).

SENSORY CANAL SYSTEM AND ASSOCIATED ORGANS

The sensory canal or lateral line system consists of a sensory canal running along each side of the body and branching over the head. Associated with certain of the canals and innervated by the same nerves are the ampullary organs, which are confined to the region of the head. Allied to these latter are the pit-organs which are found mainly in the antero-dorsal trunk-region but also on the head.

Lateral Line Canal on Body.—This organ system in *Chlamydoselachus* was first described by Garman (1884.1 and 1885.2). In the later article he notes that in the open portions of the lateral canal the margins are formed by a row of flattened scales on each side of the canal, as may be seen in his Fig. 10, pl. VI (our Text-figure 18). This we have verified on our specimens, and particularly on the beautifully preserved head from Columbia University. In a later article (1888), dealing with the lateral line system of

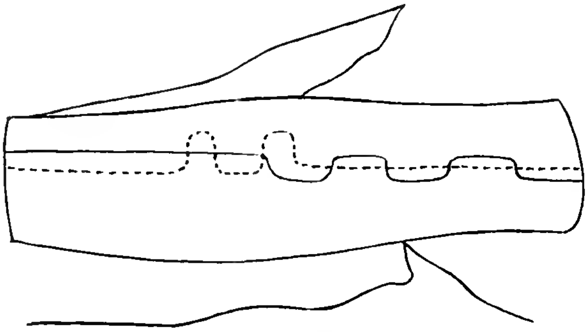


Text-figure 18
Scales (×5) from the lateral line region of the tail of *Chlamydoselachus*. Note the elongate scales which partly cover the open lateral line canal.
After Garman, 1885.2.

Elasmobranchs in general, Garman goes more into detail. However, it does not seem necessary for us to review his description further than to say that in adult fish the canal is a well-marked open groove extending from the head along each side of the body above a crease marking the dorsal limit of the body-cavity (our Figure 5, plate II). On the tail, the canal runs along the lateral surface far out on the caudal fin, as may be seen in any of the figures of the entire animal reproduced herein. On our embryos it extends clear to the tip of the tail.

Observations have been made on certain curious deviations from the normal course of the lateral line canal. Thus Garman (1887, p. 267) writes of his second fish that "the lateral line, with a few short breaks posteriorly, continued to within an inch of the end of the tail." Mrs. Hawkes (1906, p. 964) notes that "In all the specimens examined there is a tendency in the region of the dorsal fin to a departure from a straight line. In two specimens this tendency produced four distinct undulations. . . . In other cases the canal undulated slightly. No explanation of this phenomenon can be offered. This same region had on one side, in one specimen, a complete break of 5 mm." Mrs. Hawkes' illustration showing deviations from a straight line is reproduced herein as our Text-figure 19. These sinuosities are also noted by Garman (1899, p. 44) for his specimens. One of these had on one side "just above the forward end of the caudal" just such an irregularity as that figured by Mrs. Hawkes. Of one of his specimens, Dean wrote in his notebook: "In a small female *Chlamydoselachus*, July, the right lateral line was divided for a distance," and then follows a rough diagram showing the parallel doubling.

To these may be added the following observations on our three adult female fish. On the right side of No. I, about 50 mm. behind the point of the pectoral, the lateral line loops down onto the flank for a distance of 30 mm., and on the base of the tail are sinuosities for a distance of 125 mm. On the left side there is a marked looping downward just anterior to the middle point of the body proper, and there are also some sinuosities under the base of the dorsal. For fish No. II, we note nothing unusual on the right side, but on the left the lateral line curves upward under the tip of the caudal. In our largest and best-preserved fish (No.

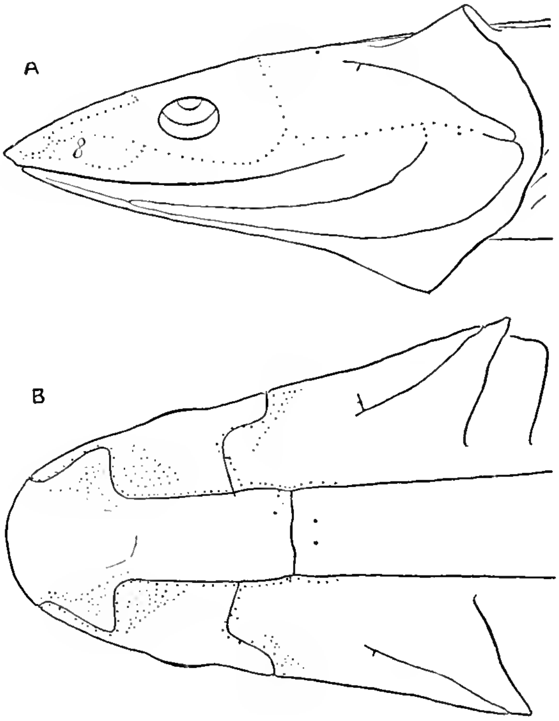


Text-figure 19
Variations in the lateral line canals of *Chlamydoselachus*. The solid line shows those on the left side, the dotted one those on the right.
After Hawkes, 1906.

III) the lateral line is beautifully clear and distinct. On the right side we find marked sinuosities on the "small" of the tail, and on the left are like sinuosities directly opposite.

Whether other sharks show such variations in the position of the lateral lines, we cannot say. At any rate we have never found them. Study of our specimens of *Chlamydoselachus* seems to indicate that variations of position are most likely to occur on the "small" of the tail. This is in confirmation of Garman's and Mrs. Hawkes' observations. These sinuosities of the lateral line in the tail-section of *Chlamydoselachus* are well portrayed in Ito's colored figure (our Text-figure 5). Possibly these variations may be taken as indications of the plasticity of this lowly shark. Following her remarks on these variations, Mrs. Hawkes pertinently states:

> The conclusion arrived at from these facts is that the lateral line system of *Chlamydoselachus* is primitive as regards (1) the open condition of a portion of the canals; (2) the cutaneous rather than subcutaneous position of the canals; (3) the entire absence of tubules in many places. In the occipital and hyomandibular regions, however, the system tends to a considerable complexity. Again there are indications, in the occipital and lateral canals, of either a vestigial or rudimentary complexity.



Text-figure 20

The sensory canals and pores on the head of *Chlamydoselachus*: A, in lateral; B, in dorsal view. The letters designating the canals and pores in the original figure have been erased since in the main they do not agree with present-day nomenclature. For the modern terminology see Allis in Text-figure 21, and Figure 7, plate II.

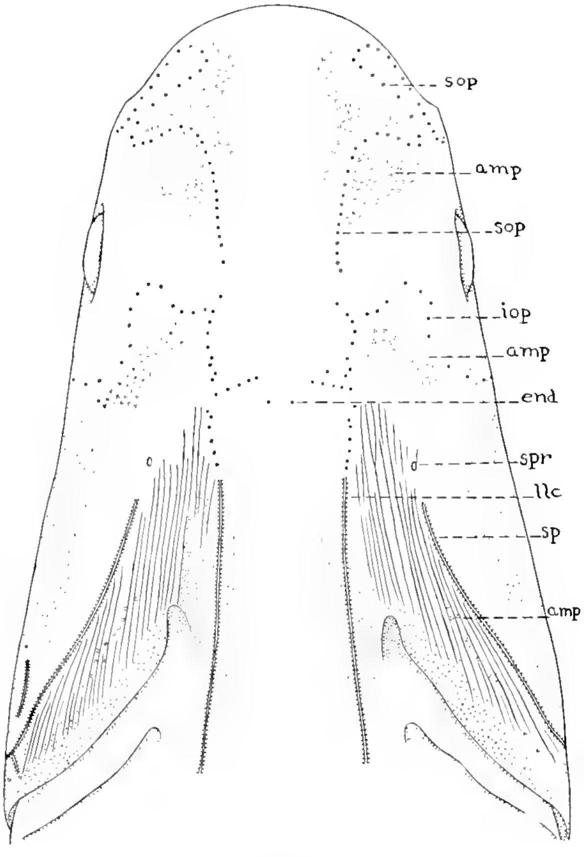
After Garman, 1888.

CANALS, PORES AND PIT ORGANS ON HEAD.—On the head of *Chlamydoselachus* are found many branches of the lateral line system, some open and some closed. These were first figured and described for *Chlamydoselachus* by Garman (1888) in the general paper on the lateral line system in Elasmobranchs above referred to. Garman's figures showing the distribution of these are reproduced herein as our Text-figure 20. The letters giving Garman's designations of these canals, pores and pit-organs have been erased from these figures since they do not agree with present-day practice.

The first critical description of the lateral line and head-canal system of *Chlamydoselachus* is that given by Mrs. Hawkes (1906, p. 960–964) in connection with her work on the cranial and spinal nerves of this fish. She has renamed the head-canals on the basis of their innervation, using the method now generally employed by comparative anatomists.

The latest and best-illustrated work on the lateral line system and associated organs on the head of *Chlamydoselachus* is that of Allis (1923, pp. 195–203). We reproduce his plates as our Text-figure 21 and Figure 7, plate II. It is outside the plan and purpose of this paper to discuss the details of the distribution of the whole sensory canal system on the head of our fish. They are clearly shown in our reproductions of Allis's figures and in the explanation of his lettering of his drawings, and any one seeking an exact description of them is referred to his text.

Intimately associated with the lateral line system on the head of *Chlamydoselachus* are the pores of the ampullae of Lorenzini and of the pit-organs. The distribution of these organs and canals is adequately portrayed by Garman (our Text-figure 20), and by Allis (our Text-figure 21 and Figure 7, plate II).



Text-figure 21

Dorsal view of the head of *Chlamydoselachus*, showing the external openings of the ampullae of Lorenzini and of the latero-sensory canals.

amp, ampullary pores; *end*, pore of the endolymphatic duct; *iop*, infra-orbital latero-sensory pores; *llc*, lateral line canal of body; *sop*, supra-orbital latero-sensory pores; *sp*, spiracular latero-sensory canal; *spr*, spiracle.

Redrawn after Allis, 1923.

THE TAIL OF THE FRILLED SHARK

As we shall see later, the Japanese call *Chlamydoselachus* the "lizard shark," probably because of its elongate slender body terminating in a long slender pointed tail. The tail of our fish includes all those structures posterior to a transverse plane cutting through the cloacal opening. The tail is compressed laterally and on its anterior portion bears the dorsal and anal fins. The hinder part of the tail bears the caudal fin, and its structure will be more conveniently described later in connection with that organ. However, we here give some measurements. Garman's first specimen (1884.1) lacked the tip of the tail, but of his second, which was 1220 mm. (48 in.) long, he wrote (1887) that "the tail was a little more than one-fourth of the total length." In Collett's (1910-mm.) specimen, the tail from the anterior base of the anal measured 470 mm. (24 per cent), a fair agreement with Garman. However, Bragança's (1904) measurement was a 405-mm. tail on a 920-mm. specimen. Here the tail measures 0.44 of the total length.

The measurements for our much shrunken and wrinkled adult female specimens follow. No. I is 1350 mm. long and has a tail measuring 531 mm. or 39 per cent of the total length. The tail of No. II is 555 mm. long, the total length 1485 mm. The tail then equals 0.37 of the whole length. In No. III, the "over all" length is 1550 mm., and the tail measures 650 mm. or 0.42 of the whole length. These proportions are startling, but they have been taken over and over again until we are sure that they are correct. One has to see the fish to realize just how much of it is tail (not merely caudal fin).

THE FINS OF *CHLAMYDOSELACHUS*

The fins are very soft and flexible, and while primitive in structure they are typically elasmobranch in character. From the natural history point of view, the most interesting facts about them are the absence of the first dorsal; the bunching of the pelvics, the anal and the single dorsal well behind the middle point of the body; and lastly the peculiar shape and structure of the tail and the tail-fin.

PAIRED APPENDAGES

Like most fishes our shark has both pectoral and pelvic fins. As in Elasmobranchs generally, the pelvic fins are modified in the male to form the claspers or copulatory organs.

Pectoral Fins.—The low-placed pectoral fins are of moderate size and are broad and rounded. Both front and hinder margins are convex—the hinder one the more so—and these curves meet at the extremity of the fin in an obtuse angle. This is true of the three adults and the six embryos in the American Museum, and it is the form portrayed in all the figures reproduced herein, save Günther's (Plate I, figure 1) where the fin is shown in oblique view. These fins are remarkably flexible in comparison with the pectorals of other sharks.

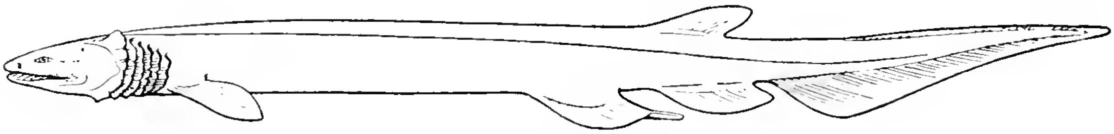
Pelvic Fins.—These fins are placed somewhat behind the middle point of the body, measured from tip to tip. They are larger than the pectorals and are even more broadly rounded. The base of each fin is unusually broad, in the female equalling about twice the depth. These proportions are found in our embryos and are portrayed (sometimes imperfectly) in the figures already given. The elongate base is especially well shown in Collett's figure of his female specimen reproduced in our Plate I, figure 3. Garman (1885.1, p. 4) says that in his female specimen each pelvic fin "ends in an acute point behind the vent," as may be seen in our Text-figure 1 and Figure 16, plate V. We find this true in our specimens, although the point is hardly so acute as is shown in Garman's figure.

Myxopterygia.—In the male, the bases of the pelvics are even longer than they are in the female, since in the male these fins are modified to form the claspers, copulatory organs, or myxopterygia. In fact, the edges of the fins reach nearly to the ends of the appendages. In *Chlamydoselachus* these organs were first studied and figured by Günther (1887), but since they do not show in his drawing of the entire fish (our Plate I, figure 1), because the body is drawn with the tail bent to the left, Günther had them figured in ventral view (Figure 17, plate V). So far as we know, there are but three other figures of male specimens: Doflein's (1906) from Japan, Bolivar's (1907) from Spain, and Goodrich's without designation of source. Both Doflein's and Bolivar's figures (Plate I, figures 2 and 4) portray the claspers as being much larger than they appear in Günther's drawing.

Goodrich's figure[5] seems to us more normal and for that reason is reproduced herein as Text-figure 22. Our adult specimens are unfortunately all females, and our embryo males have only rudimentary claspers, so we are unable to add anything here. Günther's brief statement of the external conditions is as follows:

> The membranous margin of the ventral [pelvic] fin of the male is attached to the outer and upper side of the clasper, leaving only the terminal third of the latter free, as is the case in the Notidanidae generally, whilst in other sharks the fin and the clasper are separated by a more or less deep notch.

The only other investigator who has studied the claspers is Goodey (1910, pp. 563–567). His work is chiefly anatomical and will be reviewed in another paper. He gives some measurements, which are of interest in themselves and because they seem to be the only ones ever made. His male fish was 1300 mm. (52 in.) long. The length of girdle and appendage (myxopterygium) was 214 mm. (8.5 in.), the appendage was 112.5 mm. (4.5 in.) long, but the free part was only 48 mm. (1.9 in.) long. The greatest width of the appendage was 14 mm. (0.6 in.) and the greatest width across the fins 125 mm. (5 in.). Goodey notes that, compared with the pectorals, the pelvics and appendages are quite large, that this size is mainly in the fin since the appendage is very short, and that the skin covering the terminal part of each appendage is very soft and is entirely lacking in the dermal spines ordinarily found on this organ in other Elasmobranchs.



Text-figure 22

Lateral view of a male *Chlamydoselachus*. Note the length of the claspers in comparison with those shown in Figures 2 and 4, plate I, and in Figure 17, plate V.

After Goodrich, 1909.

As may be inferred from Günther's figure of the pelvic fins and claspers (our Figure 17, plate V), and from Goodey's measurements and descriptions, these latter organs are very primitive and simple in make-up when compared with the elaborate structures usually found in the more highly specialized sharks and rays. This is an additional proof of the lowly position of this shark.

UNPAIRED FINS

Leaving the paired fins, we now turn to the unpaired ones which present several features of interest from a natural history point of view.

DORSAL FIN.—Unlike most sharks, *Chlamydoselachus* has but one dorsal fin. This is placed far back and apparently corresponds to the second dorsal of other sharks. This

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[5] E. S. Goodrich. Vertebrata Craniata (Cyclostomes and Fishes). In Lankester, E. R. Treatise on Zoology, 1909, vol. IX, fascicle 1, (*Chlamydoselachus*, pp. 140–142, figs.).

position of the dorsal fin allows a more sinuous motion of the forepart of the body. Garman (1885.2, p. 13) speaks thus of the "comparatively small dorsal":

> This fin begins above the origin of the anal, as is indicated by the peculiar armature of the upper edge, and gradually rises backward to terminate in an acute point about opposite to a similar point on the anal fin. Both upper and lower (anterior and posterior) margins are curves which meet in the apex.

For illustrations showing this fin, as well as the anal and caudal fins now to be described, see Text-figure 1 and Figures 1 and 2, plate I. The matter of the "armature" will be taken up later in considering the like structure on the dorsal edge of the caudal fin.

ANAL FIN.—This fin, in most sharks a relatively small structure, is in *Chlamydoselachus* an unusually large one. Originating a short distance behind the cloaca and immediately underneath the origin of the dorsal, its tip extends backward to the point of origin of the ventral lobe of the caudal. Arising from a base unusually long for a shark, the total length of this fin is about three times its depth. It has a smoothly rounded outline, except that in some specimens an acute angle is formed by its posterior extremity. However, in two of our fish this point is rounded. This fin is well shown in Garman's drawing (our Figure 16, plate V) and in Günther's lithographed figure (our Figure 1, plate I). From the size of the anal fin, we judge that it is of considerable use in locomotion.

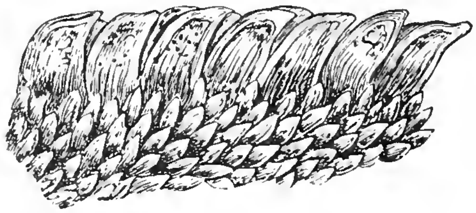
CAUDAL FIN.—In sharks this fin includes the hinder portion of the tail. In *Chlamydoselachus* the caudal fin is such a unique structure, and there is so much diversity in the figures and descriptions of it, that it has been necessary to study it with much care. The published figures and descriptions will be taken up in chronological order, and then our own observations will be presented.

Garman's first illustration (1884.1), shown in our Text-figure 1, portrays a tail-fin having a gentle curve upward, with a rudimentary dorsal fin-lobe devoid of rays, and on the ventral surface a large fin-lobe with many rays. His second and more finished drawing (1885.2) shows these structures better (see our Figure 16, plate V). The tip of the tail of this first specimen ends abruptly as if it had been bitten off. This, apparently, he did not recognize until he examined his second fish, when he wrote a short note (1887, p. 267) correcting his oversight. Here he says that the tail of his first specimen was "deformed and incomplete; the deformity in all likelihood being of embryonic origin." The particular thing to which we wish to call attention here is that in both his figures the tail-fin is bent upward shark-fashion.

Günther (1887) in our Figure 1, plate I, portrays the tail of *Chlamydoselachus* as a long, slender, pointed organ, with a serrated dorsal edge, extending the line of the body straight backward, but in its hinder half (which comprises the tail-fin) drooping slightly below this line. The tail-fin has a rudimentary dorsal lobe. This fin-lobe begins under the tip of the dorsal and increases gradually in height until well toward the end of the tail. At the tip it becomes continuous with the ventral lobe of the caudal fin. In Günther's figure the dorsal lobe of the caudal fin has a serrated edge which might be interpreted as due to projecting fin-rays, but it is really what Garman (1885.2, p. 3) calls an "armature" comparable to that found anterior to, and on the upper (free) edge of, the dorsal fin. This "armature" on dorsal and caudal is explained by Garman (1885.2, p. 7) as follows:

> The upper edge of the tail and its posterior border, to the lateral line, are armed by a sharp edge of scales. The edge is formed of two rows—one from each side—of broad, thin, subquadrangular scales, which have met on the median line and become so closely applied as to appear a single ridge. Each scale entering into the construction of the edging is opposed to two others, in this manner imbricating or breaking joints [our Text-figure 23]. . . . Similar scales guard the front or upper edge of the dorsal.

This description fits our adult fish save as to the matter of the abbreviated posterior border of the tail at the end of the lateral line. Here the healing of the wound in Garman's specimen had brought the scales across the stump. In our three specimens the tails are fairly complete and the imbricating scales ("armature") of the caudal fin grow smaller toward the posterior end and finally disappear entirely. For the last three or four inches of the tail, the dorsal edge of the caudal fin is made up of the fine dermal fin-rays held together by the membrane of the fin. There are still scales on the sides of the fin.



Text-figure 23
The scales (×5) from the upper part of the caudal fin. Note the imbrication of the large scales on the edge to form the "armature."
After Garman, 1885.2.

Garman (1884.1, 1885.2) shows (our Text-figure 1, and Figure 16, plate V) a mutilated tail-fin with the ventral lobe deeper anteriorly, diminishing only very gradually and ending in a fine point below the tip of the solid part of the fin. Günther (1887) shows a large ventral lobe, deepest anteriorly, where it begins above the tip of the anal, and becomes gradually lower to the tip of the tail where it is confluent with the dorsal lobe (our Plate I, figure 1). In this ventral lobe the fin-rays are plainly visible, as they are in one of Garman's drawings.

Of the three figures reproduced from photographs of *Chlamydoselachus*, Collett's (Figure 3, plate I) is the largest and clearest. Here the tail-fin, although somewhat dried and wrinkled, has a gentle upward bend like that portrayed by Garman. On the dorsal surface is found the remnant of the narrow dorsal fin-lobe. The ventral lobe is deep in front and tapers backward toward the end of the tail. The fin-rays are quite apparent in this lobe.

Of Iberian fish, Bolivar's photograph (1907), shown herein as Figure 4, plate I, was made from a badly shrivelled specimen. In general the tail is similar to that in Günther's figure. Bertrand (1926) reproduces a photograph of his apparently fresh specimen (see Figure 5, plate II herein). The tail of this fish is very much like that of Günther's specimen—apparently straight. The tail is either especially posed that way or appears straight because this heavy-bodied fish has the trunk rotated away from the camera in such fashion as to straighten the tail. This we judge from the high position and the curvature of both the lateral line and the crease marking the upper limit of the abdomen.

Other figures, presumably drawings, to which reference must be made for the structure of the caudal fin will now be considered. Doflein's figure (our Figure 2, plate I) is well drawn save that the pectorals are pointed and the claspers are very large. The caudal is sinuous, as is the whole body of the fish. This is presumably the artist's conception. Mertens' sketch (1921) is made from a stuffed skin. Here the fins are shrivelled and the tail has the shark-like bend with a decided droop at the tip (see Text-figure 4). The next figure to be considered is Lozano Rey's (1928), reproduced herein as Text-figure 5. So far as we can judge, this figure is apparently redrawn from Günther's plate (our Figure 1, plate I). The body instead of being curved is drawn straight, and the tail curves slightly upward, the tip alone having a barely perceptible droop. Last of all is Ito's drawing (our Text-figure 5), which shows the tail-fin slightly bent upward above the axis of the body. The dorsal lobe is very inconspicuous, the ventral lobe is larger but hardly so large as shown in other figures. Noticeable is the great thickness of the muscular part of the tail between the lobes. This seems to be accentuated in this drawing.

We now come to a consideration of the caudal fins of our three adult female specimens. First it must be said that these fish have been in alcohol and formalin for twenty-five or thirty years, coiled up in barrels, hence we cannot be sure as to the form of the caudal fin with reference to the axis of the body. We can only describe them as they appear today. Fish No. I (1350 mm.), laid out as naturally as possible, has a caudal fin with a slight upward bend, nearly as marked as that in the specimen figured by Garman. This fin (of fish No. 1), measured from the origin of the lower lobe to the tip, is 330 mm. long. No. II (1485 mm.), handled in the same way, has the caudal fin continuing the line of the body backward but drooping in its hinder half. It is almost a counterpart of that figured by Günther. Taken as above, it measures 335 mm. with the very point of the tip missing. No. III (1550 mm.) has the caudal fin very much crumpled and the lower lobe much torn, but it has a complete tip. This fin seems to extend in line with the axis of the body, very like the fin on Bertrand's or Lozano Rey's specimens. Measured as above, its length is 395 mm. The caudal fin of the specimen brought from Japan by Doctor White droops at the tip very much like that portrayed by Mertens (our Text-figure 4).

In our adult specimens, the upper lobe of the caudal fin arises at a point just below the tip of the dorsal fin and directly over the origin of the ventral lobe of the caudal; it increases very gradually in height until it reaches its maximum about two-thirds of the distance from its origin to the tip of the tail. It maintains this height almost to its extremity, where it becomes continuous with the lower lobe. Fin-rays are apparently lacking in approximately the anterior third, but are present though not distinctly visible in surface views throughout the posterior part of this lobe.

The ventral lobe of the caudal fin is very much larger than the dorsal lobe. Deepest at its anterior end, and becoming lower posteriorly, it is continuous with the dorsal lobe at the tip of the tail. Accordingly it has a gently flowing outline (Plate I, figure 1). In all three of our adult specimens the fin-rays are remarkably distinct in the ventral lobe, and the same thing is true of the six large embryos in our collection.

There is now to be considered the matter of the notch toward the posterior end of the ventral lobe of the caudal fin, a feature common to practically all sharks. Of it Garman says (1885.2, p. 4) "the tail . . . fin is not divided into lobes by a notch in its lower border." If the reader will now turn to Garman's figure (our Text-figure 1) he will see why this statement was made. However, in his article on the tail of the unmutilated specimen (1887, p. 267) Garman says nothing of any caudal notch, merely stating that the tail "tapered to a sharp extremity." Furthermore in 1913 (p. 15), in his last description of the tail of *Chlamydoselachus*, he writes: "Caudal long, pointed, . . . subcaudal deep anteriorly, narrowing backward, not separated by a notch from the tip." In this he agrees with Günther's figure (our Figure 1, plate I). On the other hand, in Collett's photograph (our Figure 3, plate I), there is shown what seems to be a notch in the hinder part of the ventral lobe of the caudal. A similar notch (?) is shown in Bolivar's photograph (1907.2, Pl. 5), our Figure 4, plate I. However, in both cases this may be wholly or in part the result of rough handling and of drying.

In the other published figures of *Chlamydoselachus*, the conditions with regard to the caudal notch may be briefly stated as follows. Doflein's figure, presumably drawn in Japan from a fresh specimen, shows a slightly sinuous tail with no sign of a notch (our Figure 2, plate I). The illustration in Mertens' article (1921), reproduced as Text-figure 4, shows an upwardly bent tail with a drooping tip without a notch. Bertrand's photograph (1926) shows a straight tail with a lappet at the tip, which is set off ventrally by a notch as may be seen in our Figure 6, plate II. Lozano Rey's (1928) portrayal (reproduced in our Text-figure 6) is almost identical with Günther's figure (our Figure 1, plate I). Lastly, Ito's drawing (our Text-figure 5) shows a tail without a sign of a notch.

Examination of our adult specimens gives the following facts. No. I has an almost perfect tail with the point lacking dermal fin-rays and therefore consisting of the hard central part of the tail. It has no notch and is almost a duplicate of the tail of Bertrand's fish (our Figure 5, plate II). In fish No. II, the tip of the tail has been broken and torn (much as in Collett's specimen), hence we cannot say whether or not it had a notch. No. III, our largest specimen, has a very long slender tip about equally "feathered" with dermal fin-rays above and below, somewhat as in Günther's illustrations (our Plate I, figure 1). It has no notch and is very similar to the tail figured by Bolivar (our Figure 4, plate I). The tails of our six embryos show widely differing tips, which will be described in a future article on the embryology of *Chlamydoselachus*.

In all the figures and descriptions of the tail of *Chlamydoselachus* given above, and in our own material, we find this organ unusually long and tapering. In many specimens it continues the axis of the body nearly straight backward, in others it has a decided upward bend as in most sharks. The dorsal lobe is always insignificant in size, the ventral always relatively large. We believe that an upward slant of the tail is the normal position while swimming. This must be the case in order to bring the large ventral lobe into line with the anal fin and with the body to keep the fish on a generally straight course.

The close association of dorsal, anal and pelvic fins with the caudal, gives the creature a fulcrum on which to straighten its body in striking forward to seize its prey. This was first suggested by Garman. In ordinary swimming, right and left strokes of the caudal will send the body forward with the sinuous motion common to all slender fishes.

FOOD OF *CHLAMYDOSELACHUS*

Comment has already been made that the large mouth with its distensible jaws fits *Chlamydoselachus* for taking in animals of a diameter approximating its own. The large and equally distensible gullet would offer no particular resistance to the backward passage of such large prey. The three-cusped backwardly hooked brier-like teeth would make escape impossible for any soft-bodied animal impaled thereon. Indeed they make difficult the work of exploring the mouth and counting the teeth, as we can affirm. Any handling of the mouth is sure to result in many painful pricks and scratches.

After studying these structures, Garman well remarks (1884.1, p. 55) that they "leave little room for doubt that the food of the creature was such as possessed comparatively little hardness in the way of mail or other armature." Garman's first specimen was partially eviscerated, the stomach and major part of the intestine being gone, and so he could not make any observations on the food of the fish. He did not dissect his second fish. Günther dissected the stomach and intestine of at least one of his specimens, but these organs were empty. Collett (1897.1) certainly dissected his huge specimen, for he states that the stomach was empty. Apparently no one else made such dissections, until Mrs. Hawkes published her investigations in 1907. But as she gives no notes on food, it would seem that her specimen also was empty of food remains. Mertens (1921, p. 176) was the next investigator to dissect the alimentary canal of the frilled shark, also with negative results so far as food contents are concerned. He expressly states that the entire canal was empty. Last of all, Deinega (1925) studied the visceral anatomy. His text is in Russian, but his English résumé refers only to structure, and we doubt if there is any indication of the character of the food.

We have opened the stomachs and intestines of our three adult sharks hoping to find undigested fragments which would indicate the nature of the food of this fish. In the stomach, small and large intestines of No. I there were, aside from some parasites described in the next section, only small quantities of finely divided flocculent brownish material which we were unable to identify under the microscope. In No. II the stomach and small intestine were empty, and in the spiral gut there was only a very small amount of finely divided material which likewise defied microscopical analysis. In No. III the stomach was empty, and the finely divided material in small intestine and spiral gut contained nothing recognizable as organic matter. Doctor White's specimen was eviscerated before it came into her hands, so no information about the food can be had from it.

We have stated elsewhere from Dean's notes that, occasionally at least, squid were used as bait in fishing for *Chlamydoselachus*, and that some specimens were caught by the use of this bait. Presumably, squid form part of the natural food of the fish.

PARASITES OF THE FRILLED SHARK

Two investigators have found parasites in *Chlamydoselachus.* Within the cardiac chamber of his first specimen, Garman (1885.2, p. 19) found, figured, and described a parasitic worm attached to the lower side of the auricle. This parasite was identified by Dr. E. L. Mark as an undescribed species of *Tetrarhynchus.* The specific name *wardii* was given to it in honor of Mr. H. A. Ward, who procured the fish in Japan.

Collett (1897.1, p. 15) writes thus of parasites in his huge fish: "The stomach was empty and did not contain any parasites. Amongst the spiral valves, on the other hand, there were hundreds of a small Cestoid; it was, besides, occupied by a single short and thick Trematoid." These cestodes belonged to the genus *Monorygma*, but they formed a new species to which the name *M. chlamydoselachi* was given by Dr. Einar Lönnberg (1897). The trematode was not positively identified but was thought to be *Distomum veliporum.*

In our fish No. I, we found in the cardiac region of the stomach three roundworms ranging in length from about 3 to 6 in., and in the small intestine (the bursa entiana) five roundworms varying from 2.5 to 5 in. long. It was clear that they belonged to the group Nematoda, but for further identification they were submitted to Prof. H. W. Stunkard of New York University who reports on them as follows:

> I have been able to clear the nematodes from the intestine of *Chlamydoselachus*, and find that they are all females. The largest ones are sexually mature, and the smaller ones are still immature. They obviously belong to the family Ascaridae, but since no males are present it is not possible with certainty to make more detailed identification.

BREEDING HABITS OF *CHLAMYDOSELACHUS*

Elsewhere note has been made of the myxopterygia or claspers which are modifications of portions of the pelvic fins in the male. These copulatory organs, though structurally very primitive in *Chlamydoselachus* (see Figure 17, plate V), indicate that fertilization is internal. This, however, gives no clue to the particular method of reproduction, since in all known sharks, egg-layers and viviparous forms alike, impregnation is internal. Although in many of its structures *Chlamydoselachus* is one of the most primitive of the existing sharks, in its breeding habits it is among the most specialized.

VIVIPAROUS MODE OF REPRODUCTION

Chlamydoselachus is viviparous. This was presumably recognized by its discoverer, Döderlein, in 1881, as we learn from Röse (1895) whose 340-mm. (13.4-in.) embryo came from the body (*Leibe*) of one of Döderlein's specimens. The structure of the reproductive organs will be dealt with in a later article; here we are interested in them only in that they protect and bring forth living young.

Garman's original specimen was partially eviscerated, and in his preliminary paper (1884.1) he does not refer to the reproductive organs. However, in his monograph (1885.2) he figures (upside down) and describes the fragments of the reproductive system left by the fishermen in the process of evisceration—the badly preserved and much torn ovaries, and the oviducal organs lacking the hinder portions. Of one of the oviducts, Garman notes that it was "greatly distended, possibly with young that had hatched within it." Further he says, in describing the nidamental gland, that "The distended condition of the oviduct is the only reason for supposing the eggs to be hatched before extrusion, after the shells have been supplied." This conjecture was later proved to be correct.

Röse (1895), as has been noted in the opening paragraph of this section, first made known that the embryos are carried within the body of the mother. Collett's first specimen (1890), a young female, was eviscerated. However, his second fish (1897), also a female, the largest but one ever taken, was in perfect condition but presumably not gravid. Collett quotes Röse to the effect that *Chlamydoselachus* is viviparous, but it seems very doubtful to us if his own specimen showed this.

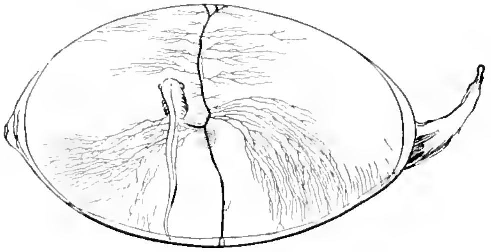
The man who first definitely and clearly demonstrated viviparity in *Chlamydoselachus* was Nishikawa (1898). Here are his own words: "*Chlamydoselachus anguineus* is viviparous, and the breeding season is spring, extending from about the end of March to the beginning of June." He gives a brief description of eggs in the blastula stage, and specifically states that: "The youngest batch of embryos was obtained from a specimen 170 cm. long. . . . There were six embryos, 32, 35, 43, 48, 50, and 60 mm. long respectively." Each embryo was attached to a large yolk-sac.

As pointed out by Nishikawa, the size of the egg in comparison with the size of the parent fish is remarkable. His photograph of a female fish and twelve or more large eggs, presumably cut out from her body, was originally reproduced on unsuitable paper and is therefore lacking in detail; but it is the only figure known to us showing in one view both the adult female fish and its eggs, hence we have reproduced this poor half-tone as our Text-figure 2. The main outlines of both fish and eggs have been retouched to make them sufficiently clear to illustrate the impressive size of the eggs. Since the eggs are so enormous they are necessarily few in number. Of his specimens Nishikawa says:

> The right oviduct [the only one he found fertile] is very much distended and contains 3–12 eggs, these numbers being the limits observed in seven specimens. The oviduct is only 60 cm. [23.6 in.] long, and one can imagine the degree of its distention when as many as twelve eggs, each 11–12 cm. [4.3–4.7 in.] long, are contained in it.

This is indeed remarkable when one compares the long slender body of the fish, of nearly uniform size from shoulder-girdle to pelvic fins, with the broad bodies of ordinary sharks which have large abdominal cavities. Where can room be found for these huge eggs? Here note our Figure 5, plate I, of Bertrand's female specimen, which, because of its full abdomen, we believe to have been gravid. Even larger in body-size is the female *Chlamydoselachus* portrayed by Ito (1931) (our Text-figure 5). This fish has a greater abdomen than any other female figured herein (and we have reproduced every original figure known to us), even greater than Bertrand's. We presume that Ito had before him an actual specimen, and we can only explain this distended abdomen as due to a large amount of ingested food, or to the presence of eggs in the uterus. Of the two conjectures we prefer the latter.

Nishikawa's drawings (his figures 1 and 2) show that the egg of *Chlamydoselachus* has an egg-case produced at one end into a long tapering curved process or hook, and at the other end into a smaller mound-like excrescence. One of the hooks is plainly shown in Text-figure 24. Such an egg-case is to be expected in this primitive form. But one would not expect viviparity in a shark with so many primitive characters, since oviparity seems to have been the primitive method of reproduction among the sharks. Dean himself recognized this fact, for he says in his one communication (1903) on *Chlamydoselachus*, after commenting on the huge size of the eggs, that it is a very archaic type. He adds: "that it was, however, until recently an egg-depositing shark is apparent from the character of the horn-like capsule (with rudimentary tendriliform processes) which the egg still retains."



Text-figure 24
Egg-shell, egg, and embryo of *Chlamydoselachus* shown in one-half natural size.
After Nishikawa, 1898.

With Dean's visits to Japan in 1900–1901, and 1905, the knowledge that *Chlamydoselachus* is viviparous became widespread. Elsewhere it is noted that Dean records the capture of 39 specimens. We know that 12 of these were males, and 27 were females. Dean's fragmentary notes show that 11 females carried 53 eggs in the "uteri." Also, we learn from his notes that other embryonic material was collected and shipped to him. Suffice it to say that Nishikawa's article (1898) and Dean's first visit to Japan shortly thereafter (1900) settled forever the question of viviparous reproduction in the Japanese frilled shark.

The young are born alive, are evidently of large size at the time of parturition, and when they emerge from the cloaca of the mother they are able to forage for themselves. Röse's not-yet-extruded young specimen was 340 mm. (13.4 in.) long. The largest of our six embryos are 320 mm. (12.6 in.) long and 374 mm. (14.7 in.) over all. These are uterine embryos, for though the yolk-sac has been removed from the first, attached to the second (the largest embryo that we have examined) is a huge yolk-sac 80 mm. (3.1 in.) in its longest diameter after being in preserving fluid about 30 years. How large the young are at birth can only be conjectured—we would hazard the guess that they are at least 600 mm. (24 in.) long. When one realizes that there may be as many as 12 embryos in one uterus, one can visualize the tremendous distention of the body of this slender shark during gestation. One can then understand better the huge abdomens of Bertrand's and Ito's fish (our Figure 5, plate I; and Text-figure 5).

In the above paragraphs we have brought together all the data known to us bearing on the subject of the breeding habits. Dean's notes on our fish are very fragmentary. In the notebook labelled CHLAMYDOSELACHUS, we find pages having headings for what was intended to be a natural history of the fish, but nearly all are blank, as for instance is the one reading "Habits in Spawning." However, since this fish is taken at great depths, it is doubtful if we will ever know either the mating behavior or the manner of parturition. The heading quoted above may possibly indicate that Dean saw young extruded from the body of the mother after these were brought on board the fishing boats, or possibly after they were brought to the laboratory at Misaki. This is a thing not unknown in other viviparous sharks.

A final word may be said as to the methods by which viviparity is known to be effected in various Elasmobranchs. In some the embryos, enclosed in a thin diaphanous shell or membrane, lie free in the uterine enlargement of the oviduct. After the yolk is almost all absorbed, they are nourished by a milky fluid secreted by the uterine mucosa which at the time of gestation is developed into villi or thread-like prolongations. In others, having a similar egg-membrane, when the yolk is absorbed the emptied yolk-sac becomes applied to the lining mucosa of the uterus, the two develop interdigitations and there is thus formed a functional placenta—a so-called "yolk-sac placenta." By what process the young of *Chlamydoselachus* are nourished during their last stages cannot be said, since, so far as we know, full-term embryos or fetuses have never been taken. Possibly neither of the above methods is found in *Chlamydoselachus*, since in the earlier stages the egg is surrounded by a fairly thick horny egg-case, of which there are several in our material. Gudger has found that the large egg of the nurse shark, *Ginglymostoma cirratum*, likewise contained in a huge thick shell, is carried in the uterus for a long period of time. The embryos of both sharks have short yolk-cords, which seem to preclude the formation of a yolk-sac placenta. On the other hand, all the Elasmobranchs that nourish the young on a uterine "milk" or by means of a yolk-sac placenta have the eggs enclosed in the exceedingly thin diaphanous shells referred to above, which offer no resistance to the passage of fluids. Probably it will be eventually found that all the food required for the prenatal growth of the embryonic frilled shark is contained in the huge egg, the most enormous in any shark known to us. In this matter, as in many others touching the structure and habits of *Chlamydoselachus*, there is room for further investigation.

Since in this section of our article we are dealing largely with the views of earlier investigators, we have used their term "viviparity." In our opinion the method of reproduction in this shark should be called "ovoviviparity." Presumably, the egg is retained in the uterus until the young embryo is able to burst the shell. Doubtless, this useless shell is then cast out through the cloaca, while the embryo with the huge yolk-sac remains in the uterus until the yolk is all absorbed, and the young shark is fully developed and ready for birth. The question of viviparity versus ovoviviparity in *Chlamydoselachus* will be considered further in the introduction to the article on the outer development of the embryo of this shark.

BREEDING SEASON

On this subject we have information from but two men, Nishikawa and Dean. The former (1898) says "The breeding season is spring, extending from about the end of March to the beginning of June." Presumably Nishikawa means that this is the season of copulation and fertilization. Nishikawa obtained an egg having on it a blastoderm 1.3 mm. in diameter. Unfortunately he gives no date for this—it could not have been many days, possibly not many hours old. He also obtained an egg in the blastula stage, and a gastrula 3 mm. in length. Of slightly older forms he writes that "The youngest batch of embryos was obtained from a specimen 170 cm. long, which was brought to the University [of Tokyo?] on the 26th of May 1896. There were six embryos 32, 35, 43, 48, 50, and 60 mm. long respectively." From our knowledge of shark embryology, we judge that these eggs were fertilized at various times during that spring.

From Dean's scattered notes we have gleaned the following data. His earliest material consisted of three blastulae obtained on April 10. Had Nishikawa dated his embryos we could check his dates against Dean's. On April 25, 1903, Dean's collector obtained for him (from two females) twelve eggs with embryos, stages not noted. Two days later the same collector got a female with two embryos, but their stages were not noted. Again he records that on May 25 five large eggs were obtained, but nothing is said about embryos.

From the data given there can be little doubt that the breeding season (the time of copulation and fertilization) begins in the early spring—in March and April. Nishikawa says that it extends until June, but one queries if it may not extend longer, even if it may not last throughout the year as there is reason to believe that it does in many sharks.

PERIOD OF GESTATION

That gestation lasts for a year or more, we judge in part from the huge size attained by the eggs. Dean speaks of some *ovarian* eggs as 60 mm. in diameter and of others measuring 30×70 mm. That these ovarian eggs are unripe is shown by the fact that he records (but did not preserve) an embryo 390 mm. (15.3 in.) long, on a yolk-sac measuring 70×100 mm., while another embryo of 331 mm. (13 in.) sat on a yolk-sac measuring 100×111 mm. Furthermore, Nishikawa speaks of eggs found in the oviduct as measuring "each 110–112 mm. long." Also, Nishikawa recorded living eggs (not yolk-sacs), which he says were ellipsoidal in form, measuring 65–75 mm. in shortest diameter and 102–124 mm. in longest diameter. Apparently it was the egg-cases, not the eggs proper, that were measured, but one can judge, from his figures (our Text-figures 2 and 24), the size of the eggs contained therein.

The second thing leading to the belief that gestation lasts for a year or more is the great size of some embryos taken from the uterus. Dean notes "1905, early Jan., embrs. of 11.5, 15.5, 20 mm." Under date of Apr. 25, he lists embryos of "16.5, 17.5, 18.5, 19.5, 20.5, 21, 25 cm." (165–250 mm., 6.5–9.8 in.). Again "4 embrs., large, taken about May 1, 1905." And last of all "1905, Bt. in Tokyo, June 20, 317.5 mm., 331 (yolk-sac 100×111), 352, 390 (yolk-sac 70×100)"—12.5, 13.85 and 15.35 in. respectively. Our 6 embryos (Dean's material) have been in preservative for about 30 years; the yolks are much shrunken, and are almost as solid and hard as stones. The smallest embryo (190 mm., 7.5 in.) has had the yolk-sac opened and the yolk removed. The 200-mm. (7.9-in.) embryo has a yolk-sac measuring 57×75 mm. (depth and length); the 245-mm. (9.7-in.) young has a yolk-sac measuring 60×74 mm.; for the 305-mm. (12-in.) specimen, the yolk-sac is 57×83; in the 320-mm. (12.6-in.) fish, the yolk-sac (which has been cut off but preserved in the same jar) measures 64×76 mm; and in our largest embryonic specimen, 374 mm. (14.7 in.) long, the yolk-sac is 51mm. deep by 73 long.

This is a huge yolk-mass for any shark's egg, especially when we consider that the volume of this yolk has been diminished by furnishing food for the growth of an embryo 14.7 inches in length, and undoubtedly over a year in age.

In the literature we find but two references to the eggs and young of *Chlamydoselachus*, other than those already mentioned. Ziegler (1908) says that he had three small embryos, two of 25 and one of 75 mm. long. He does not give measurements of the yolk-sac. However, his student Brohmer (1909) worked on the head of the larger embryo and his text-fig. 1 shows egg and embryo "in natürlicher Grösse." The yolk-sac in this figure measures 60×110 mm. It is the only representation known to us of an entire egg, other than those found in Dean's drawings and in Nishikawa's photograph and drawings (Text-figures 2 and 24).

From the data presented, it is certain that gestation lasts at least one year and probably longer. When one realizes that these sharks live at depths of 1500 to 2500 ft., where the temperature is low, one might infer that growth of the embryo is slow as it is in fish embryos reared at low temperatures at the surface; but we have no data concerning the effect of pressure on the rate of development of aquatic organisms. Further, taking into consideration the large size of the yolk-sac in the second year, it seems possible that hatching may not take place until at least the second summer following impregnation, and indeed that it may not take place till after the little shark is quite two years old.

NOMENCLATURE OF *CHLAMYDOSELACHUS*

Generally, in fishes as in other animals, various describers have given different names to one and the same animal, hence it becomes necessary to prepare an extensive list of names, the synonymy of modern authors. However, *Chlamydoselachus* is such a definitely characterized fish that only two attempts have been made to change its name from that first given it. These will be recounted in their proper places.

SCIENTIFIC NAMES

In giving this fish the name *Chlamydoselachus anguineus*, Garman exemplified the best ideal of nomenclature—which is to make the name accurately and briefly describe the thing named. Literally translated, this name means 'snake-like cloak [-gilled] shark,' and how correct this is may be seen in Figure 1, plate I. The body is attenuate and flexible, the fins (except the pectorals) are set far back, the head is flat, the mouth is subterminal and has a wide gape, and the eye with its overhanging brow is decidedly reptilian. Thus in many respects the fish has a snake-like appearance.

The generic term comes from the Greek *chlamys*, a cloak; and *selachus*, shark. The allusion here is to the remarkable gill-covers, which as already noted extend from high on the dorsal surface of the head almost all the way across the throat—in the case of the first gill-cover entirely so. *Chlamydoselachus* is the only shark in which the first gill-covers meet to form a continuous fold across the throat. Long gill-covers are found also in the basking shark, *Cetorhinus maximus*, but in it the gill-covers, usually called "gill-straps," tend to lie flat as in any ordinary shark, or indeed in any shark other than *Chlamydoselachus*. As Figures 7 and 16, plates II and V show, what in *Cetorhinus* or any other shark are straps, here become veritable gill-covers, and so voluminous are they that they are thrown into folds, giving rise to the common name "fringe-gilled" or "frilled" shark. However, the term "cloak-gill" must be restricted to the first and most voluminous gill-cover, which as noted entirely crosses the throat.

Despite the fact that Garman (1884.1) had complied with the rules of nomenclature by publishing a figure and description of a specimen of the fish preserved in a great museum, and had given it definite generic and specific names, which as we have seen are accurately descriptive, Günther (1887), without assigning any reason, changed these to *Chlamydoselache anguinea*. However, Garman (1889, p. 43) points out that this new generic name is merely the Greek plural, and that the name should of course be put in the singular, with the specific name in adjectival agreement. Doflein (who has been quoted above) uses Günther's terminology, probably because he had not seen Garman's papers.

One other ill-founded attempt to change the name of *Chlamydoselachus* will be considered later in the section on "Affinities", where its relationship to fossil forms and its place in the system are considered.

The name originally assigned by Garman stands today, but some curious errors in the spelling have crept into the texts of certain foreign authors. Thus Bolivar (1907) spells the specific name *anguinus*, and the indexer of the volume in which Bolivar's article appears writes "*Chlamidoselachus anguineus* Garner." Seabra (1913) writes the generic name in two places *Chlamydocelachus*. Bertrand (1926) makes the same error as Bolivar in writing the specific name, while Maurer's article (1913) prints the specific name *anguinens* on his plate. All these are undoubtedly mere typographical errors.

VERNACULAR NAMES

This fish is so sparingly taken (even in Iberian waters) that, so far as we know, nowhere save in Japan has it any vernacular name. There it is called *Rabuka*. We find this vernacular name in Doctor Dean's notes and in some of the systematic works on Japanese fishes. The word means Silk Shark. This name may possibly be given because its fins, especially the anal and the sub-caudal, are thin and delicate in structure and probably have a waving motion in the water. The Japanese call it also *Tokagizame* or Lizard

Shark, presumably because of its reptile-like head and long slender body and tail. Another Japanese name is *Kagurazame* or Scaffold Shark. This last name we get from Jordan and Fowler (1903). For its significance we can offer no suggestion.

The facts that Doflein (1906) designates this fish as *Schlangenhai* and that Mertens (1921) calls it *Krausenhai*, do not controvert the statement that there are no vernacular names except the Japanese ones known to us, since these terms are merely the German for "snake shark" and "frilled shark" respectively.

AFFINITIES OF *CHLAMYDOSELACHUS* WITH EXTINCT SHARKS

So hot a controversy raged over the supposed relationships of the frilled shark to fossil forms that we think it best to set forth with some care the positions and arguments of those involved in order to show the steps leading to the final conclusion.

Garman's general remarks on the subject are to the point and make an interesting and valuable introduction to the matters considered in this section. His first description of *Chlamydoselachus* (1884.1) appeared on January 17, 1884. In this paper he names our shark and places it in the family Chlamydoselachidae. He remarks on its "embryonic look" and says that this calls for a comparison with fossil selachians, among which however he found none "at all near." He then concludes as follows: "However, the type is one which produces the impression that its affinities are to be looked for away back, probably earlier than the Carboniferous, when there was less difference between the sharks and the true fishes." This thought is repeated and emphasized in his next paper (February 1, 1884) where he adds (1884.2): "I am inclined to consider this [shark] the type of a new order, to which the name Selachophichthyoidi might be given, and which stands nearer the true fishes than do the sharks proper." The erroneous idea that *Chlamydoselachus* "stands nearer the true fishes than do the sharks proper" is possibly based on the presence of such structures as the nearly terminal mouth with the hinges of the jaws at a point behind the skull, and the operculum-like first gill-cover which is continuous across the throat and "free from the isthmus."

SUPPOSED RELATIONSHIPS WITH *CLADODUS*, AND WITH *DIDYMODUS* OR *DIPLODUS*

Garman has been quoted to the effect that he could find no fossil representatives of the selachians "at all near" to *Chlamydoselachus*, although in *Cladodus* of the Devonian, he found (1884.1, p. 55) "a form with teeth somewhat similar, a median and two lateral cones on each tooth, but the cones are straight instead of curving backward and the enamel is grooved or folded instead of smooth." This was also repeated in Garman's second paper (1884.2, p. 117). Garman cautiously called these teeth "similar" and spoke of their mere "resemblance."

Cope, however, did not share Garman's caution. He had not seen Garman's specimen, nor indeed anything pertaining to the teeth of *Chlamydoselachus*, except Garman's figures (identical save for size) in the *Bulletin of the Essex Institute* (1884.1), and in *Science* (1884.2), in which a tooth is represented in three aspects, but so much reduced in size that the minute denticles between the primary cusps are hardly visible under a reading glass. The drawing (the same was used for the figures in both journals) of a tooth may be seen in our Text-figure 1 reproduced in the exact size in which it appeared in *Science*. Nevertheless, Cope, having examined this figure only, proceeded to set forth the following dictum (March 7, 1884.1, p. 276) as to the name and affinities of this shark:

> The figure of the teeth which he gives shows the animal characterized by Mr. Garman to be a species of the genus *Didymodus* (Cope) . . . equal to *Diplodus* (Ag.) . . . , which has hitherto been supposed to be confined to the Carboniferous and Permian periods. The species possesses two, three or four denticles. Material in my possession enables me to fix the position of this genus. . . . *Didymodus* becomes by this discovery the oldest living type of vertebrate.

To this Garman replied on March 21 (1884.3, p. 345) that in *Diplodus* Ag. the median cone remains rudimentary and the secondary cones are enlarged (as may be seen in our Text-figure 25), while in *Chlamydoselachus*, as Garman's figure (our Text-figure 10) shows, the median and lateral cones are very large and the secondary ones rudimentary. Garman then suggested that:

> The propriety of placing living species in fossil genera of so long ago on account of resemblances in a single organ, such as a tooth only of a selachian, is to be questioned. . . . Material in my possession will enable me . . . to prove conclusively that *Chlamydoselachus* does not belong to the genus *Didymodus* of Cope (*Diplodus* Ag.), and that it was hardly safe to announce *Didymodus* as the 'oldest type of Vertebrata' until more was known about *Chlamydoselachus*.

Text-figure 25
Two teeth of *Diplodus gibbosus* Agassiz. A, drawn natural size, has the central cusp very much smaller than the lateral ones. B, much enlarged, has in the center what Agassiz calls a "bouton."
After Agassiz, 1843.

In the same issue of *Science* (March 21), Gill (1884.1, p. 345) took a hand in the controversy. He agreed with Garman that *Chlamydoselachus* is the representative of a new family (Chlamydoselachidae), and of a new order for which he suggested the possible name Pternodonta. However, he dissented from the idea that there are any affinities between *Chlamydoselachus* and *Cladodus*, but agreed with Cope in thinking that *Chlamydoselachus* did have a relative in the Carboniferous *Diplodus* Ag. (*Didymodus* Cope). He did not think that the two were congeneric. Gill considered *Chlamydoselachus* to be near the primitive line from which both sharks and bony fishes have diverged.

Cope, in the *American Naturalist* for April, 1884, again stated (1884.2, p. 413) that the teeth of *Chlamydoselachus* are "identical with those of the genus above named [*Didymodus* Cope = *Diplodus* Ag.]. The species should then be called *Didymodus anguineus*." How far he was in error may be seen by comparing teeth of *Diplodus* *gibbosus* Ag. (our Text-figure 25) with those of *Chlamydoselachus*. In *Diplodus* the two lateral cusps are large and blunt, the central one almost rudimentary, as may be seen in Text-figure 25A. Agassiz[6] shows another tooth of this extinct shark (our Text-figure 25B). Here the two outer cusps somewhat approach the shape of the teeth of *Chlamydoselachus*, but between them is a rudimentary structure called a "button" by Cope. Let us contrast these teeth with one from *Chlamydoselachus* (Text-figure 10). Here we have a central long rather slender cusp, flexible even in the fossil form (Lawley, 1876), and at its base are the two rudimentary cusps, while outside of these are the two lateral cusps which are almost as large as the central one. We cannot see any essential likeness.

Gill at first was inclined to acquiesce in Cope's views of the relations of *Didymodus* or *Diplodus*, but in his next communication (April 11) he brought his unrivalled knowledge of the literature of fishes to bear on the question. He traced (1884.2, p. 429) the history of these names, noted that Cope in 1883 had substituted the former name for the latter, and concluded with the statement that "The distinguished naturalist [Cope] was evidently not acquainted with the researches of his predecessors." Furthermore Gill was able to show that the names *Diplodus* and *Didymodus* are synonymous with *Pleuracanthus*, or with the names of other related forms of the family Pleuracanthidae, all members of which had prominent dorsal spines. Gill was of the opinion that *Didymodus* not only has neither generic nor family relationships with *Chlamydoselachus* but that it belongs to a different order. Lastly he ventured the prediction that a study of the anatomy of *Chlamydoselachus* would show structures most like those of the Notidanidae, but probably more primitive—a relationship now generally accepted.

Following the publication of Gill's note, Cope studied the literature, and acknowledged (May 30) that "On some points I stand corrected." Recognizing the fact that *Diplodus* had a dorsal spine, he agreed (1884.3, p. 645) that *Chlamydoselachus* must be separated from it on account of the structure of the dorsal fin, but he queried "whether such a spine is concealed in *Chlamydoselachus* or not." To this the answer is that there is none. Furthermore, it may be remarked that the Pleuracanthids seemingly lack a well-developed dorsal fin, and that the spine referred to is attached to the dorso-posterior region of the skull.

However, on March 7, 1884, Cope had read before the American Philosophical Society a paper on the skull of *Didymodus*, based on the study of twelve crania from the Permian of Texas. In his paper published in the *Proceedings* (July 1), he again affirmed (1884.4, p. 588) that the teeth of this shark do not differ generically from those of *Chlamydoselachus*, but that the fishes must be separated on the differences in structure of the dorsal fins. His text does not indicate that he had ever seen the teeth of *Chlamydoselachus*, and his figures of the teeth of *Didymodus* certainly show no generic resemblance to those of *Chlamydoselachus*. This will be recognized when one compares his figure of a tooth of

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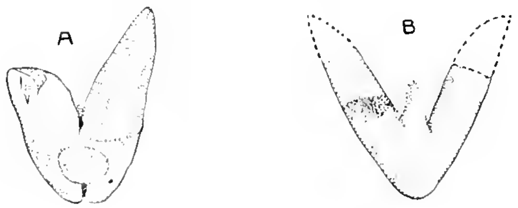
[6] Agassiz, L. Recherches sur les Poissons Fossiles. 1843, Atlas, Tome III, plate 22b, figs. 1 and 4 (*Diplodus gibbosus*), fig. 11 (*Cladodus mirabilis*), and fig. 21 (*Cladodus acutus*).

Didymodus (our Text-figure 26A) with those of *Chlamydoselachus*. Our Text-figure 26B is a copy of another figure of a *Didymodus* tooth on the same plate. Of it Cope said "Superior tooth of external row, without apices of two of the cusps; from the palatine bone of the specimen represented in fig. 5 . . . anterior view." The natural size of this tooth was 7 mm. To facilitate comparison we have had it drawn to the same scale as the other tooth. From a comparison of these figures with Garman's drawing of the tooth of *Chlamydoselachus* (our Text-figure 10), it is plain that there is here no generic relationship whatever.



Text-figure 26
Teeth of *Didymodus*: A, of *D. compressus* Nwb. in natural size (note the "button"); B, of *Didymodus* sp. 7 mm. long, but enlarged to same size as the other tooth (28 mm.). Note the button and the small central cusp.
After Cope, 1884.4.

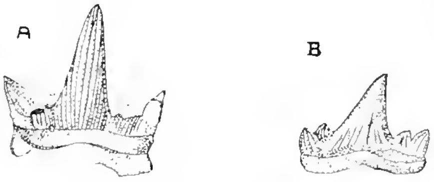
In September, 1884, Garman read before the American Association for the Advancement of Science at Philadelphia a paper (1885.1) in which he presented the evidence that "Under dissection the skeletal structure shows quite as emphatically as the dentition that the claim of Professor Cope that this shark belongs to his genus *Didymodus* is not based on knowledge of the animal," which Garman thought most nearly related to *Heptabranchias* (*Heptanchus*). Confronted with the evidence (possibly dissected material, almost certainly drawings), Cope conceded his error, as we see in Garman's note in *Science* of November 28, 1884, that he "agreed with me that the two genera belong to different orders, and that . . . the nearest known allies of *Chlamydoselachus* were the Cladodonts of the Sub-Carboniferous and the Middle Devonian" (1884.4, p. 484).

Gill in *Science* (Dec. 12, 1884) congratulated Garman on having settled the *Didymodus-Chlamydoselachus* controversy as he (Gill) had predicted it would be settled. However, he dissented as to the relationship of the Cladodontidae and Chlamydoselachidae, but he refrained from any discussion (1884.3, p. 524).

In July, 1885, Garman published his full memoir on the frilled shark. On the basis of his extensive dissections, Garman said that it was not hard to determine that *Chlamydoselachus* is "near to the outlying genera, *Hexanchus* and *Heptranchias*" among recent sharks. However, since it is more unlike the ordinary sharks than they, it lies still "farther from the main body of the Galei."

In the matter of the relationships of *Chlamydoselachus* to the early selachians, Garman said (1885.2, p. 27) that "A further study of both extinct and recent forms enables me to speak still more positively in asserting that *Chlamydoselachus is* [sic] a Cladodont." *Cladodus* is best known from its teeth, and while these bear a general resemblance to those of *Chlamydoselachus*, with which the reader is now familiar, they differ in many details. In Text-figure 27 we have reproduced teeth of *Cladodus mirabilis* and *C. acutus* from Agassiz. In both teeth there is a central large broad-based cusp, with two or three lateral cusps on each side; the outer cusps in each case are larger than the intermediate ones but lower than the central cusp. Furthermore the enamel of all cusps, main and lateral, is grooved or striated, in strong contrast to the smooth enamel of the teeth of *Chlamydoselachus*.

It seems to us that while the teeth of *Cladodus* are constructed on the same fundamental plan as those of *Chlamydoselachus*, they are much more primitive and more like dermal denticles (Text-figures 13 and 17). This is evident in the stoutness of all the spines, the lesser development of the outer lateral spines, the retention of the fluting of the surface, and the lesser degree of development of the enamel.



Text-figure 27
Teeth of *Cladodus* (×1?): A, of *C. mirabilis* Ag.; B, of *C. acutus* Ag. Note lengths of secondary cusps and striations on all cusps.
After Agassiz, 1843.

In the paper just referred to, Garman (1885.2) passed some strictures on Cope's article (synopsized on our p. 307) dealing with the skull of *Didymodus*. So in the *American Naturalist* for September 1885 (pp. 878–879), Cope complained strongly that Garman had made such comments, saying in reply: "The surprise which these criticisms occasion increases when it is understood that they are derived 'from a study of the illustrations' [of the teeth of *Didymodus*] and not of the specimens themselves." In fairness it must be noted that all Cope's pronouncements on the affinities of *Chlamydoselachus* were based solely on Garman's drawings published in *Bulletin Essex Institute*, Jan. 17, and in *Science*, Feb. 1, 1884, and reproduced herein as Text-figure 1 in the exact size in which they appeared in *Science*. Possibly, however, he had later seen Garman's more complete drawings (1885.2, July) of the fish, its teeth, and its various organs. Furthermore in this same note (1885, p. 879), Cope complained that Garman alleged that he (Cope) had replaced the name *C. anguineus* by *Didymodus anguineus*, and stated positively that "I have never proposed or used this name at the places cited, or elsewhere." However, he evidently forgot that he had stated (*American Naturalist*, April, 1884, p. 413) that the name *C. anguineus* could not stand and that "The species then should be called *Didymodus anguineus*."

This controversy was reviewed by J. W. Davis, the eminent English paleichthyologist, whose experience fitted him admirably to pass on the merits of the question. After comparing the structures of *Pleuracanthus* (=*Diplodus*=*Didymodus*) and *Chlamydoselachus* and finding them very different, Davis (1885) concluded that "The resemblance of the teeth as first insisted upon by Professor Cope is only a superficial one and rests simply on the accidental circumstance of each having three denticles."

To make matters still clearer we are reproducing from Davis' paper on the Pleuracanthidae,[7] his drawings of five teeth of *Pleuracanthus laevissimus* Ag. (=*Diplodus gibbosus* Ag.) in natural size (Text-figure 28). These show considerable variation in form

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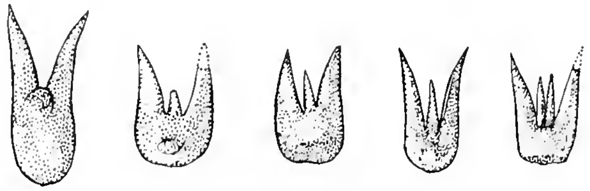
[7] Davis, J. W. On the fossil fish remains of the Coal Measures of the British Isles. Part I, Pleuracanthidae. *Sci. Trans. Roy. Dublin Soc.*, 1892, 2. ser. **4** (*Pleuracanthus laevissimus* Ag. =*Diplodus gibbosus* Ag., p. 726, pl. LXV, figs. 5, 7, 11, 13, 15).

and size, but are evidently teeth of the same species of shark. Study of them fails to show any generic relationships with *Chlamydoselachus*. Of these teeth, Davis wrote:

> The teeth of *Pleuracanthus laevissimus*, Ag., vary greatly in form; there are two principal cones, circular, or more or less compressed, with or without lateral cutting edges, sometimes striated. The cones are divergent, and frequently exhibit a slightly sygmoidal curvature. Between the two outer denticles is a smaller intermediate one [sometimes two], which may be short and compressed or comparatively long and slender. On the posterior surface behind the smaller intermediate denticles is a 'button,' which forms the seat on which the anterior part of the base of the succeeding tooth rested. The "button" is of irregular size, sometimes prominent, at others scarcely discernible, which is probably due to the different relative positions occupied by the teeth. Base broad, extending backwards, inferior surface more or less flattened.



Text-figure 28
Five teeth of *Pleuracanthus laevissimus* Ag.(= *Diplodus gibbosus*) in natural size, to show variations in size, shape and secondary cusps.
After Davis, 1892.

Then after describing with some care the varying details of the teeth of several species of *Cladodus*, all of which have the same general form, Davis concluded with the following summation (1885, pp. 112–113):

> Our knowledge of the fossil forms of *Cladodus* does not lead us to infer that the teeth of *Cladodus* differed in form to any extent comparable with those of the existing *Chlamydoselachus*. There are no fossil examples known to be associated with the ordinary form of *Cladodus* similar to those of either the anterior [rows of] recurved teeth or the posterior ones with a single denticle as in the recent fish, and the question naturally arises as to whether the correspondence in the form of one portion of the teeth of *Chlamydoselachus* is sufficient to justify the assumption that the latter is the existing type of a group of sharks hitherto considered to be extinct since the Carboniferous period. The resemblance is no doubt striking, and the discovery of intermediate forms in the secondary or tertiary formations will be a great assistance in guiding the palaeontologist to a correct estimation of its value, but at the present no such evidence exists and whilst the immense value of the discovery of the fish cannot be too fully appreciated, it may be well to await fresh evidence before finally deciding that *Chlamydoselachus* is a descendant from the fossil Cladodonts.

With regard to this matter of a single denticle, it should be understood that in *Chlamydoselachus* teeth with a single denticle are comparatively few, since they occur only in the angle of the jaw, where teeth with one or two denticles are sometimes found. Because these teeth are few and presumably not fully developed they should not figure largely in the comparison.

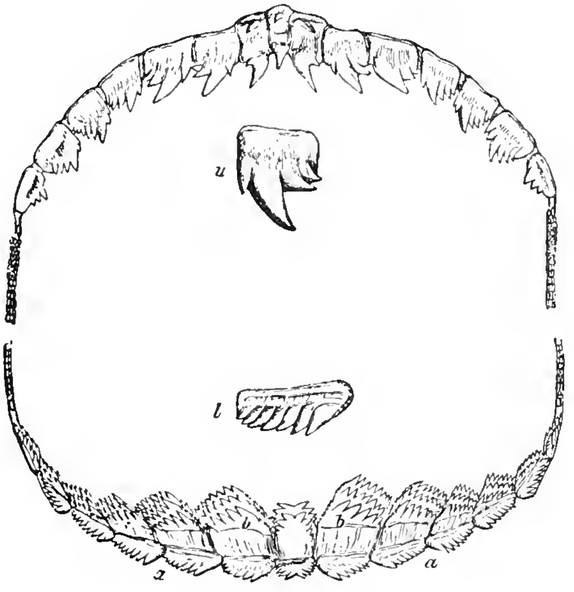
We have presented the facts concerning the affinities of *Chlamydoselachus* to fossil forms as they have been set forth by the contenders, freely quoting their very words. To these statements have been added others which we believe to bear on the matter.

These statements have all been checked against the figures of the teeth referred to, and we believe that, so far as we can judge from the structure of the teeth, *Chlamydoselachus* has no generic relationship with *Diplodus* (=*Didymodus*). With regard to its affinities to *Cladodus*, Dr. W. K. Gregory comments as follows: "Some authors regard *Chlamydoselachus* as a living representative of the cladodont sharks of the Devonian and Carboniferous periods, but later investigations indicate that it is only a deep-water specialization of a Mesozoic group."

The teeth of *Chlamydoselachus* (Text-figure 10) are barb-like, prehensile, and alike in both jaws. Those of *Heptanchus* (Text-figure 29) are adapted for cutting as well as holding, and are not alike in upper and lower jaws. The decided differences between the teeth of *Chlamydoselachus* and *Heptanchus*—forms which are in many important respects closely related—serve to weaken our faith in the validity of phylogenetic deductions based on a comparison of present-day fishes with fossil forms that are known only by their teeth. Generally speaking, in living fishes family differences in the teeth are great, generic differences are considerable, while specific differences are slight. But it should also be borne in mind that the form of teeth is mainly an adaptive character, very subject to parallelisms.

FOSSIL CHLAMYDOSELACHIDS

Interestingly enough, while the controversy above epitomized was raging, all the contestants were unaware that as early as 1876 the fossil teeth of a true *Chlamydoselachus* had been described. In fact this was not known until Davis called attention to it in 1887, when the controversy had died down. Furthermore, since our work on this article began, the fossil tooth of another species of this genus has been found. Both of these finds will now be described.



Text-figure 29
Dentition of *Heptanchus* (*Notidanus*) *indicus* Cuv.
a, teeth in function; *b*, teeth in reserve; *u* and *l*, upper and lower single teeth (×1).
From Goodrich after Günther.

CHLAMYDOSELACHUS LAWLEYI FROM NORTHERN ITALY

Great numbers of fossil sharks' teeth have been found in northern Italy, and in 1876 Roberto Lawley described many of these. Among them were certain remarkable ones from the Pliocene beds of Orciano in Tuscany. These he figured and described without assigning any name to them. In our Text-figure 30 we reproduce his drawings in the exact size in which he published them—i.e., *1b* is in natural size, the others are approximately twice as large (using *1b* as the standard). Here follows his description as translated from the original Italian:

> As seen in fig. *1a*, the root of a tooth has two [posterior] branches; these are joined for almost their whole length, but in front of the line of junction, the central spine arises, as in Fig. 1, and forms with the two lateral cusps a complete tooth. The apex of each spine is composed entirely of dentine and is transparent; the spines are flexible, fig. 1c, and the root forms almost a right angle with them. We have two complete teeth, and seven more or less mutilated specimens, but all are similarly formed and recognizable. All came to me from Orciano, where they seem to be very rare. I have never seen a similar tooth in a living creature nor in pictures either of fishes or reptiles.

Since these teeth were incidentally described and were not assigned to any named shark, it is not surprising that Lawley's description was lost sight of. However, the publication of Garman's articles, including figures and descriptions of the teeth of *Chlamydoselachus*, aroused great interest in the fish and its relationships to various fossil forms, as we have shown. Lawley's discovery was made generally known to English-speaking scientists by the publication of a short article by Davis in 1887. Davis noted that Lawley knew of no living or fossil form having similar teeth. But he (Davis) affirmed that, when these teeth are compared with the teeth of the frilled shark from Japan (the Madeiran specimen of 1889 had not yet been captured), it may clearly be seen that they carry the same generic characters, regardless of the fact that the fossil teeth are twice as large as the teeth of the present-day form. Hence he proposed for this fossil form the name *Chlamydoselachus lawleyi*, in commemoration of Lawley's discovery.

Text-figure 30
Fossil teeth of *Chlamydoselachus lawleyi* from the Pliocene of Orciano, Tuscany, Italy.
1 and *1b* teeth viewed from above; *1a* from below; *1c* in lateral view. Note the lack of secondary cusps. (*1b*, nat. size; all others ×2).
After Lawley, 1876.

Comparison of the teeth in Lawley's plate (Text-figure 30) with Garman's drawing (Text-figure 10), whether looked at from the front, side or below, shows plainly that these teeth are congeneric. The whole general conformation is the same, even to the depressions hollowed out under the anterior bases of the roots. The cusps of the teeth of *C. lawleyi*, if correctly drawn, are slenderer than those of *C. anguineus*, and are slightly bulbous at the base. Again the posterior parts of the base are not so long, slender and pointed as are these parts in the modern form. However, these differences are trifling, and may be due in part to imperfections or to changes inherent in the process of fossilization. The thing which is of specific value is the absence, from the spaces between the cusps of *C. lawleyi*, of the rudimentary or secondary cusps found in *C. anguineus*. Differences of size between the teeth of *C. lawleyi* and those of *C. anguineus* will now be considered.

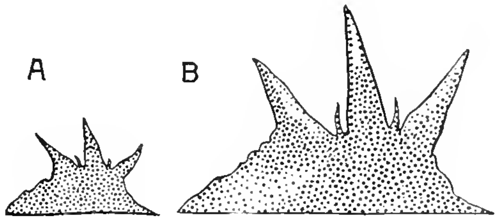
Davis (1887) stated that the teeth of *C. lawleyi* are twice as long as those of *C. anguineus*. To this we cannot agree. The teeth in Lawley's figure *1b* (our Text-figure 30) are said in his text to be "grand. nat." The central cusp measures 7.5 mm. exactly. The teeth in Garman's drawing are said to be "six times nat." They measure 32.5 mm. exactly, and in natural size must have been 5.4 mm. Careful measurements of the middle cusp of the front teeth of our specimens give the following results: No. I (1350 mm. long) has teeth varying from 4.5–5 mm.; No. II (1485 mm.), 4.5–5.5 mm.; No. III (1550 mm.), 4.5–5 mm.; the Columbia Univ. head, 4–4.45 mm. long. These measurements are accurately made on perfect teeth (central cusps) in and around the symphysis of each jaw. Many of these central teeth are broken, some with merely the fine points gone. Care has been taken to avoid measuring these latter. There is here some variation, as is to be expected, and it is interesting to note that our largest specimen does not have the largest teeth. Also it should be recorded that the teeth grow shorter progressively in the rows approaching the corner of the jaws. Generally speaking, these front teeth average about 4.8 mm., or 0.6 mm. smaller than the size given by Garman for the central cusps of the teeth of his fish, but 2.7 mm. smaller than the central cusp figured from one of the two perfect teeth of C. *lawleyi*.

CHLAMYDOSELACHUS TOBLERI FROM TRINIDAD ISLAND

Some years prior to 1928, Aug. Tobler collected on the island of Trinidad and deposited in the Musée d'Histoire Naturelle of Basel, Switzerland, a curious three-pronged fossil tooth. This was submitted to Maurice Leriche for study, and in 1929 he published a short article in which he gave it the name *Chlamydoselachus tobleri*.

This tooth was found in a calcareous marl, tuff-like in appearance and containing Globigerina remains, which had been ejected by the mud volcano Chagonary in the island of Trinidad, Lesser Antilles. According to Leriche, the horizon is certainly Tertiary, and more closely is either Oligocene or Miocene.

This tooth, of which the central cusp is 6 mm. long, is figured in natural and twice natural size. The half-tone screen was very coarse and the paper very soft, hence the figure is very poor, showing everything without perspective. There is no modelling of these teeth in the figures; both are shown as perfectly flat. We have had the figure carefully copied both in its natural size and in enlarged form, and reproduce these drawings as our Text-figure 31. Contrasted with C. *lawleyi* (Text-figure 30) the cusps are much straighter, much heavier, more uniformly tapering from base to tip, more sturdy in every respect. However, the thing which most distinctly differentiates *tobleri* from *lawleyi* is the presence of a pair of long and slender secondary cusps on either side of the central cusp. As already stated, there are no secondary cusps in *lawleyi*. So far as we can discern from Leriche's figures, in *tobleri* all the cusps are practically straight, not curved as in *lawleyi* and *anguineus*.



Text-figure 31
A fossil tooth of *Chlamydoselachus tobleri* from the Tertiary of Trinidad Island: A (×1); B (×2).
After Leriche, 1929.

Comparison of the tooth of C. *tobleri*

(Text-figure 31) with that of C. *anguineus* (Text-figure 10) shows that in front view the tooth of *tobleri* is somewhat like that of *anguineus* in having a central cusp, with very small slender secondary cusps separating it from the two large lateral ones. However, the whole tooth (as shown in the drawing) has an enormously broad base, unlike that of *anguineus;* the large cusps are stiff and blunt, while the secondary cusps are very slender compared to the short blunt ones of *anguineus.*

The teeth of C. *tobleri* (central cusp) are markedly larger than those of C. *anguineus* (6 mm. as compared with our average of 4.8 mm.). They are slightly shorter than those of C. *lawleyi*, which are 7.5 mm. long in Lawley's lithographed plate, where they are marked "grand. nat."

CLASSIFICATION OF THE FRILLED SHARK

The outcome of investigations as to the relationships of *Chlamydoselachus* has been to establish the family to which our shark belongs, and to determine its relationships to the other primitive sharks, *Hexanchus*, *Notorhynchus* (*Notidanus*) and *Heptranchias* (*Heptanchus*). These latter are all included by Garman (1913) in his family Hexeptranchidae, which with the family Chlamydoselachidae constitutes the very primitive selachian group Hexanchoidei. We feel that we cannot do better than to quote Garman's (1913) brief statement of family and generic characters.

Family CHLAMYDOSELACHIDAE

Garman assigns the family characters in the following concise terms:

> Body elongate, slender. Head broad, depressed. Eyes lateral, without a nictitating membrane. Nostrils distinct from the mouth. Mouth anterior, without labial folds; teeth with broad, backward-extended bases and slender cusps. Spiracles small. One dorsal [fin], not preceded by a spine. An anal fin. No pits at the root of the caudal. Margin of first gill cover free across the isthmus. Intestine with a spiral valve. Pterygoquadrate not articulated to postorbital process of the skull [cranium], hyomandibular elongate.

Genus *CHLAMYDOSELACHUS*

The family Chlamydoselachidae is monogeneric, and here follows Garman's brief characterization of the solitary genus:

> Six gill openings, margin of first free across the isthmus. Mouth very wide, longer than the skull, without labial folds. Teeth raptorial, similar in the two jaws, each with a broad base and three slender, curved, subconical cusps, with or without rudimentary cusps at their bases, no median teeth in the upper series; a median series on the symphysis below. Eyes lateral, elongate. Fins broad, caudal [usually] without a notch.

Species: *TOBLERI, LAWLEYI* and *ANGUINEUS*

C. *TOBLERI.*—A recently determined species based on a single tooth collected in the Tertiary of the island of Trinidad, Lesser Antilles. The tooth is differentiated from that of the present-day form mainly by the broad base and by the presence of the needle-like secondary cusps.

C. *LAWLEYI.*—The first discovered fossil form was named by J. W. Davis in 1887 from a description by R. Lawley (1876) of two complete and seven fragmentary teeth from the Pliocene of Tuscany. These teeth much more closely resemble those of the recent fish, the chief difference being that they lack the secondary cusps found in C. *anguineus* on either side of the main cusp. They definitely belong to a species apart from the next.

C. *ANGUINEUS.*—The present-day species, the subject of this paper and of others to follow, is usually accepted as the lowest living member of the great group Elasmobranchii. The external characters of this fish are dealt with throughout our paper *in extenso*, and for that reason it seems best to quote Garman's brief characterization (1913), inserting some corrections based on our studies:

> Body long, slender, subcylindrical, compressed behind the vent, which is behind the middle of the total length. Head broad, wider than high, slightly convex. Snout broadly rounded, hardly extending beyond the jaws. Nostrils lateral, behind the forward end of the mouth. Eye rather large, elongate, about midway from eye [*sic*—angle of jaw?] to end of snout, near a vertical from the mid-length of the mouth. Spiracle very small, distance behind the eye about equal to distance from eye to end of snout. Mouth very large, extending as far backward as the skull [cranium]; upper and lower jaws of equal length. No labial folds. Teeth small, similar in both jaws, several of each row in function; each tooth with three long, slender, curved, backward directed cusps. A small cusp at [each side of] the base of the middle cusp is not always [?] present. Bases of teeth broad, each with two prongs reaching backward beneath the base of the next tooth in the row. Upper jaw with [approximately] fourteen rows on each side, no median row. A median row on the symphysis of the lower jaws [jaw] with [approximately] thirteen rows on each side of it. Pterygoquadrate attached to the skull [cranium] in front of the postorbital process, between the eyes. Gill openings six, very wide, oblique [?], in front of the pectorals; those of the two sides narrowly separated on the isthmus, which is crossed by the free margins of the first gill cover.
>
> Pectorals moderate, broad, rounded. Dorsal small, base opposite and shorter than that of anal. Anal larger than ventrals, tip reaching origin of caudal. Caudal long, pointed, armed on upper edge by modified scales, subcaudal deep anteriorly, narrowing backward, not [often] separated by a notch from the tip.
>
> Uniform [?] brown [darker on dorsum and on margins of fins].

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PLATE I

NATURAL HISTORY OF *CHLAMYDOSELACHUS ANGUINEUS*

PLATE I

DRAWINGS AND PHOTOGRAPHS OF *CHLAMYDOSELACHUS ANGUINEUS*

Fig. 1. A 1473-mm. female fish from Yeddo Bay off Tokyo.
From a lithograph. After Günther, 1887.

Fig. 2. A 1500-mm. (?) male specimen from the Odawara Bank (?), Sea of Sagami, Japan. Note the large myxopterygia.
From a drawing. After Doflein, 1906.

Fig. 3. A 1910-mm. female shark from the Varanger Fjord, Arctic Coast of Norway.
From a photograph. After Collett, 1897.

Fig. 4. A 1140-mm. male fish from off Corunna, Spain. Note the large claspers.
From a photograph. After Bolivar, 1907.

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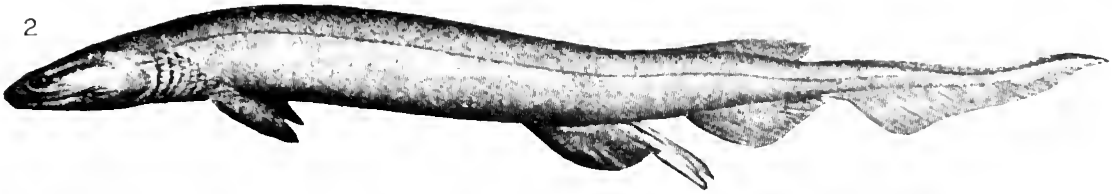

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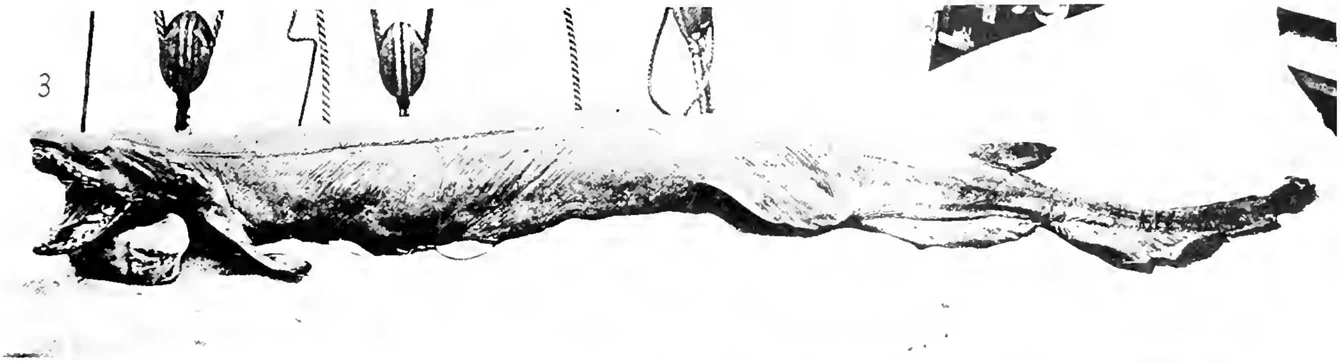

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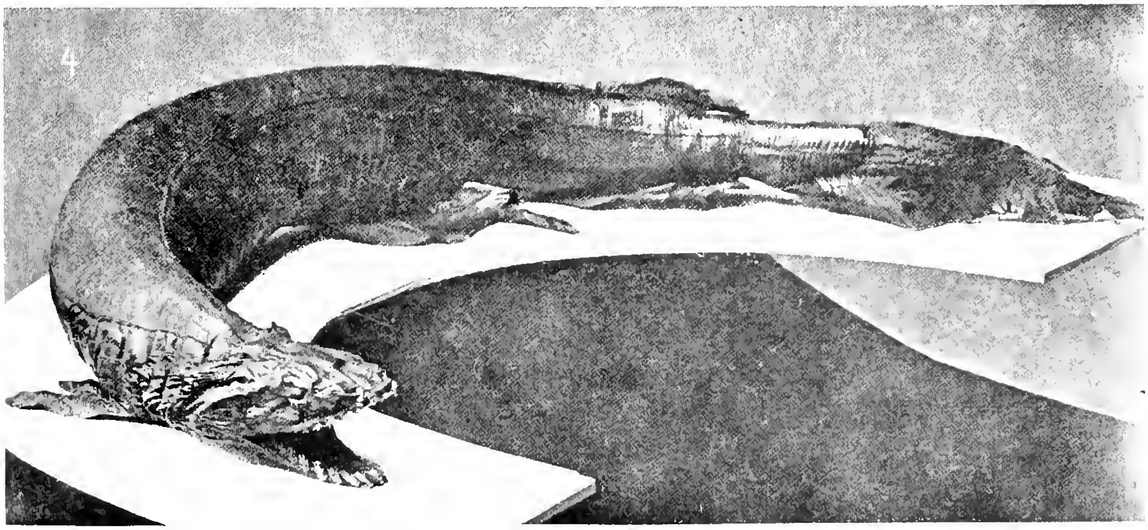

PLATE II

NATURAL HISTORY OF *CHLAMYDOSELACHUS ANGUINEUS*

PLATE II

A PHOTOGRAPH OF *CHLAMYDOSELACHUS* AND DRAWINGS OF TWO HEADS

Fig. 5. An 1860-mm. female taken off San Sebastian, Spain. From the very full abdomen we believe this to have been a gravid female.

After Bertrand, 1926.

Fig. 6. A drawing of the head of the fish of Figure 3, plate I. Note teeth, tongue, nostrils, eye, spiracle, and gill-covers with their supports.

After Collett, 1897.

Fig. 7. A drawing of the head of *Chlamydoselachus* from the left side.

amp, pores of the ampullae of Lorenzini; *ana*, anterior nasal aperture; *ang*, angular latero-sensory canal; *gul*, gular lateral line canal; *iop*, infra-orbital latero-sensory pores; *jug*, jugular latero-sensory canal; *llc*, lateral line canal of body; *or*, oral latero-sensory canal; *sop*, supra-orbital latero-sensory pores; *sp*, spiracular latero-sensory canal; *spr*, spiracle.

After Allis, 1923.

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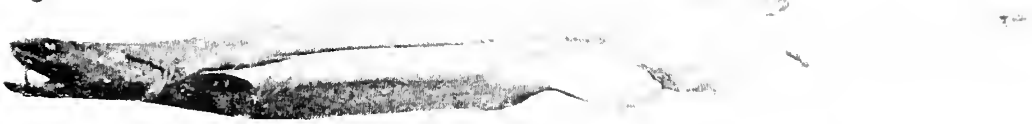

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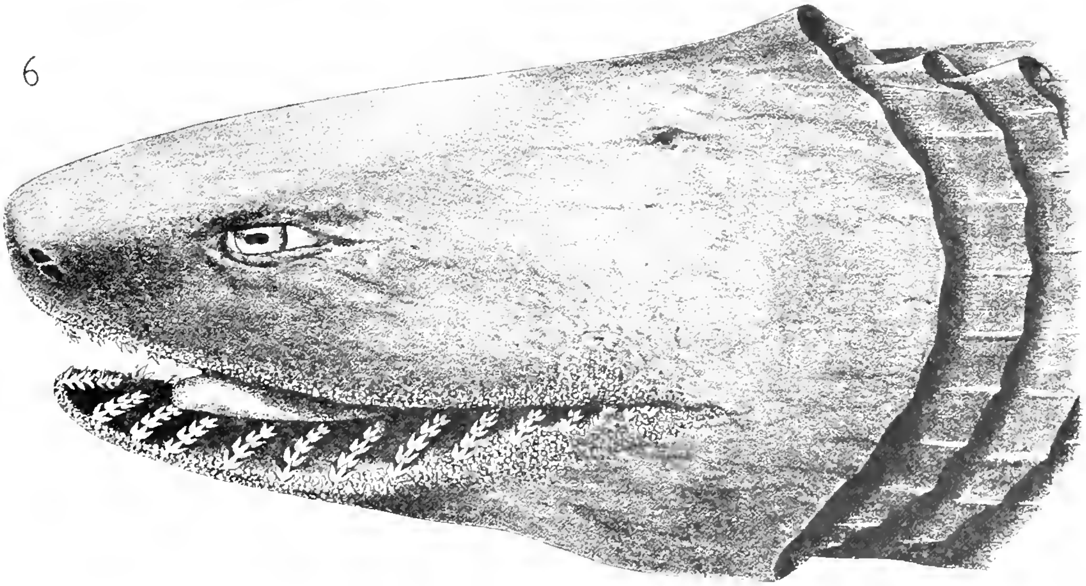

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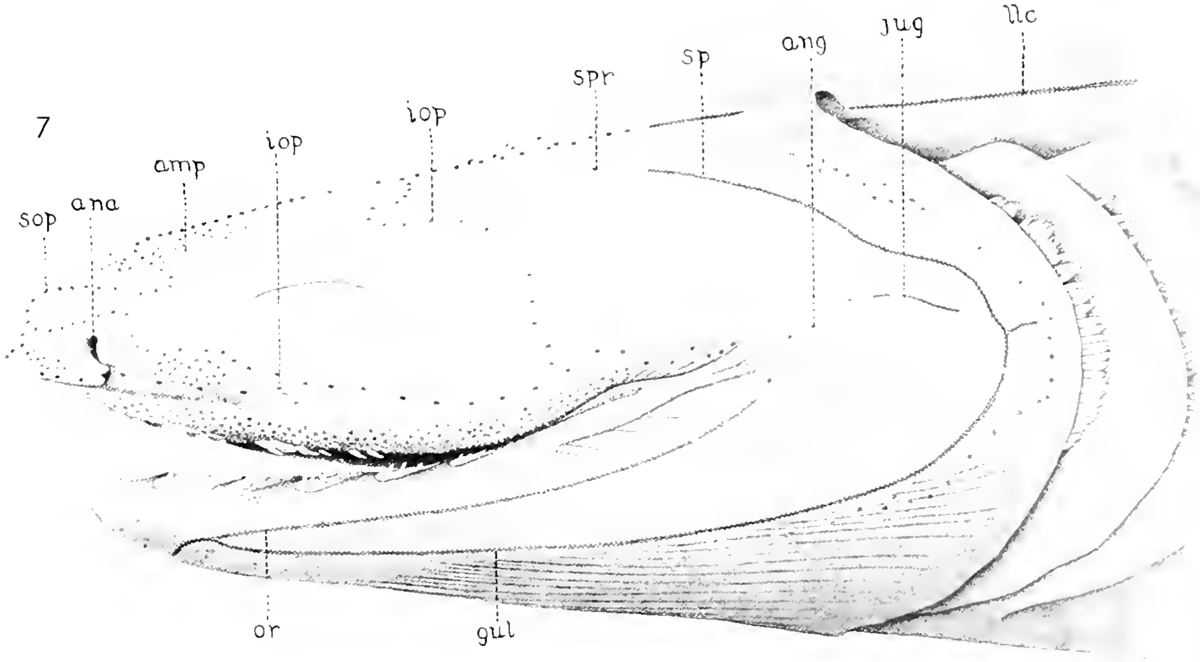

PLATE III

NATURAL HISTORY OF *CHLAMYDOSELACHUS ANGUINEUS*

PLATE III

OPEN MOUTHS OF THREE SPECIMENS OF THE FRILLED SHARK

Fig. 8. Mouth, tongue and teeth of a 1220-mm. fish. From a drawing of the specimen first described.
After Garman, 1885.2.

Fig. 9. A similar view of another fish. From a drawing of a head supplied by Bashford Dean.
After Allis, 1919

Fig. 10. The widely distended mouth of the head from Columbia University. Specimen supplied by Doctor Dean. Note the double row of small teeth near the center of the upper jaw.
From a photograph, A. M. N. H.

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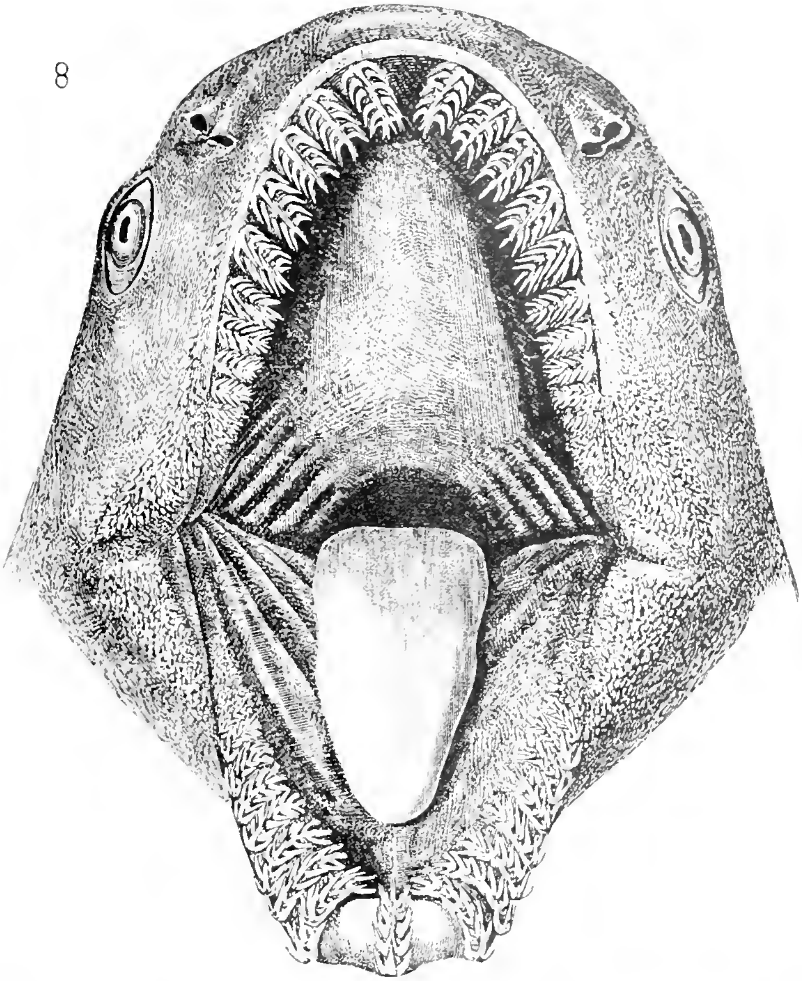

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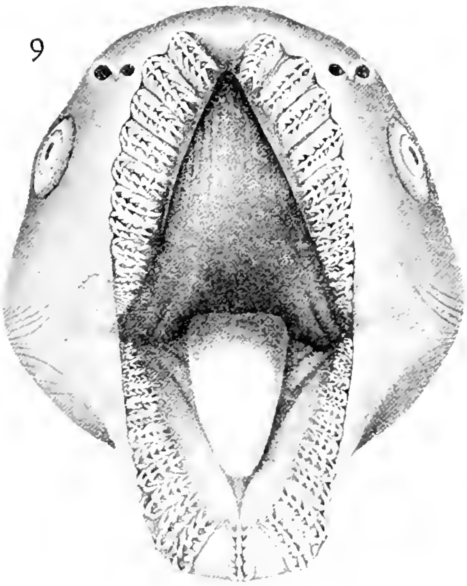

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PLATE IV

NATURAL HISTORY OF *CHLAMYDOSELACHUS ANGUINEUS*

PLATE IV

BREATHING VALVE AND TEETH OF *CHLAMYDOSELACHUS ANGUINEUS*

Fig. 11. The angular breathing-valve of the 1485-mm. specimen in the collections of the American Museum.
From a photograph, A. M. N. H.

Fig. 12. The somewhat rounded breathing-valve of a 1550-mm. specimen in the American Museum.
Note the very small teeth at the base of the valve.
From a photograph, A. M. N. H.

Fig. 13. The greatly enlarged anterior end of the upper jaw of the specimen from Columbia University.
Note the crescentic breathing-valve, and the double row of half-sized teeth near
the symphysis of the jaw-cartilages.
From a photograph, A. M. N. H.

Fig. 14. Anterior end of the upper jaw of Doctor White's specimen (see page 253) showing the single row
of half-sized teeth near the symphysis.
From a photograph, A. M. N. H.

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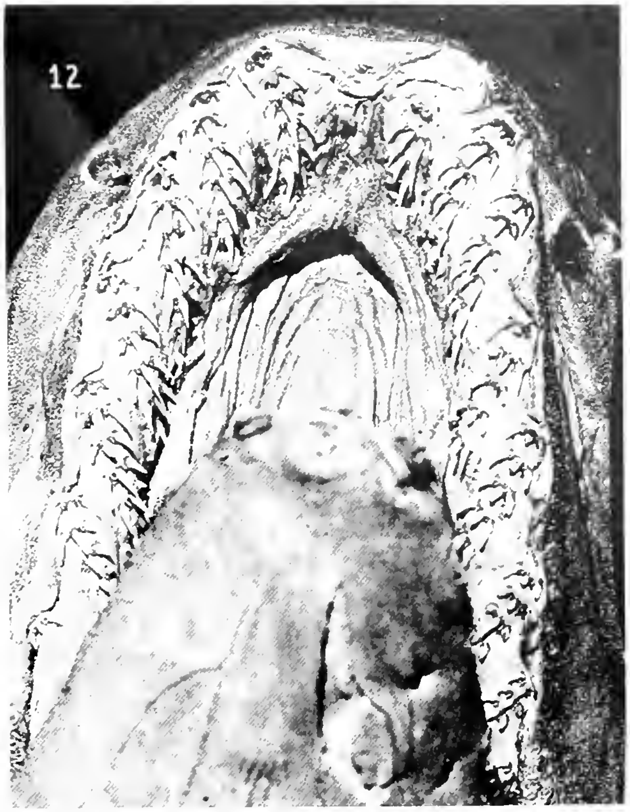

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PLATE V

NATURAL HISTORY OF *CHLAMYDOSELACHUS ANGUINEUS*

PLATE V

CHLAMYDOSELACHUS, ITS BREATHING VALVE, TEETH, AND PELVIC FINS

Fig. 15. Breathing-valve and some of the teeth of the 1350-mm. specimen in the American Museum.

From a photograph, A. M. N. H.

Fig. 16. Detailed drawing of the shark seen in outline in our Text-figure 1 (page 249).

After Garman, 1885.2.

Fig. 17. Pelvic fins, myxopterygia, and cloacal aperture of a 1474-mm. male fish. Note the shortness of the claspers or myxopterygia.

After Günther, 1887.

Fig. 18. Pelvic fins, abdominal pores, and cloacal aperture of a 1220-mm. female fish.

After Garman, 1885.2.

Fig. 19. Cloacal aperture and abdominal pores of American Museum specimen No. I, a 1350-mm. female fish. The abdominal pores are here nipple-like structures. That on the right is perforate, that on the left has no opening.

From a photograph, A. M. N. H.

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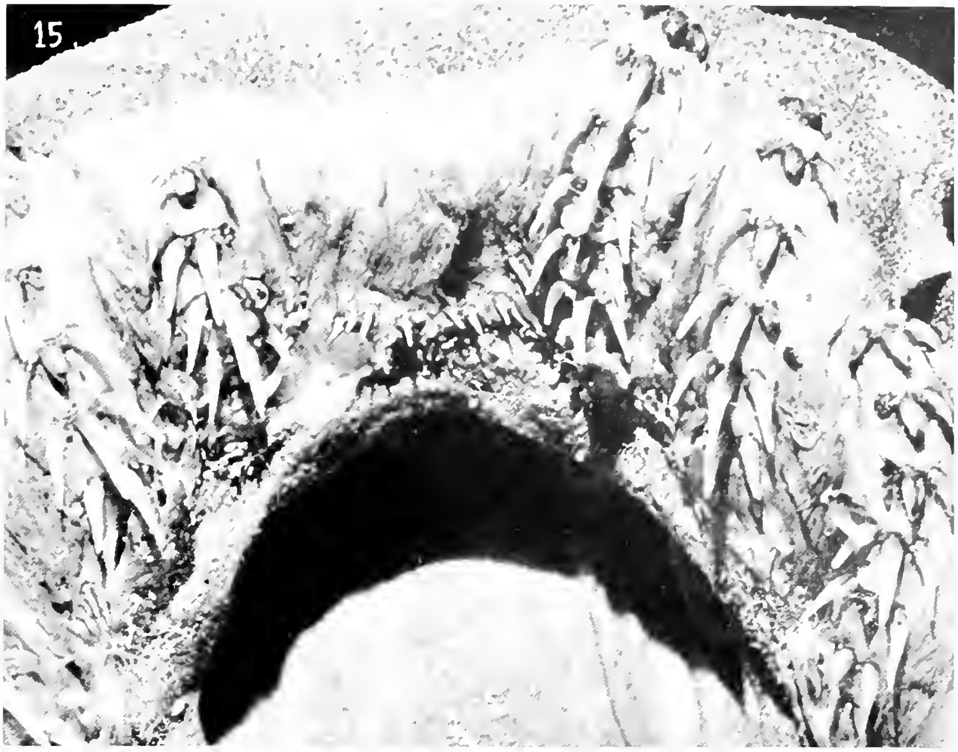

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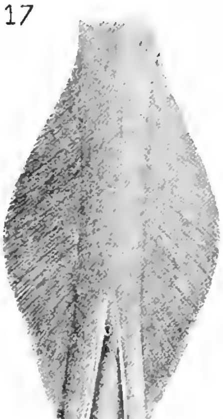

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THE
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ARCHAIC FISHES

Edited By

EUGENE WILLIS GUDGER

ARTICLE I

MEMORIAL OF BASHFORD DEAN

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NEW YORK
PUBLISHED BY ORDER OF THE TRUSTEES

Issued December 15, 1930

THE
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ARCHAIC FISHES

Edited By
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THE SEGMENTATION OF THE EGG OF THE MYXINOID, *BDELLOSTOMA STOUTI*, BASED ON THE DRAWINGS OF THE LATE BASHFORD DEAN

By EUGENE WILLIS GUDGER
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NEW YORK

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Boston University School of Medicine

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A CONTRIBUTION TO OUR KNOWLEDGE OF THE ARTHRODIRA

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Curator of the Paleontological Museum
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ARTICLE V

THE NATURAL HISTORY OF THE FRILLED SHARK *CHLAMYDOSELACHUS ANGUINEUS*

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PUBLISHED BY ORDER OF THE TRUSTEES

Issued November 23, 1933

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ARCHAIC FISHES

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